Understanding and predicting global change impacts on migratory birds

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I am a part of all that I have met.

Alfred Lord Tennyson

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Abstract

This is a publication-based dissertation comprising three original research studies (one published, one submitted and one ready for submission; status March 2019). The dissertation introduces a generic computer model as a tool to investigate the behaviour and population dynamics of animals in cyclic environments. The model is further employed for analysing how migratory birds respond to various scenarios of altered food supply under global change. Here, ecological and evolutionary time-scales are considered, as well as the biological constraints and trade-offs the individual faces, which ultimately shape response dynamics at the population level. Further, the effect of fine-scale temporal patterns in resource supply are studied, which is challenging to achieve experimentally. My findings predict population declines, altered behavioural timing and negative carry-over effects arising in migratory birds under global change. They thus stress the need for intensified research on how ecological mechanisms are affected by global change and for effective conservation measures for migratory birds. The open-source modelling software created for this dissertation can now be used for other taxa and related research questions. Overall, this thesis improves our mechanistic understanding of the impacts of global change on migratory birds as one prerequisite to comprehend ongoing global biodiversity loss. The research results are discussed in a broader ecological and scientific context in a concluding synthesis chapter.

Zusammenfassung

Dies ist eine publikationsbasierte Dissertation, welche aus drei wissenschaftlichen Originalstudien (eine publiziert, eine eingereicht und eine einreichbar; Stand März 2019) besteht. Die Dissertation stellt ein generisches Computermodell bereit, um das Verhalten und die Populationsdynamik von Tieren zu untersuchen, welche saisonale Umweltbedingungen erfahren. Mit diesem Computermodell untersuche ich in der vorliegenden Thesis, wie Zugvögel auf verschiedene Szenarien veränderter Nahrungsverfügbarkeit reagieren, welche im Rahmen des globalen Wandels wahrscheinlich sind. Dabei werden ökologische und evolutionäre Zeitskalen berücksichtigt. Außerdem werden biologisch bedingte Einschränkungen und Zielkonflikte einbezogen, welche das einzelne Individuum erfährt, die aber letztendlich auch das Geschehen auf Populationsebene bestimmen. Weiterhin studiere ich mit dem erstellten Computermodell am Beispiel des Weißstorchs, wie sich feinskalige Zeitmuster in der Nahrungsverfügbarkeit auf Zugvögel auswirken. Solche Studien würden eine enorme experimentelle Herausforderung darstellen. Die im Rahmen dieser Dissertation entstandene frei verfügbare Modellierungs-Software kann nun für andere Taxa und verwandte Forschungsfragen eingesetzt werden. Nach meinen Ergebnissen ist im Zuge des globalen Wandels mit verstärkten Populationsabnahmen bei Zugvögeln zu rechnen, sowie mit Änderungen im zeitlichen Verhaltensablauf und nichtlinearen negativen Carry-over-Effekten. Dies verdeutlicht, wie wichtig es ist, die vom globalen Wandel betroffenen ökologischen Mechanismen näher zu erforschen sowie effektive Schutzmaßnahmen für Zugvögel zu entwickeln. Allgemein erhöht die Dissertation unser mechanistisches Verständnis davon, wie sich der globale Wandel auf bedrohte Zugvogelarten auswirkt und damit die globale Biodiversität beeinflusst. Die Forschungsergebnisse werden in einem abschließenden Synthese-Kapitel zusammenführend diskutiert.

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1 General introduction

1.1 Global change – the main driver of biodiversity loss

Biodiversity, the “variety of life” on Earth (Gaston, 2000), is increasingly affected by human activity (Leadley et al., 2010; Pereira et al., 2010). Humans have converted the globe’s surface to fulfil their demands for food, shelter, energy, and mobility, thus profoundly influencing the Earth system’s many interacting components (McGill et al., 2015; Vitousek et al., 1997). They induced “global change”. Involving land conversion, resource overexploitation, pollution and species invasion, global change encompasses many of the main drivers of ongoing biodiversity loss (Hoffmann et al., 2010; Leadley et al., 2010; Pereira et al., 2010; Sala et al., 2000). It also involves climate change, which is predicted to rapidly increase its impact during the 21st century, becoming the key driver of future changes in biodiversity (Maxwell et al., 2016; Pereira et al., 2010; Thuiller, 2007). Indeed, it has been suggested that we are approaching a global extinction crisis, with humanity being responsible for the sixth mass extinction of species within the last 540 million years (Barnosky et al., 2011).

By the early 21st century, scientists no longer debate whether the anthropogenic emission of greenhouse gases such as CO2 is provoking climate change (IPCC, 2013). According to the Intergovernmental Panel on Climate Change (IPCC), climate change encompasses increasing global temperatures, altered atmospheric and material cycles, ocean acidification, ice melt, sea level rises, and intensified extreme weather events (IPCC, 2013). The rate, magnitude, and direction of these climatic changes and their associated indirect effects and risks will vary across the planet but clearly operate globally (Garcia et al., 2014; IPCC, 2014, 2013; Thuiller et al., 2011). Thus, climate change has the potential to affect pristine regions that are far from other human influences but are important for the Earth’s climate and biodiversity, such as primeval forests or arctic regions (Beaumont et al., 2011; Brierley and Kingsford, 2009). Moreover, various facets of climate change interact via positive feedback loops, accelerating climate change even further (IPCC, 2013). For instance, increased global temperatures are causing permafrost melt, leading to the release of additional greenhouse gases and additional heat absorption of the ground beneath, which in turn is accelerating global warming (IPCC, 2013). Consequently, humanity is causing rapid but long-lasting changes to the Earth’s climate system.

Further, the wide-ranging consequences of global change, including climate change, go beyond their physical manifestations by influencing the biosphere and human society (Bellard et al., 2012; Díaz et al., 2006; Jetz et al., 2007; McGill et al., 2015; Parmesan and Yohe, 2003). Observed changes in the abundance and distribution of species have been attributed to global change, as well as altered behavioural patterns and species interactions (Jetz et al., 2007; McGill et al., 2015; Raimo and Aleksi, 2017). For example, mounting evidence indicates that the number of different species existing on Earth, i.e. global species richness, is declining due to global change (Ceballos et al., 2017, 2015; Pimm et al., 2014), meaning that extinction rates are outpacing speciation rates. Indeed, current extinction rates are significantly higher than those from fossil records (Barnosky et al., 2011; Pimm et al., 2014). Converting wilderness to farmland and pasture in particular has been shown to negatively impact global biodiversity, with an increasing signature of climate change (Newbold et al., 2015). Species' abundances are further in decline (Sanderson et al., 2006), which is not captured by focusing on species richness (Hillebrand et al., 2018).

Indeed, species richness represents only one aspect of biodiversity, which also encompasses other important qualities like functional, genetic, phylogenetic, and phenotypic diversity (CBD, 2014; Díaz et al., 2013; Pereira et al., 2013). The noted effects of human activity on biodiversity vary not only with the type of biodiversity or the type of human impact considered, but also with scale (McGill et al., 2015). Analysing biodiversity trends at local and regional scales have invoked an enduring debate whether these reflect global trends (Cardinale et al., 2018; Gonzalez et al., 2016; Newbold et al., 2015; Primack et al., 2018; Vellend et al., 2017). In some regions such as many islands, local and regional species richness is actually increasing due to the establishment of new species (Hillebrand et al., 2018) and for some species the IUCN Red List status has improved (Hoffmann et al., 2010), highlighting a potential for successful conservation measures (Hoffmann et al., 2010; Johnson et al., 2017). Additionally, different taxa, populations, and trophic levels are unevenly affected by global change (Böhm et al., 2013; Both et al., 2009; Schipper et al., 2008; Stuart et al., 2004; Thackeray et al., 2016). Despite such complexities there is large scientific consensus that a biotic homogenization of the world is taking place at larger spatial scales (Primack et al., 2018; Thuiller et al., 2011).

Conserving biodiversity is predicted to make ecosystems more stable and resilient to change (Cardinale et al., 2012; Jiang and Pu, 2009; van der Plas, 2019). Every species fulfils a specific function in the ecosystem and is part of various interacting ecosystem processes (MEA, 2005). When a species presents high genetic and phenotypic diversity, it is likely more adaptable to a rapidly changing world (McGill et al., 2015). However, declining species' abundances and, eventually, extinctions can induce community-level changes that potentially threaten the functioning and stability of the whole ecosystem (Brook et al., 2008; Strona and Bradshaw, 2018). In particular, extinction processes are likely amplified by co-extinction processes, meaning that consumer species follow their resource species' fate (Strona and Bradshaw, 2018). When species go extinct, not only their unique gene pool might be lost but also various free benefits a functioning ecosystem is providing to humanity, i.e. ecosystem services such as provisioning of food, pollination or pest control (Mace et al., 2012; MEA, 2005). Accordingly, biodiversity declines are expected to be detrimental for human-wellbeing (Johnson et al., 2017), apart from ethical concerns about causing species extinctions (May, 2010).

Apart from decreasing in abundance and going extinct, natural population can respond in two different ways to a changing environment: they can shift their range by moving (or being moved) or they can adapt to their new, altered environmental conditions (Holt, 1990; Pulido and Berthold, 2004). Range shifts towards the poles represent a widely documented response of organisms to climate change (Maclean et al., 2008; Parmesan and Yohe, 2003; Perry et al., 2005; Root et al., 2003). Adaptive responses refer to adjustments in morphology, physiology, or behaviour to meet the new requirements posed by the altered environment (Pulido and Berthold, 2004). Two main underlying mechanisms of adaptive response are discussed in the scientific literature: evolutionary adaptation and phenotypic plasticity (Charmantier and Gienapp, 2014; Gienapp et al., 2008; Merilä and Hendry, 2014).

Evolutionary adaptation is genetic change driven by natural selection (Merilä and Hendry, 2014). One of the most well-known examples of evolutionary adaptation to anthropogenic environmental change is the peppered moth (*Biston betularia*) in industrial England, where the air pollution supposedly selected for darker wing colour because they provided a better camouflage (Kettlewell and Ford, 1956). Another evolutionary adaptation facilitated by human influences is the newly developed migratory route of German blackcaps, which started migrating to Great Britain instead of the Iberian Peninsula in the 1960s (Bearhop et al., 2005; Berthold et al., 1992). This behavioural change was not only found to have a genetic basis and to be associated with fitness benefits (e.g. larger clutch sizes), but it also leads to a temporal segregation of breeding populations overwintering in either Britain or distant Spain (Bearhop et al., 2005; Berthold et al., 1992). Despite this example and though evolutionary changes can occur quite rapid in some taxa, the rate of microevolution has been estimated to be relatively low for vertebrates (Gienapp et al., 2008).

Phenotypic plasticity, in contrast, is the potential of a single genotype to produce different phenotypes under different environmental conditions (Merilä and Hendry, 2014). For example, many migratory bird species return earlier to their breeding grounds and advance their breeding activities in warmer springs (Gordo, 2007; Lehikoinen and Sparks, 2010). Phenotypic plasticity allows beneficial short-term responses to novel environmental conditions and may thus buffer a population from negative global change effects (Visser, 2008). Though many observed changes in natural populations are interpreted as plastic response to environmental change, the relative role of genetic versus plastic responses is still debated, as well as potential interactions between the two mechanisms (Charmantier and Gienapp, 2014; Gienapp et al., 2008; Merilä and Hendry, 2014).

Nevertheless, any adaptive response represents a time-dependent process and different temporal, spatial and entity scales need to be crossed in order to grasp how global change affects biodiversity, ranging for example from individual life-histories over ecological to evolutionary timescales (Garcia et al., 2014; Pulido and Berthold, 2004). Accordingly, an important question when assessing the vulnerability of a species to rapid global change is not whether that species can find an adequate response to global change, but whether it can do so in time before going extinct – given the environmental and evolutionary constraints it experiences (Visser, 2008). Similarly, global change features different temporal signatures (Garcia et al., 2014). On the one hand, many facets of global change happen gradually, e.g. global mean temperature is gradually increasing and land all over the world is continuously degrading (e.g. IPCC, 2013; Leadley et al., 2014; MEA, 2005). On the other hand, global change incorporates discrete short-term changes in the environment such as sudden land conversions or intensifying extreme weather events like droughts (e.g. IPCC, 2013; Leadley et al., 2014; MEA, 2005). Extreme events are unpredictable, rare, and abrupt short-term changes, whose effect on the life cycle of individuals up to whole ecosystems is typically disproportional to their short duration (Jentsch et al., 2007; Jentsch and Beierkuhnlein, 2008). Nevertheless, simple events can also leave their fingerprint in a population by increasing mortality, reducing reproductive success, and altering species interactions (Jentsch et al., 2007). Further, they may have long-lasting effects within the life-history of individuals, when the influence of an event within one season carries over to subsequent seasons (Harrison et al., 2011; O'Connor et al., 2014). Since populations consist of individuals, such altered individual life cycles potentially scale up to shape population and community dynamics (Garcia et al., 2014). Both types of change, gradual and punctuated, pose specific challenges to the organisms experiencing them, and their potential impacts on the ecosphere are still being explored (Jentsch et al., 2007).

While there is high confidence in predictions regarding the physical impact of global change, its implications for the biosphere remain largely uncertain (IPCC, 2014). Anticipating the effects of global change on biodiversity presents major challenges. First, it requires knowledge of species and a thorough understanding of biological and ecological processes, which involves collection and analysis of massive amounts of high-quality data (IPCC, 2014). Second, we require a systemic approach that works across temporal, spatial, and entity scales: from ecological to evolutionary timescales and from the past to the future, from local to global spatial scales, from the individual to populations and communities (Bellard et al., 2012; Garcia et al., 2014). Third, there are numerous interdependencies and interactions between the biotic and abiotic environment but also within the living world itself (Garcia et al., 2014; Leadley et al., 2010; van der Plas, 2019). These must not only be identified but also be understood. Critically, given the serious threats posed by global change to biodiversity (Leadley et al., 2010; Pereira et al., 2010), it is imperative to develop a better understanding of biodiversity loss and to conserve existing biodiversity.

To this end, different scientific approaches are required, including theoretical studies and suitable model systems for analysing the causes, mechanisms and consequences of global change on biodiversity.

1.2 Threatened migratory birds – a model system for the ecological impacts of global change

A remarkable indicator of global change are birds, particularly those that migrate (BirdLife International, 2018; Møller et al., 2010). Comprising more than 10,000 known extant species (BirdLife International, 2018), birds represent the second-largest group of vertebrates on the planet, with recent phylogeny-based estimates inferring an avian diversity of greater than 18,000 species (Barrowclough et al., 2016). On average, one in five of these species is migratory, undertaking regular seasonal movements between its distant breeding and overwintering ranges (BirdLife International, 2018; Kirby et al., 2008). At high latitudes such as Scandinavia, bird species richness increases by up to 80 % during summer with the presence of migratory birds, leading to similar decreases in local species richness in the southern overwintering ranges during that time (Figure 1-1) (Somveille et al., 2013). Thus, per se, migratory birds can have a profound impact on local biodiversity.

(BirdLife International, 2018). In particular, agricultural expansion and intensification, deforestation and unsustainable logging, invasive alien species and overexploitation threaten birds around the world, while the effect of climate change is increasing and amplifying existing threats (Bairlein, 2016; BirdLife International, 2018). Migratory birds, whose life-cycle is tightly synchronised with global environmental cycles and depends on the well-functioning of multiple ecosystems (Bauer and Hoye, 2014), are particularly threatened (Bairlein, 2016; BirdLife International, 2018; Sanderson et al., 2006). It has been shown that they are affected by multiple independent risks compounding each other (Zurell et al., 2018). Birds living in agricultural landscapes and insect-feeding birds also seem to be particularly vulnerable to global change (BirdLife International, 2018; Frenzel et al., 2016; Stanton et al., 2018). Their declining populations reflect major changes in agricultural practices that also affect other taxa, for example the substantial loss of flying insects over recent decades cascading to bird populations (Fox, 2013; Hallmann et al., 2017; Thomas et al., 2004). To conclude, bird population trends mirror those of general biodiversity.

Anyhow, birds have been observed and studied for centuries and recent technical advances resulted in a rapidly growing wealth of bird data to be harnessed (Bridge et al., 2011; Lehikoinen et al., 2004; López-López, 2016). In particular migratory birds with their extraordinary lifestyle have fascinated people and scientists alike with the eldest systematic records dating from the early 1700s (Lehikoinen et al., 2004; Miller-Rushing et al., 2012). Accordingly, their abundance, distribution, behaviour, ecology, and taxonomy are quite well-known, allowing to aim for a mechanistic understanding of the global change impacts on migratory birds.

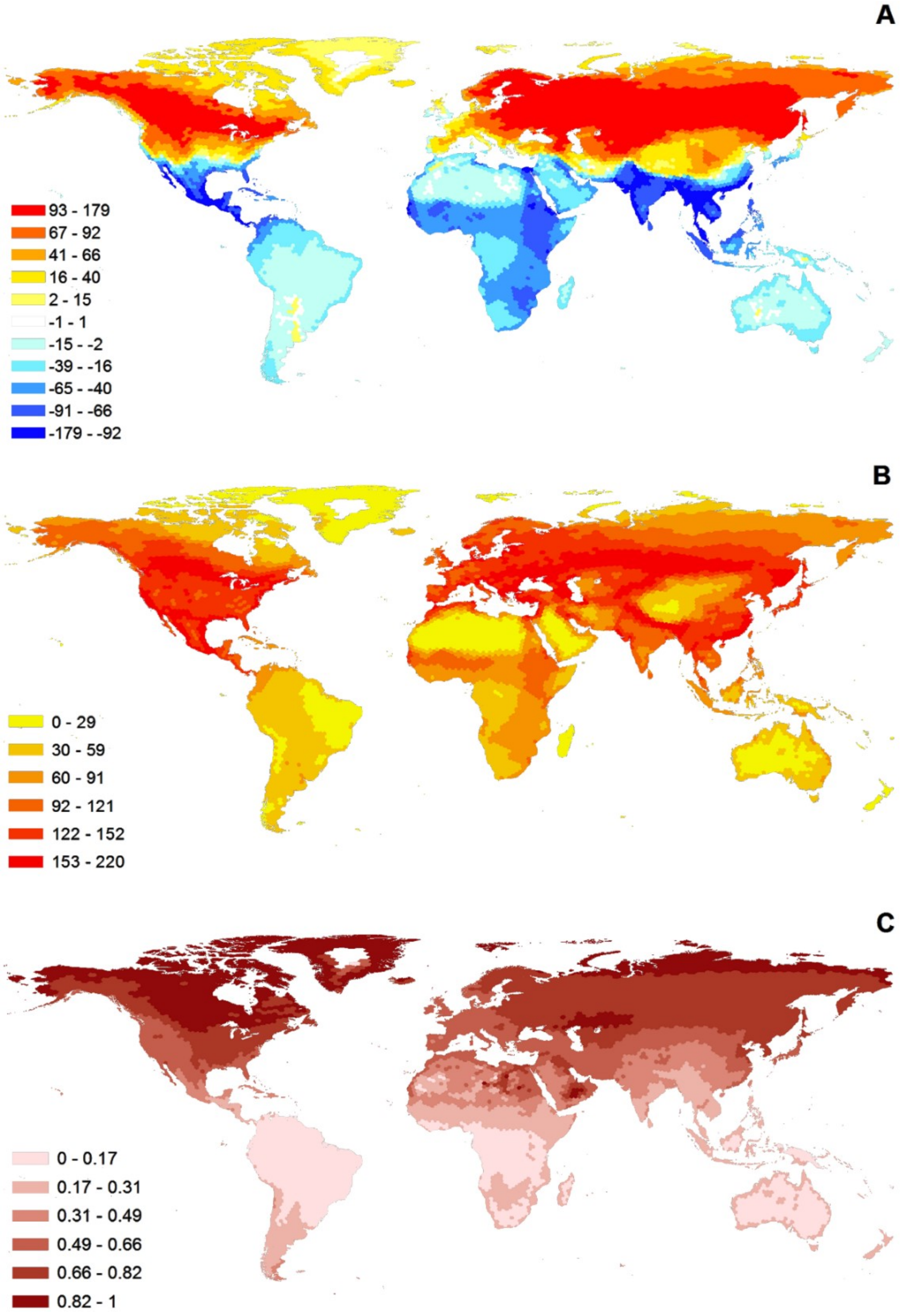

Figure 1-1: Global distribution patterns for migratory bird species. (A) Difference in species richness for the local avifauna between July and January, whereby positive values (red) indicate areas that are richer in July, and negative values (blue) show areas that are richer in January; (B) richness in migratory bird species; (C) share of migratory species compared to total number of bird species. This figure was adapted from the original paper by Somveille et al. (2013).

According to the IUCN Red List index for birds, one in eight bird species is threatened with extinction (IUCN, 2018) – mainly due to global change

Birds in general and migratory birds in particular further fill different functions in the food chain and provide various important ecosystem services (Şekercioğlu, 2006; Şekercioğlu et al., 2004). For example, they are consumers, predators, prey and recyclers, and provide major ecosystem services such as insect and pest control, pollination, seed dispersal and carcass disposal (Şekercioğlu, 2006; Şekercioğlu et al., 2004). Moreover, connecting distant ecosystems around the world (Figure 1-2), like Central European breeding and Sub-Saharan overwintering ranges, they represent important mobile links (Bauer and Hoye, 2014; Jeltsch et al., 2013). They transport nutrients and energy but also pathogens along their migratory routes, potentially influencing down-stream processes that affect biodiversity patterns (Bauer and Hoye, 2014; Jeltsch et al., 2013). Therefore, an improved knowledge on migratory birds will help improving our understanding of whole ecosystems and their vulnerability to global change.

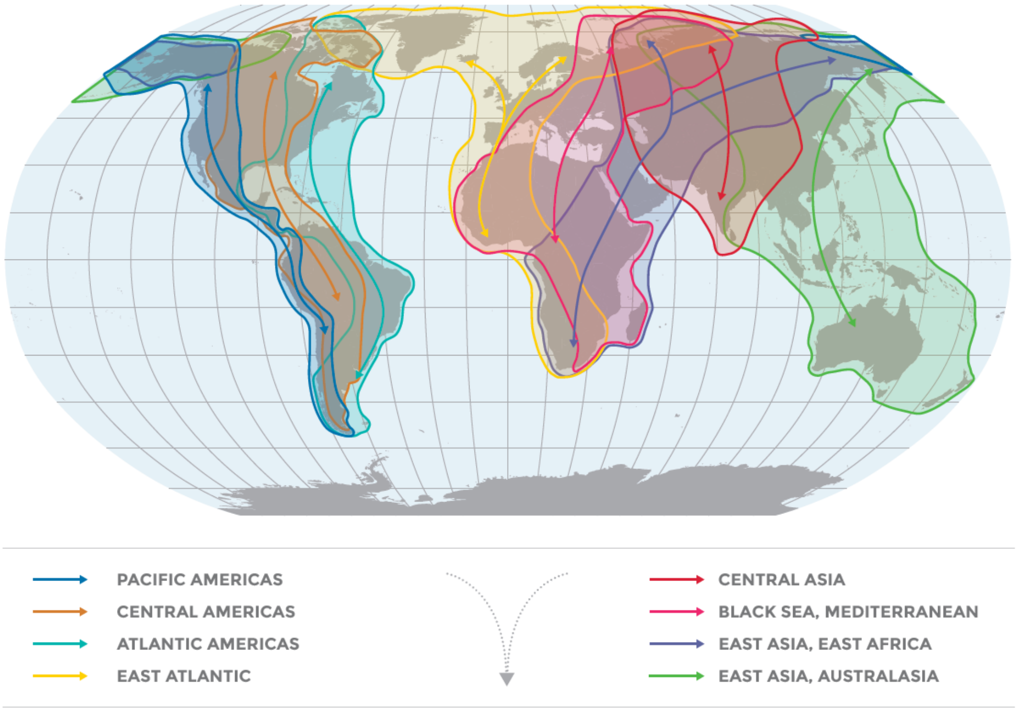

Figure 1-2: Generalized global flyways of migratory land and water birds. This figure was taken from the original report by BirdLife International (2018).

Additionally, the high mobility of birds generally, and migratory birds in particular, leads to comparatively quick responses to environmental change (BirdLife

International, 2018). The most prominent examples of such responses in migratory birds are an altered timing of life-history events like breeding and migration, reduced migratory activity (Berthold et al., 1992; Pulido and Berthold, 2004) and range shifts (A La Sorte and Thompson, 2007; Maclean et al., 2008) that are connected to altered migratory routes and distances (Knudsen et al., 2011). For instance, many but not all migratory bird populations seem to advance spring migration and egg laying in response to climate change (Aloni et al., 2017; Dunn and Møller, 2014; Miles et al., 2017; Rubolini et al., 2007). The extent to which advancing their breeding phenology is possible and beneficial might vary among taxa and is not yet fully understood (Knudsen et al., 2011). Such temporal adjustments of behaviour can be crucial for population dynamics but are challenging to predict (Knudsen et al., 2011; Møller et al., 2008). If migratory birds fail to respond adequately to the generally advancing spring phenology of the food sources in their breeding habitats, trophic mismatches might occur that could induce population declines (Both et al., 2009; Knudsen et al., 2011; Visser et al., 2004). Similarly, temporal mismatches with respect to predator pressure, pathogen prevalence, or protective foliage cover could arise (Elmberg et al., 2014; Knudsen et al., 2011; Møller et al., 2010), highlighting the importance of understanding and predicting the effects of environmental change on migratory birds. Another example of a quick adaptive response to climate change is the poleward shifts in the winter ranges of many wader species from 1981 to 2000, which may constitute range expansion (Maclean et al., 2008). Nevertheless, migratory birds—like other species—face important evolutionary constraints in their adaptive potential to global change. These include, for example, internal constraints in behavioural decision-making, but also external constraints such as the temporal and spatial heterogeneity of climate change (Senner et al., 2018).

Altogether, migratory birds provide a valuable early-warning indicator for the effects of global change and a suitable study system to reach a deeper understanding of the impacts of global change including climate change on the biosphere. Additionally, they can serve to test and refine respective explanatory and predictive methods.

1.3 Understanding and predicting global change impacts on migratory birds

To better understand and predict how global change impacts migratory birds, we need to know how environmental factors and changes therein affect the behaviour and population dynamics of migratory birds. This endeavour can only be successful if we recognize the evolutionary constraints that migratory birds are experiencing, as well as their potential for adaptive response. Life-history theory (Section 1.3.1) provides a natural background for such questions. Further, by acknowledging that movement plays a central role in the life of migratory birds, this thesis strongly connects to the movement ecology framework (Section 1.3.2) by Nathan et al. (2008). Therefore, I will briefly summarize both life-history theory and the movement ecology framework, illustrating important terms with bird examples.

1.3.1 Life-history theory

Life history theory aims to explain how natural selection shapes the design and life schedules of organisms for achieving long-term reproductive success (Roff, 1992; Stearns, 2004, 2000). It is concerned with questions like: Why do organisms differ in their lifespans? Why do they have different numbers of offspring? Why do they reproduce earlier or later? Why do they migrate and why do they vary in their departure and arrival dates? Such genetically determined but environmentally shaped properties of an organism (lifespan, offspring size, behavioural timing etc.) with direct fitness consequences contribute to an organism’s phenotype and are termed life history traits (Varpe, 2017). Fitness describes an individual‘s success in surviving and contributing the most copies of itself in successive generations (Roff, 1992; Stearns, 2004, 2000). Typically, there exist trade-offs between different life-history traits, meaning that a beneficial change in one trait is associated with a costly change in another trait with respect to fitness (Stearns, 1989). Such trade-offs may even act inter-generationally (Stearns, 1989). For example, experimentally increased clutch size in birds decreased the survival probability of both the parents and their offspring, in addition to decreasing their future clutch sizes (Roff, 1992; Vander Werf, 1992). An organism’s set of life-history traits and its associated schedule of major life-history events (e.g. reproduction or migration) throughout its life represents the life history strategy of an organism (Houston and McNamara, 1999; McNamara and Houston, 2008; Varpe, 2017). The life-history strategy in turn may comprise an annual routine, i.e. the regular schedule of behavioural activities which are performed over the annual cycle (Houston and McNamara, 1999;

McNamara and Houston, 2008; Varpe, 2017). For instance, billions of birds undertake regular seasonal journeys between their breeding and overwintering habitat each year (Bauer and Hoye, 2014).

In classic life-history theory (as reviewed in Roff, 1992; Stearns, 2004), the evolution of life-histories including annual routines, is treated as an optimality problem (Stearns, 2000). Assuming that natural selection maximizes fitness, it should select for the optimal trait combination and behavioural schedule, maximizing long-term reproductive success in a given environment and subject to given trade-offs and phylogenetic constraints. Since environmental conditions vary spatially over the globe, different life-history strategies have evolved. Temporal variation in environmental conditions further increased the number of life-history strategies, which include adaptations to cope with unfavourable and to exploit favourable time periods in seasonal environments, respectively (Varpe, 2017). Birds accumulate fat depots or migrate to warmer regions during winter, for example, or they reproduce at certain times of the year in order to improve offspring survival (Blix, 2016). Additionally, environmental conditions can be more or less predictable and fluctuate over the years, leading to different optimal life-history strategies for uncertain environments (Kivelä et al., 2016; Tökölyi et al., 2012).

One major tool to understand the evolution of different life-history strategies is mathematical modelling. In particular, mathematical optimization and dynamic state variable models were successfully employed to this end (Clark and Mangel, 2000; Houston and McNamara, 1999; Stearns, 2000). Optimal annual routine (OAR) models as introduced by Houston and McNamara (1999) became a key tool for analysing annual routines in seasonal environments, for example. These models determine the optimal schedule for multiple behavioural activities over an environmental cycle with respect to long-term reproductive success, considering the state of the environment, the internal state of an organism such as its energetic reserves (cf. Section 1.3.2) and trade-offs between various life-history traits (Houston and McNamara, 1999). With changing environmental conditions, the fitness consequences of existing traits and behavioural schedules can be expected to change (McNamara et al., 2011), promoting the development of new life-history strategies including behavioural strategies. Indeed, organisms that do not update their life-history strategy might be threatened by population declines and extinctions (McNamara et al., 2011; Thomas et al., 2001).

Meanwhile, further modelling approaches involving evolutionary game theory or explicit density- and frequency-dependence have been developed (e.g. Barta et al., 2008, 2006; Stearns, 2000). Though optimality models have not failed in their predictions, such model approaches represent the logical next step in life-history theory from a theoretical point of view. However, their empirical success is still under evaluation and they are even more challenging to apply than OARs because of their increased complexity (Barta et al., 2008, 2006). Still, with global change rapidly altering the planet's environmental conditions, mechanistic modelling approaches that are grounded in life-history theory are required (Pereira et al., 2010) to provide a better understanding and more reliable predictions of the global change impacts on natural populations.

1.3.2 The movement ecology framework

Organismal movements play a key role for the fate of individuals up to the dynamics of whole communities (Jeltsch et al., 2013). The movement ecology framework by Nathan et al. (2008) describes the interplay between individual movement and the environment (Figure 1-3), aiming to facilitate a holistic understanding of the causes, mechanisms, patterns and consequences of movement. It focuses on the individual and encompasses four components: external factors and the internal state, navigation capacity and motion capacity of the individual, which together result in the realized movement path of an organism.

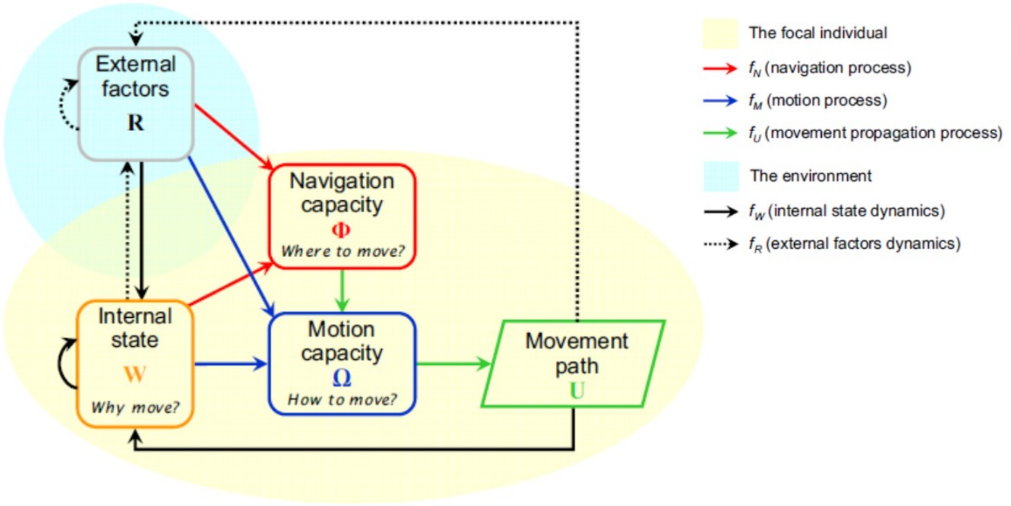

Figure 1-3: Conceptual framework for movement ecology with its basic components: external factors (blue background) that affect the internal state, navigation capacity and motion capacity of the focal individual (yellow background), resulting in its movement path. Arrows indicate the occurrence and direction of relationships between these factors. This figure was adapted from the original paper by Nathan et al. (2008).

An individual’s movement emerges from external and internal factors. External factors are influences from outside the animal that affect its movement. These can be biotic, such as seasonally high food supply provoking migratory movements, or abiotic, such as atmospheric weather conditions influencing the path and timing of migration. Internal factors, by contrast, relate to the individual itself. Nathan et al. (2008) distinguish three basic components of movement: the internal state (“why move?”), the navigation capacity (“where and when to move?”) and the motion capacity of an individual (“how to move?”). The internal state reflects the unmet needs and goals of an individual, and accounts for its physiological and neurological state. For example, if a bird has low energetic levels, it will feel hungry and start moving in search of food in order to improve its energy balance. The navigation capacity allows the individual to orient itself in space and time and to control its movement in order to achieve its goal including interfering goals. For example, a hungry bird might direct its movement towards a detected food source or decide to wait since there exists a stronger interfering goal such as hiding from a predator or avoiding bad weather. The specific manner in which the individual moves is determined by its motion capacity. The motion capacity encompasses fine-scale movement patterns like different hunting movements that depend on the specific prey to gross-scale movement modes like flying or walking. Finally, the observable movement path emerges from this interplay of movement components and external factors.

One important process within the movement ecology framework, which also plays a major role for my work in this thesis, is the navigation process. Here, navigation capacity, internal state and external factors together determine which movement decisions are made. Each movement and hence movement decision is associated with certain costs and payoffs, such as those relating to the individual’s survival, energy balance, or reproduction success. Accordingly, natural selection will act on it alongside to the underlying behavioural strategy, optimizing them with respect to an appropriate measure of fitness like survival or reproductive success. Hence, optimal annual routine modelling (cf. Section 1.3.1) can be applied to study how environmental factors shape movement decisions.

Integrating the optimality perspective of evolutionary and behavioural ecology, the movement ecology framework considers how movement is shaped over ecological and evolutionary timescales, fostering a deeper understanding of animal movement. It also suggests that the taken movement path operates on the environment – an idea that has been refined by Jeltsch et al. (2013), who incorporated various mechanisms into the framework by which movement interacts with biodiversity.

1.4 Research objectives

As alluded to above, we still do not fully understand how ongoing global change is and will be affecting the behaviour and population dynamics of migratory birds. However, such knowledge is crucial for predicting future population dynamics and identifying vulnerable populations in order to develop effective conservation measures. It also is a prerequisite to understand and anticipate the impacts of global change on general biodiversity patterns. Thus, with this thesis, I aim to improve our understanding of the impacts of global change on migratory birds and to advance our ability to predict their responses to expected environmental change. In particular, my objective is to investigate how changes in food supply as they can be expected under global change will influence the population size and the behavioural timing of migratory birds over ecological and evolutionary timescales. I further seek to clarify, what carry-over effects can be expected from predicted intensifying droughts in the overwintering habitat of many migratory birds as these will scale-up to affect population dynamics.

To this end, I implement a dynamic mechanistic model that allows to determine optimal animal life-history strategies in cyclic environments and to simulate emergent behavioural patterns and population dynamics of a population following the computed behavioural strategy in a given environment. Abstracting global change to altered environmental food supply, I employ this model to analyse the potential impacts of expected food changes on modelled migratory birds, as well as the required adaptive responses to keep population sizes stable. I consider two signatures of global change, namely gradual versus punctuated changes, and two temporal scales, specifically an ecological or short-term and an evolutionary or long-term timescale. Further, I revert to bird functional types, namely a stork and a falcon type. Since the functional traits of a species reflect its ecological strategy (Westoby et al., 2002), functional types naturally link mechanistic models of species' response to environmental change (Jeltsch et al., 2008). They also produce more general results than individual- or species-specific approaches and ease scaling-up from individuals to ecosystems (Blaum et al., 2011; Chave, 2013; Zakharova et al., 2019). Further, there exist promising studies demonstrating the potential of using animal functional types in mechanistic modelling (Kearney et al., 2010; Scherer et al., 2016; Teckentrup et al., 2018). The stork and falcon bird functional type selected for this dissertation are both long-distant migrants for which enough biological data is available to parametrize the implemented model.

1.5 Outline of thesis

The core part of this publication-based thesis is structured into four chapters, thereof three thematically related but independently readable research papers that summarize my findings and one synthesizing chapter that discusses my work in a wider ecological and scientific context. One of these research papers is published in Ecography (Schaefer et al., 2018 / Chapter 2), one has been under review and was invited to be resubmitted to Oikos (Chapter 3) and one has been under review and was invited to be resubmitted to Movement Ecology (Chapter 4). Since the papers are co-authored, they are written in first-person plural. However, being the lead author of all articles, I performed the main work and was predominantly responsible for the study design, the model development, the model implementation, the computations and simulations, the result analyses and the writing. Nevertheless, I want to acknowledge the support of my co-authors in terms of invaluable discussions, data provision, and proof-reading.

In **Chapter 2**, I introduce the software *sOAR* (Schaefer et al., 2018), which represents a powerful and user-friendly implementation of the well-established framework of optimal annual routine modelling. The generic open-source software allows for the determination of animals' optimal behavioural strategies in cyclic environments, as well as the simulation of emerging behavioural patterns and dynamics of a population following this strategy. It helps to improve our understanding of how complex behaviours evolve and how behavioural decisions are constrained by internal and external factors experienced by the animal. Such knowledge is crucial for anticipating potential species' response to global environmental change. *sOAR* is particularly suited for theoretical studies of bird migration. For example, it includes options to differentiate between costs of active and passive flight into the optimal annual routine modelling framework, as well as options to consider periodic wind conditions affecting flight energetics. A user manual and two illustrative examples are included in the software package.

In **Chapter 3**, I am particularly interested in potential global change impacts on migratory birds over ecological and evolutionary time scales. Analysing two contrasting bird functional types using *sOAR*, I find that the advancement of spring phenology in migratory birds is an optimal response to global change, whereas model populations, which do not adapt their behavioural strategy to the altered environment, decline in most cases. The falcon type shows higher phenotypic plasticity in its behavioural strategy, but at times this counteracts optimal behavioural adaptation. The results further indicate that observed advances of spring phenology cannot be explained by phenotypic plasticity but suggest adaptive response. They highlight a need to disentangle the role of phenotypic plasticity, microevolution and other adaptive mechanisms like social learning in observed behavioural responses. Sociality and flight mode could indeed be important overlooked factors that may improve predictive models for identifying vulnerable migratory bird species. Apart from that, decreasing food levels during the breeding phase as well as in the overwintering location significantly affected population dynamics of the studied bird functional types.

In **Chapter 4**, I explore the effects of altered overwintering food supply until the breeding season in Central European white storks, which follow the currently optimal behavioural strategy. The results showed that annual routine modelling is a valuable tool for studying carry-over effects, which are difficult to assess experimentally in migratory birds. Hereby, overwintering conditions significantly affected population dynamics depending on the timing, duration and strength of resource events. Under decreased food supply, breeding was delayed, fewer birds started a brood and they had lower energetic reserves when doing so, especially late breeders. Equivalent food surplus had the opposing effect. Additional to these carry-over effects (COEs), intra-seasonal effects occurred that can indirectly influence subsequent breeding performance, e.g. food shortages immediately reduced energetic reserves and increased mortality rates later in winter. The pre- and post-migratory phase turned out to be particularly important. Contrary to experimental findings, model birds had low mid-winter reserves. This indicates that even a mobile and opportunistic feeder like the white stork experiences food supply in the African overwintering regions as highly unpredictable, so that winter fat depots and a nomadic lifestyle might be fostered at evolutionary timescales.

In **Chapter 5**, I synthesize my findings and discuss them in a wider scientific context. I evaluate how OAR modelling can be employed for global change research and address the challenges to be met when working with complex models. I discuss how population declines, altered behavioural patterns and carry-over effects in migratory birds as predicted in this thesis relate to and advance the scientific literature, while assessing their meaning for general biodiversity patterns. Advancing theoretical ecology, I further propose how the movement ecology framework by Nathan et al. (2008) can be developed further so that it operates smoother across temporal and entity scales. To assist the conservation of migratory birds, which is highly necessary according to my results, I outline a mechanistic-based indicator of vulnerability based on my work. Finally, I reveal worthwhile future directions of research to reach a deeper mechanistic understanding of different ecological phenomena and to predict global change impacts on the biosphere.

2 sOAR: A tool for modelling optimal animal life-history strategies in cyclic environments

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2.1 Abstract

Periodic environments determine the life cycle of many animals across the globe and the timing of important life history events, such as reproduction and migration. These adaptive behavioural strategies are complex and can only be fully understood (and predicted) within the framework of natural selection in which species adopt evolutionary stable strategies. We present *sOAR*, a powerful and user-friendly implementation of the well-established framework of optimal annual routine modelling. It allows determining optimal animal life history strategies under cyclic environmental conditions using stochastic dynamic programming. It further includes the simulation of population dynamics under the optimal strategy. *sOAR* provides an important tool for theoretical studies on the behavioural and evolutionary ecology of animals. It is especially suited for studying bird migration. In particular, we integrated options to differentiate between costs of active and passive flight into the optimal annual routine modelling framework, as well as options to consider periodic wind conditions affecting flight energetics. We provide an illustrative example of *sOAR* where food supply in the wintering habitat of migratory birds significantly alters the optimal timing of migration. *sOAR* helps improving our understanding of how complex behaviours evolve and how behavioural decisions are constrained by internal and external factors experienced by the animal. Such knowledge is crucial for anticipating potential species' response to global environmental change.

2.2 Introduction

Life on earth is subject to various geophysical cycles such as the solar day or the seasons (Numata and Helm 2014). In response to these cycles, many animals display rhythmic patterns of behaviour (Numata and Helm 2014). For example, migratory birds respond to seasonal environments by undertaking regular long-distance journeys between breeding and wintering habitat (Alerstam 1990). Such grand-scale behavioural patterns can only be fully understood and protected from global change if the complete behavioural cycle, as embedded into the periodic environment, is considered from an evolutionary and mechanistic perspective (Helm et al. 2013, Visser 2010, Wilcove and Wikelski 2008). Life history theory (see Stearns 2004 for review) predicts that natural selection and other evolutionary forces led to the evolution of optimal behaviours that ensure highest fitness in terms of long-term reproductive success (McNamara et al. 2001) under the given ecological constraints.

In mathematical biology, game theoretic approaches help to understand complex decision-making processes that lead to the maximization of fitness and the evolution of optimal strategies (Houston et al. 1988, McNamara et al. 2001, Parker and Smith 1990). Notably, stochastic dynamic programming (SDP) can be applied, which is a well-known method for solving multi-stage decision problems (Bertsekas 2005, Parker and Smith 1990). In periodic environments, we face the additional problem that behavioural cycles need to be closed (Clark and Mangel 2000, Hostetler et al. 2015, Houston and McNamara 1999). To this end, the optimal annual routine (OAR) modelling framework has been introduced (Houston and McNamara 1999, McNamara et al. 1998). Grounded in state-based life history theory, it assumes that evolution shapes the behaviour of animals by natural selection and that an animal takes its behavioural decisions based on knowledge of its environment as well as its own state. These assumptions allow for an optimization-based approach like SDP to identify state-dependent optimal life-history strategies of organisms under cyclic environmental conditions (McNamara and Houston 2008).

Although the OAR framework is suited for a broad range of research questions and has many advantages over other modelling approaches, the number of actual implementations is small (Feró et al. 2008). One major reason for this might be the complexity of such models, which require time and expertise for model development and implementation. Here, we present the software package *sOAR* (Figure 2-1) that provides an open source implementation of the original OAR framework by Houston and McNamara (1999). We further extended the framework by certain optional features that are crucial for studying bird migration and account for flight ability and wind-dependent migration costs. *sOAR* provides a computationally fast and ready-to-use OAR software, which is implemented in a modular manner in C++ allowing easy adjustment for specific research questions.

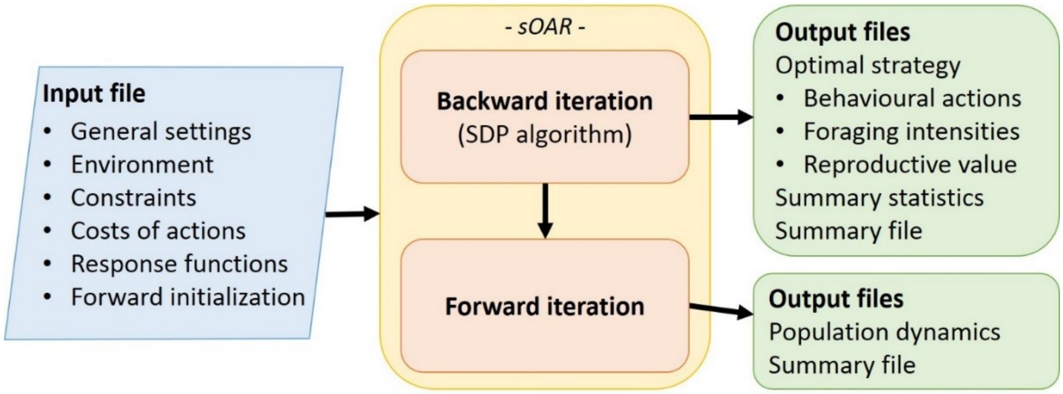

Figure 2-1: sOAR flow of use. User-defined settings provided by an input file are illustrated in the blue box, while the green boxes give an overview of the output files generated by the internal backward and forward iteration of sOAR (orange box).

2.3 Theoretical Background

The key ingredients of stochastic dynamic programming (SDP) are state variables, decisions and a currency to evaluate decisions. The set of possible decisions, or available behavioural activities, at time t depends on the state X_t of the animal. The main objective is finding the optimal strategy that maximises pay-off, for example the long-term reproductive success (Houston and McNamara 1999, Mangel 2015). The optimal strategy takes the short- and long-term costs and benefits of any particular decision into account, as well as the associated probability of surviving the activity and the probability that the animal's state is changed by a certain increment when the activity is performed (Mangel, 2015). The decision costs can depend on internal (e.g. metabolism) but also on external constraints (e.g. food availability) (Bauer and Klaassen, 2013).

The development of state X_t of an organism at time t under the given constraints, costs and benefits is modelled as a discrete-time dynamical system with usually nonlinear difference equations of the form

$$\boldsymbol{X_{t+1}} = \boldsymbol{F}(\boldsymbol{X_t}, \boldsymbol{A_t}, \boldsymbol{W_t}), \quad \boldsymbol{t} = \mathbf{0}, \mathbf{1}, \dots, \boldsymbol{T} - \mathbf{1} \text{ with } \boldsymbol{X_0} = \text{const.}, \qquad (1)$$

where A_t is the vector of decision variables to be selected in the process, $W_t$is a random parameter with given probability distribution, T represents the time horizon, X_0 is the initial state and F is a function specifying the system's transitions in state with time. In general, though the concrete result of a given action will be unknown, the probability distribution of states X_{t+1} resulting from state X_t and action A_t taken at time t can be estimated (Bertsekas, 2005).

Subject to this random sequence of constraints (eq. 1), a planned sequence $\{A_t^*\}_{t=0}^T$ of behavioural decisions conditional on the sequence of realized states shall be selected that maximizes the payoff. By Bellman's Principle of Optimality (Bellman, 1957) and the law of iterated expectations, the maximum payoff $V(X_t)$ to be expected given state $\mathrm{X_t}$ is

$$V(X_t) = \max_{A_t}\{U(X_t, A_t) + \lambda\mathbb{E}[V(X_{t+1})]\},$$

where $\mathrm{U}(X_t, A_t)$ is the utility or immediate reward of being in state X_t performing action A_t and $\mathbb{E}[V(X_{t+1})]$ represents the expected value of being in state X_{t+1} at the next time step. The discounting factor λ equals one when a population is following an assumed evolutionary stable strategy. Thus, if the optimal payoff at final time T is given ($V(X_{t+1}) = V(X_T)$), the expected maximum payoff can be calculated recursively for each combination of state and time by using the appropriate transition probabilities between states X_t and X_{t+1} (eq. 1) and maximizing only the immediate utility $U(X_t, A_t)$ in each case at a time. Simultaneously, the optimal sequence $\{A_t^*\}_{t=0}^T$ of decisions for all potential sequences of states that could realize is obtained, i.e. the optimal strategy.

For computational reasons, the optimal strategy is usually computed by backward induction, starting from the known (or desired) end state and moving backwards in time until convergence. Hereby, suboptimal solutions are omitted during the search as illustrated in Houston et al. (1988). In the context of optimal annual routine modelling, the terminal reward $V(X_T)$ is assumed to equal one for all possible states. Further, consecutive periodic time cycles are connected by setting the state and payoff at the end of one cycle equal to the state and payoff at the beginning of the next cycle (Houston and McNamara 1999). Iterating over successive time cycles to convergence may then result in the best strategy maximizing the expected number of descendants left in the distant future. Once the optimal strategy has been computed, it can be applied in simulations of population dynamics or individual life histories under the optimal strategy, e.g. for predictive modelling.

2.4 Model description

The model considers the behaviour of a female animal and its female descendants over a specified number of periodically reoccurring stages or decision epochs respectively. For example, the animal has to make behavioural decision at each week of an annual cycle. The animal itself is described by the state variables energy reserves, health condition (optional), age of offspring, experience, location, and migratory state (optional). Their uniform discretization is user-defined, whereby the location variable is currently implemented for up to two different sites. An overview of the implemented state variables is provided in Table 2.1 and Table S 2.4-1.

Table 2.1: Overview of state variables and behavioural actions implemented in sOAR, and of user-defined costs, constraints and response functions. Italic entries indicate optional settings.

State Variables:	Energy reserves, *health condition*, experience, age of offspring, location, *migratory state*
Actions:	Forage, start reproduction, care for offspring, subsist, *migrate*
Fixed costs and constraints:	Reproduction costs and constraints, growth and role of experience, maximum lifespan, basal metabolic rate, food availability, grade of stochasticity, *wind conditions*, *migration costs and constraints*
Response functions:	Metabolism, predation, *immune response*, *flight energetics*

At the beginning of each stage the animal selects a behavioural action (Table 2.1). For an animal without dependent offspring these are either initiating reproduction, subsisting or migrating (optional). Potential activities of an animal with dependent offspring are caring for the offspring or abandoning it. Simultaneously, the animal must choose a foraging intensity at each decision epoch, ranging from zero (no feeding) to one (maximum possible energetic intake of available resources). If an animal with dependent offspring cannot forage with sufficient intensity to balance the offspring's energy needs, this is abandoned.

Each behavioural action is associated with the following costs that influence the animal's future state (Table S 6.1-1): metabolic energy costs that increase with foraging intensity, and additional energetic costs for reproduction and migration. If health condition is included in the model, it will also be affected by costs for metabolism, reproduction and migration. Further, there are expected energetic gains from foraging that increase with foraging intensity, food availability and experience. Energy intake is coupled to experience assuming that young animals may have a lower foraging efficiency than adults. The coupling happens via a parameter θ with $0 < \theta \leq 1$, which scales the actual energy intake of an animal with low experience such that it will be a certain fraction of the intake of an animal with full experience. The parameter θ implicitly accounts for density dependence and is usually adjusted during computations until the population growth rate equals 1, meaning the population is in a stationary state with constant population size (see Houston and McNamara 1999, *sOAR* User Manual).

The animal faces different sources of mortality: starvation, predation and disease (optional). Starvation and disease correspond to reserves and health condition dropping to their minimum level. The user-defined predation rate can increase with foraging intensity and higher levels of reserves. It is specified for each location and the migration period, respectively, and may include a background mortality. Disease risk rises with decreasing values of the health variable. If this variable is enabled, a background mortality for disease is determined in *sOAR* that reflects the maximum life expectancy of the species. If a parent animal dies, its dependent offspring dies, too.

sOAR can be run as a pure reproduction model or can optionally include migration between two locations. In both models, environmental food availability is specified by a periodic function of time and location. Migratory costs can be time and reserves dependent but since migrating model animals cannot forage, these user-defined costs need to integrate potential energy gains through foraging for species that in reality feed during migration. We introduced an option to read in periodic migratory costs from file, which can mirror cyclic wind conditions like thermals that allow energy-efficient soaring flight of avian migrants. However, in principle this option allows time-dependent migration costs for any animal. Additionally, the respective share of active (flapping) and passive (soaring/gliding) flight regarding total flight costs is determinable. Migration may span several decision epochs but must be completed without pause once started. During that time, the state variable indicating the state of migration increases while the location variable indicates the place of origin until the last week of migration upon which the animal will be relocated and the migratory state be reset.

To determine the optimal strategy, behavioural actions are evaluated in terms of their associated long-term reproductive success. Subsequently, the computed optimal strategy can be employed in Markov chain iterations (forward iteration). The values of the resulting steady state distribution represent the probability of an individual or the proportion of a population that follows the optimal strategy to be expected in any particular state-time combination. Thus, population dynamics under the optimal strategy emerge from the simulation allowing to analyse behavioural timing, proportions of a population performing a behaviour, age structures, mortality patterns and the development of mean reserves and health condition.

A detailed model description and instructions on running *sOAR* are provided in the User Manual (*sOAR* User Manual). Figure 2-1 illustrates the workflow of *sOAR* including required inputs and produced output files, while Figure 2-2 provides a model overview.

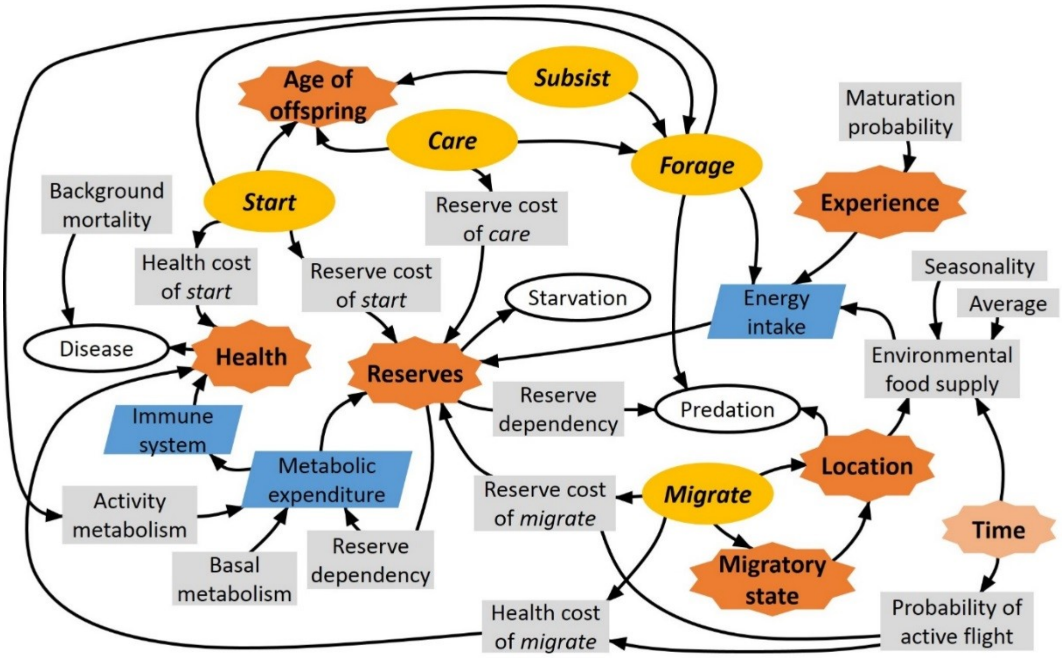

Figure 2-2: Model overview for sOAR depicting the implemented interdependencies (arrows) between state variables (orange stars), behavioural activities (blue boxes), user-defined input parameters (grey ellipses), internal sub-models (yellow ellipses) and sources of mortality (white ellipses).

2.5 Illustrative examples

We illustrate *sOAR* by simulating the effect of seasonality in the wintering habitat on the timing of migration and reproduction in a migratory bird. Using a hypothetical migratory bird we show *sOAR*'s capability to determine a complete life-history strategy based on differing cyclic environmental conditions at two distinct locations representing the breeding and wintering habitat. Ecologically, the example reveals how the degree of seasonality in the wintering habitat may alter the optimal timing of migration and reproduction. Moreover, it shows that the optimal timing of behaviour depends on the state of the animal and that different degrees of synchrony between adult and juvenile behaviour might arise from different environmental conditions.

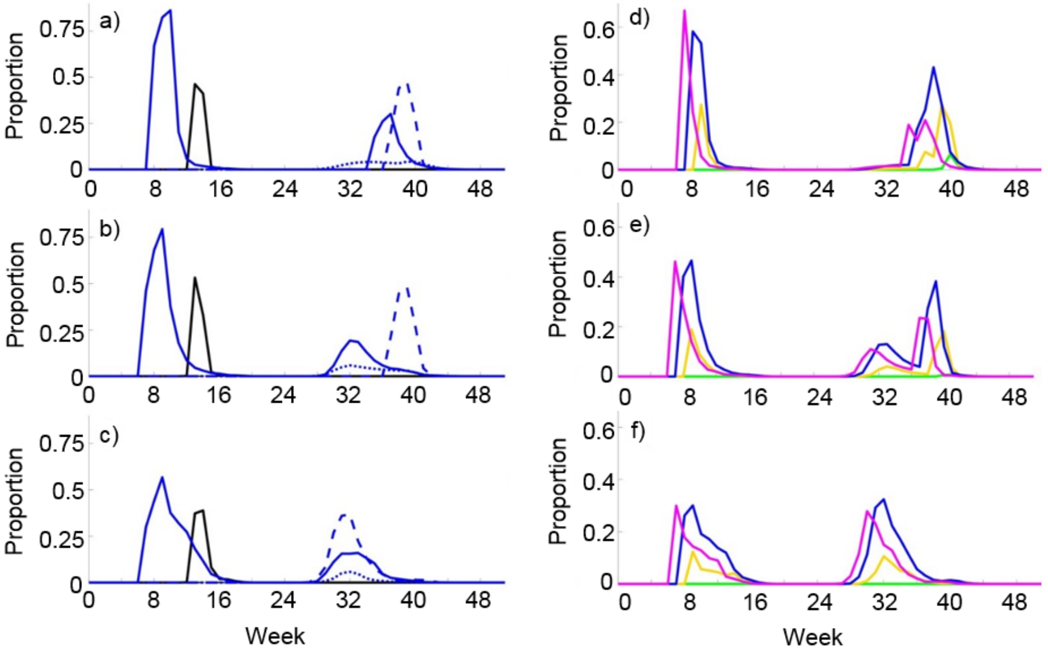

Figure 2-3: The timing of behaviour with respect to different experience (a-c, left) and reserve classes (d-f, right) for different degrees of seasonality in wintering grounds, ranging from very low seasonality of high tropics (top) to intermediate seasonality of subtropics (bottom), whereas seasonality of breeding grounds was very high as in temperate zones. Graphs represent the proportion of a population following the optimal strategy that performs a certain behaviour or has a certain condition over the year. Left: The timing of migration (blue), especially autumn migration, varies with seasonality in the wintering habitat, in contrast to the breeding period (black). Varying seasonality can induce synchronic or differential migration between individuals with low (dashed), medium (dotted) or high (solid) experience. Please note that only individuals of the highest experience return from wintering location in spring and attempt breeding. Right: The level of reserves on the onset of migration is depicted from high to low in pink, blue, yellow and green. Regardless of other factors, an early departure is optimal when reserves are high. This figure was adapted from the original by Schaefer et al. 2018 to ensure readability in this thesis.

In the example, both the health variable and the migration option were enabled. Biological parameter settings (Table S 6.1-2) were oriented at a medium-sized long-distant migrant as from the genus Falco, employing active flapping flight. The two locations can be interpreted as a temperate and a more tropical location in the same hemisphere, meaning that seasonal food availability (following a sine curve) was synchronised but the tropical location showed much lower seasonality despite the same yearly average. We computed the optimal behavioural strategy for three scenarios with different degrees of seasonality in the wintering habitat such that the maximum potential energy gain from foraging in the two locations differed by approximately 25 % (subtropics), 30 % and 35 % (high tropics) during peak times (Figure S 6.1-1). Sample scripts and detailed instructions are provided in the supporting information.

The preferential departure date of autumn migration varied depending on seasonality of food supply in the wintering habitat whereas the onset of spring migration and breeding was very similar across scenarios. For lower degrees of seasonality in the wintering location (high tropics compared to more seasonal subtropics), the timing of autumn migration varied considerably between experience classes (Figure 2-3 a,b,c), and depending on the level of reserves (Figure 2-3 d,e,f) and health condition (not shown). Timing of spring migration was overall less variable because the optimal timing of spring migration is more influenced by conditions in the breeding habitat and because only mature birds return to summer grounds to attempt breeding, as emerging during the solution of the model. At the same time, the time window of spring migration was longer when overwintering in more seasonal subtropics because building up reserves after strenuous autumn migration was less effective than in tropics because of the more pronounced resource low during winter. Hence, overall, differences in seasonal food availability between different locations may induce large variances in migration patterns. No major differences in the optimal timing of the breeding period occurred but the highest food abundance coincided with the hatching of the young for all settings.

We note that time slots of favourable wind conditions might be similarly important in driving the timing of migration in soaring and gliding birds since passive flight can decrease their energy consumption during migration considerably (Pennycuick 1972), which can be further explored using *sOAR*.

A second example illustrates how the optimal number of brood cycles per year of non-migratory birds decreases with increasing fledging age of the offspring (Figure 2-4), parameter settings and configuration file see Table S 6.1-3 and the *sOAR* User Manual). Here, the migration option and the state variable of health condition were not included in the model. The *sOAR* software has further been tested on the optimal annual routine models of Houston and McNamara (1999) and a migration model oriented at McNamara et al. (1998). The results were consistent with those published except for minor differences which we attribute to potential differences in the actual implementation of the model and in selected model settings regarding e.g. the convergence criterion and stochasticity settings for energy reserves and health condition. The respective configuration files and some visual results can be found in the *sOAR* User Manual.

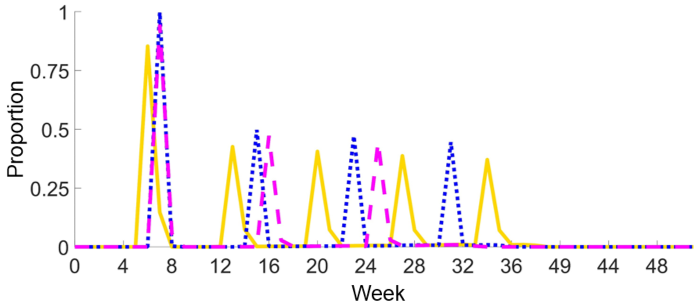

Figure 2-4: The optimal timing of initiation of breeding activities when the offspring becomes independent from the parent bird at the age of 3 (solid yellow), 4 (dotted blue) or 5 (dashed pink) weeks. Other model parameters than age of independence were kept constant. With increasing age of independence the optimal number of brood cycles decreases.

2.6 Conclusion

sOAR provides a powerful and user-friendly implementation of the optimal annual routine framework by Houston and McNamara (1999) for computing optimal life history strategies of animals under periodic environmental conditions and simulating their population dynamics given such a strategy. Facilitating theoretical studies of animal behaviour, it will improve our understanding of how natural selection shapes trade-offs in animal behaviour within cyclic environments. We further extended the original framework to differentiate between the costs of active and passive flight and to consider periodic wind conditions acting on birds during migration. This will allow studying the timing of migration between obligate soaring vs. flapping birds, or studying ontogenetic differences in birds where soaring vs. flapping flight is age dependent (Hake et al., 2003).

Our main illustrative example showed how the optimal timing of spring and autumn migration may vary with environmental food supply at a site. Such insights are particularly interesting in the face of global change that may differently alter food availability in different regions. Changing environments may render current behavioural strategies of migrants and other animals suboptimal with potentially negative effects on population dynamics such that, in the long-term, a new optimal strategy should be adapted in order for a population to persist. Such facets, the consequences of suboptimal behaviour or the development of new behavioural strategies, can be easily explored using *sOAR*. Also, individual variation can be explored within OAR frameworks and be compared to empirically observed movement data, for example by means of telemetry (Feró et al. 2008). To illustrate usage and ease application, the software package *sOAR* includes descriptions and configurations for two illustrative examples as well as two examples from the literature (Figure 2-3, Figure 2-4 and *sOAR* User Manual).

The following list provides a summary of potential applications of *sOAR* (cf. Feró et al. 2008) whereby additional sites and processes such as molt or explicit density-dependent effects (Barta et al., 2008) or thermoregulation could be integrated into future versions of *sOAR*:

- Analysis of life-history constraints under global change
- Prediction of potential new adaptive behavioural strategies
- Theoretical studies of carry-over effects at the population level
- Analysis of phenotypic variation in a population within a life-history context
- Studies of functional groups of organisms
- Combining life-history models with large-scale datasets that are becoming increasingly available nowadays

Overall, such analyses will contribute to better understanding the different constraints on movement and behaviour of individuals and the consequences for population and community dynamics (Jeltsch et al. 2013, Nathan et al. 2008).

2.7 Acknowledgements

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2.8 Data Accessibility

The *sOAR* application as ready-to-use binary distribution and as source distribution, with detailed manual, the configuration file used in this paper and sample R and Matlab scripts for processing the output, is accessible at https://sourceforge.net/projects/soar-animal-behaviour.

2.9 References

Supplementary material (Appendix ECOG-03328 at < www.ecography.org/appendix/ecog-03328 >). Appendix 1–5.

3 Advancement of spring phenology in migratory birds is an optimal strategy under global change but are adaptive mechanisms overlooked?

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Key-words:	Behavioural strategies, migratory birds, full annual cycle model (FAC), global change, optimal annual routine, phenotypic plasticity, population dynamics, stochastic dynamic programming

3.1 Abstract

Migratory birds are increasingly affected by global change, with changes in population size as well as phenology. Yet, not all species appear to be advancing breeding phenology, and the extent to which advancing phenology is possible and beneficial might vary among taxa. Here, we use optimal annual routine modelling for investigating evolutionary shaped behavioural strategies of migratory birds under current and future environments. Exploring associated phenological shifts in behavioural timing, we aim to reach a deeper understanding of the response of migratory birds to global change and to advance research on the underlying mechanisms and unexplained variation. The model is parameterised for white storks and small falcons, which differ in longevity, body mass, flight mode and breeding span. We determine the timing of migration and breeding for various food scenarios under global change, assuming either adaptation of the optimal behavioural strategy to altered food conditions or adherence to the traditional behavioural strategy, which has become suboptimal under global change. In nearly all analysed scenarios, stable populations of both bird types employing the new optimal strategy had an advanced spring migration and breeding phenology whereas populations, which did not adapt their behavioural strategy to the altered environment, declined in most cases. Phenotypic plasticity in the behavioural strategy was higher for the falcon type, but at times counteracted optimal behavioural adaptation. Our results indicate that observed advances of spring phenology cannot be explained by phenotypic plasticity but suggest adaptive response. Further, not only food decreases during the breeding phase but additionally in the overwintering location significantly affected population dynamics. The study illustrates the various effects of global change on the population dynamics and behavioural strategy of migratory birds. It also highlights a need to disentangle the role of phenotypic plasticity, microevolution and other adaptive mechanisms like social learning in observed behavioural responses.

3.2 Introduction

We currently witness large changes in the size and phenology of migratory bird populations, which is commonly attributed to global change (Both et al., 2004; Stephens et al., 2016). While many migratory bird populations seem to be declining due to warming climate and altered land use, others are of stable size or even increasing (Bairlein, 2016; Stephens et al., 2016). Additionally, many but not all populations seem to advance spring migration and egg laying (Aloni et al., 2017; Miles et al., 2017; Rubolini et al., 2007) whereby the extent to which advancing breeding phenology is possible and beneficial might vary among taxa (Knudsen et al., 2011). The intra- and interspecific variation in the response of migratory bird species is studied intensely and various ecological, geographical and life-history factors have been tested as predictors of species' vulnerability (Knudsen et al., 2011; Lehikoinen et al., 2004; Usui et al., 2017). Additionally, there now exist several theoretical models to predict climate-related changes in population dynamics and migratory phenology (Bauer et al., 2008; Taylor et al., 2016; Tökölyi et al., 2012). However, a substantial part of variation in the response of migratory bird populations to global change remains unexplained (Knudsen et al., 2011; Usui et al., 2017). It is further unclear, to what degree changes in bird migration phenology represent phenotypic plasticity or microevolution (Charmantier and Gienapp, 2014), reflecting that a full mechanistic understanding of the potential response and inherent limitations of migratory birds has not been reached yet and that important ecological mechanisms might have been overlooked.

Successful conservation of migratory bird populations under global change, however, will require both robust assessments of species' vulnerability as well as species' adaptive potential within a mechanistic framework. For that, it is necessary to better understand the evolution of life-history strategies and the selection pressures and constraints mediating individual behaviour. Visser et al. (2008) suggest that annual routine models (McNamara and Houston 2008) could be used to compute optimal reaction norms, which relate a range of environments to a spectrum of phenotypes for a particular genotype. This would help to assess the behavioural plasticity of migratory birds and whether observed behavioural changes are actually adaptive. The optimal annual routine (OAR) framework introduced by Houston and McNamara (1999) employs mathematical optimization techniques for computing the optimal life-history strategy and resulting population dynamics based on various biological parameters and ecological constraints within a given environment. It is grounded in state-dependent life-history theory and works with stochastic dynamic programming as dynamic optimisation technique. An important characteristic of it is that it considers animal behaviour and associated trade-offs over the full annual cycle (FAC).

Here, using an existing annual routine model (Schaefer et al. 2018), we aim to advance the exploration of phenological shifts in migratory birds and shed light on the behavioural strategies of animals as well as their plasticity in changing environments. According to state-dependent life-history (McNamara and Houston, 1996), individuals differ in their state and available behavioural options at a particular time. As a result, individuals also differ in performed behaviour and individual life histories with direct consequences for reproductive success and survival. For example, it was shown that migratory birds arriving at an optimal timing to the breeding grounds can have more offspring (Kokko, 1999; Tryjanowski et al., 2004).

Since behaviour has an inheritable genetic component, the underlying behavioural strategy will be subject to evolution by natural selection and should be optimized to increase long-term reproductive success in the population under the given constraints and trade-offs. Accordingly, Houston and McNamara (1999) define the optimal behavioural strategy to maximize fitness in the population and assume that the strategy's fitness indicates the fitness of the genotype that codes for the strategy. The behavioural strategy hereby is a rule, which specifies the action to take by an organism at a certain time depending on the state of its environment and its own internal state. When the actions are performed, they constitute the observable behavioural phenotype.

The optimal behavioural strategy is dependent on the given environment and represents a quasi-equilibrium situation. Changes in the environment may cause deviations from this quasi-equilibrium. These might result in short-term population growth if the behavioural strategy proves (still) beneficial or might lead to population declines if the behavioural strategy proves suboptimal. Eventually, the individuals will adapt a new optimal behavioural strategy for the altered environment or go extinct. A crucial question is thus whether and how fast individuals can adapt a new optimal behavioural strategy given inherent biological constraints and environmental predictability. For vertebrates, the rate of microevolution has been estimated to be quite low (Gienapp et al., 2008). Phenotypic plasticity on the other hand, which is incorporated in the OAR framework, might also allow migratory birds to respond to altered environmental conditions (Gibbin et al., 2017; Visser, 2008). However, plastic behavioural changes can only be beneficial in the short-term, helping to buffer the population from negative effects, and might even hamper adaptive evolution (Visser 2008). This is because the old reaction norm of a genotype will not be suited for the altered environment anymore (Visser, 2008). Thus, the short-term as well as the long-term perspective are relevant for identifying populations at risk and for designing appropriate conservation measures.

In the present study, we employ an existing optimal annual routine model (Schaefer et al. 2018, Houston and McNamara 1999), to investigate the population dynamics and the phenology of two distinct migratory bird populations under environmental change when assuming sub-optimal behaviour (following the historically shaped life-history strategies) and when assuming adaptation to the new equilibrium situation. The modelled migratory bird types represent two typical long-distance migrants, for which comparatively comprehensive data are available to parametrize the model: white storks and small falcons like Eurasian hobby. The theoretical approach allows for a deeper understanding of how species-specific optimal reaction norms, the phenotypic plasticity, and behavioural adaptation may determine population response to global change. Such an understanding will be crucial for interpreting observed changes and for identifying and anticipating potential human-wildlife conflicts caused by global change. It includes assessing whether observed behavioural changes are plastic or adaptive and how much adaptation of behavioural strategies would be necessary for migratory bird populations to persist in the future.

3.3 Material and Methods

3.3.1 Bird types

We study two migratory bird types of Central Europe, which employ distinct flight modes during migration and can be expected to differ in their behavioural strategy and behavioural plasticity due to differences in temporal and energetic constraints throughout the year. The first bird functional type (T1) is oriented at the white stork. This large and long-lived species has long breeding periods and is thus strongly constrained by time and additionally by the availability of thermal updrafts that are required for its energetically efficient soaring-gliding flight mode during migration. The second bird type (T2) is taken from Schaefer et al. (2018) and a composite of several small falcon species like the Eurasian kestrel, Eurasian hobby or European red-footed falcon. Functionally it represents a smaller, shorterlived species with shorter breeding periods and an active flight mode during migration, leading to comparably lower time- and wind-constraints but larger energetic costs during migration. Both bird functional types are described by various state variables, parameters and functions capturing their biology in the model (Table 3.1). A detailed justification of selected parameter values including references can be found in Appendix Section 6.2.1.

Table 3.1: Model parameters and formulas including their baseline values for the stork (T1) and falcon (T2) functional type, whereby when only one value/formula is given, it holds for both functional types (a detailed justification of selected parameter values including references can be found in Appendix Section 6.2.1).

Parameter	**Symbol**	**Value / Formula T1 (white stork)**	**Value / Formula T2 (small falcon)**
State and stage variables:			
Range of energy reserves	x	$\in [0,10], \in \mathbb{N}$	
Range of health condition	y	$\in [0,10], \in \mathbb{N}$	
Range of experience	e	$\in [0,2], \in \mathbb{N}$	
Age of any offspring	a	$\in \left[-1, a_{incub} + a_{indep}\right], \in \mathbb{Z}$	
Location	o	$\in [1, n_{loc}], \in \mathbb{N}$	
State of migration	s	$\in \left[-1, s_{migr} - 1\right], \in \mathbb{Z}$	
Week of year	t	$\in [0,51], \in \mathbb{N}$	
General biology:			
Background mortality by disease	M_{bg}	0.00055	0.0016
Basic metabolic cost	c_b	1.7	2.0
Foraging intensity	u	$\in [0,1]$	
Energetic cost of subsistence	$c_{subsist}$	$c_b(1 + 0.01(x/10^2) + 6u^2(1 + 0.01(x/10)^2)$	
Health cost of subsistence	$h_{subsist}$	$1 - 0.2c_{subsist} - 0.01{c_{subsist}}^2$	
Environment:			
Number of locations	n_{loc}	2	
Average food availability at overwintering and breeding location (F1-base)	A_{food}	$[1.0, 1.0]$	
Degree of seasonality of food at overwintering and breeding location (F1-base)	ε	$[0.3, 0.7]$	
Background predation for both locations	M_{bgpred}	$[0.004, 0.002]$	$[0.01, 0.01]$
Predation risk	M_{pred}	$M_{bgpred}\,(o)u^2(1 + 0.01(x/10\,)^2)$	
Probability of active flight	p_{act}	$p_{act}(o,t)$	1.0
Reproduction:			
Duration of incubation in weeks	a_{incub}	4	4

Age of independence in weeks	a_{indep}	9	6
Energetic cost of starting a brood	c_{start}	1.53	0.5
Energetic cost of incubation	c_{incub}	0.63	1.5
Energetic cost of brood care	c_{care}	6.0	7.0
Health cost of starting a brood	h_{start}	1.0	1.0
Number of offspring	n_{brood}	2	2
Fitness of offspring at independence	f_{indep}	0.5	0.5
Computed equilibrium value for foraging efficiency of inexperienced young	θ	0.7381	0.8123
Probability of experience growth	p_{exp}	0.01	0.02
Migration:			
Duration of migration in weeks	s_{migr}	3	3
Energetic cost of active flight	c_{act}	4.0	2.0
Energetic cost of passive flight	c_{pas}	0.8	$n.a.$
Reserves change during migration	Dx_{migr}	$(p_{act}c_{act} + (1 - p_{act})c_{pas})(1 + 0.001x^2)$	
Health cost of active flight	h_{act}	2.0	1.0
Health cost of passive flight	h_{pas}	0.4	$n.a.$
Health change during migration	Dy_{migr}	$p_{act}h_{act} + (1 - p_{act})h_{pas}$	
Background predation during migration	M_{bgmigr}	0.004	0.01
Predation risk during migration	M_{migr}	$M_{bgmigr}(1 + 0.01x/10)^2$	

3.3.2 The model

We use the OAR model implemented by Schaefer et al. (2018) to compute the optimal behavioural strategy for a population of migratory birds in a given environment using stochastic dynamic programming. Then, the population dynamics and emergent distribution of states and behaviour within a population can be simulated by following a cohort of individuals employing this optimal strategy forward in time, either under equilibrium or non-equilibrium environmental conditions. For simplicity, we only consider female birds and their long-term number of descendants. They are characterized by the following state variables: energy reserves x, health condition y, experience e, breeding status a, location o and migratory state s. The strategy is computed for an annual cycle that is divided into $T = 52$ weeks. At the beginning of each week, birds take a decision regarding their foraging intensity and potential migratory or reproductive activities. Migration can occur between two locations. The optimal decision depends on the birds' internal state (in terms of energy, health and dependent offspring) and week t of the year.

In the following, we describe the specific model components. Further mathematical and computational details can be found in Appendix Section 6.2.2 and Schaefer et al. (2018).

3.3.2.1 ENVIRONMENT

We use two environmental variables to constrain bird behaviour, namely food availability and wind conditions during migration.

Birds can migrate between two locations representing the Northern breeding and the African overwintering habitat, which differ in resource availability. Environmental food supply $g(o, t)$ varies sinusoidal over the year with the same yearly average in both locations but higher seasonality in the breeding location (Figure 3-1 a). Consequently, the Northern breeding grounds show a distinct resource peak during summer but low resource availability during winter. The Southern overwintering grounds are also assumed to be north of the equator with a small resource peak during summer.

The wind conditions are important for the stork (T1) functional type because it employs passive flight and depends on the availability of thermals for its migration. Accordingly, we defined a time- and location-dependent probability of active flight affecting migratory costs for the T1 type. Since the formation of strong enough thermals requires warm temperatures, the probability of active flight in the breeding location is set equal to one during winter and equal to zero during summer with a linear increase over one month in spring and a corresponding linear decrease in late summer (Figure 3-1 a; details in Appendix Section 6.2.2). In the African overwintering location, the probability of active flight is set zero throughout the year.

Bird type T2 is assumed to employ only active flight such that the probability of active flight is always equal to one.

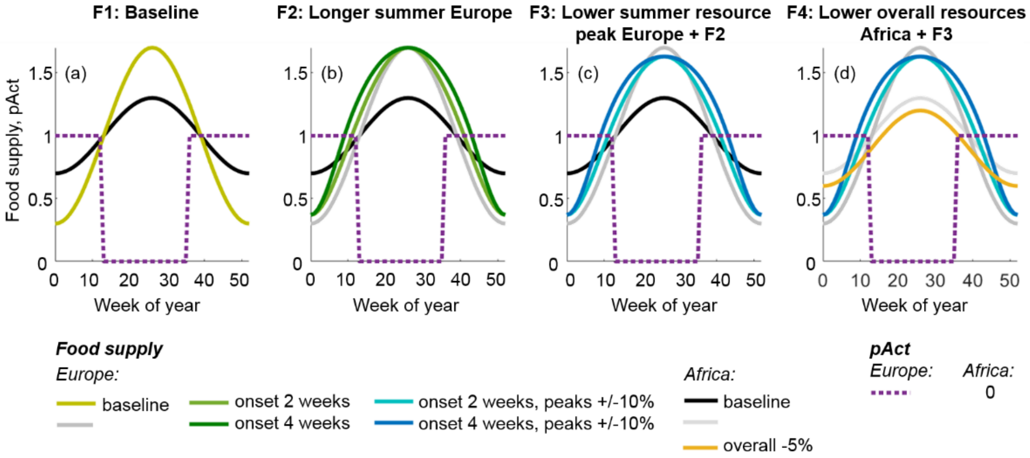

Figure 3-1: Temporal distribution of food in the African overwintering and the European breeding habitat for each of the four studied scenarios F1-F4. For scenario F2-F4, two different sub scenarios were run, in which the onset of spring and autumn was shifted by either two or four weeks. pAct represents the probability of active flight for the stork (T1) functional type, which is location- and time-dependent and here depicted for the breeding habitat.

3.3.2.2 DYNAMICS OF ENERGY RESERVES

Energetic intake

Environmental food supply $g(o,t)$, a bird's experience e and its selected foraging intensity u determine the bird's energetic intake $\gamma(e,o,u,t)$ in a given location o at a particular week t. The foraging intensity u can range from not feeding at all to feeding with full intensity, i.e. $u \in [0,1]$, and linearly scales with gross energy intake. Experience e increases with age from no experience ($e = 0$) of newly fledged young to full experience ($e = e_{max}$) of fully matured adults. Higher levels of experience are associated with higher energetic gains from foraging, assuming that newly fledged young forage less efficiently than adults. Hereby, gross energetic intake and experience are coupled via a parameter θ with $0 < \theta < 1$ that implicitly quantifies the effect of density dependence acting on the foraging success of juveniles (see Houston and McNamara 1999). In particular, if a fully experienced bird gains an energy amount γ from foraging with intensity u, a bird with experience e will have the energetic intake $\theta^{e_{max}-e}\,\gamma$ under the same foraging intensity. Then, the gross energetic intake is:

$$\gamma(e,o,u,t) = \theta^{e_{max}-e} * g(o,t) * u.$$

The value of the parameter θ is calibrated during computations such that the population following the computed optimal behavioural strategy will be of stable size (see Houston and McNamara 1999).

Energetic expenditure

The energetic expenditure $c_{subsist}(u,x)$ of a subsisting bird is a function of its foraging intensity u, body reserves x and basal metabolism c_b:

$$c_{subsist}(u,x) = (c_b + 6u^2) * \left(1 + \left(0.01\,\frac{x}{x_{max}}\right)^2\right)$$

Additional energetic costs (c_{action}) arise from demanding behavioural activities, namely from initiating breeding (c_{start}), incubation (c_{incub}), brood care (c_{care}) and migration (c_{migr}). The average level of energy reserves at the beginning of next week $t + 1$ is

$$x_{t+1} = x_t + \gamma(e,o,u,t) - c_{subsist}(u,x) - c_{action},$$

where c_{action} is either any of the extra demanding activities or zero when the bird chooses to subsist only. A bird that has dependent young must forage with sufficient intensity $u_{crit}(t) \leq u \leq 1$ to ensure their survival. Otherwise, the brood is abandoned and dies.

3.3.2.3 DYNAMICS OF HEALTH CONDITION

Reproduction and migration activities also impose fixed health costs on a bird. However, its health condition can improve when activity and thus metabolic expenditure is low. Here, the average health condition of a non-migrating bird at week $t + 1$ is

$$y_{t+1} = y_t - h_{action} + (1 - 0.2c_{subsist}(u, x) - 0.01(c_{subsist}(u, x))^2,$$

where $c_{subsist}(u, x)$ is the metabolic expenditure of subsistence and h_{action} represents potential extra health costs ($h_{start}, h_{migrate}$) for initiating breeding or migrating during time t to $t + 1$.

3.3.2.4 REPRODUCTION

The breeding status of a bird is denoted by the state variable $a \in [-1, a_{max}]$, where a_{max} is the age at which the brood becomes independent. Birds that have no brood ($a = -1$) and are not migrating ($s = -1$) may start a brood any time of the year. Initiating a brood is associated with above-mentioned costs and will change the breeding status to $a = 0$ at the next time step $t + 1$. The action is followed by a subsequent voluntary period of incubation and brood care, which both decrease the parent bird's reserves. To prevent starvation of its brood, the parent bird must provide it with sufficient food $\gamma(e, o, u_{crit}, t)$. Otherwise, the brood dies while the parent bird's breeding status is reset to $a = -1$. If the parent bird continues brood care, its breeding status is incremented by one ($a_{t+1} = a_t + 1$). If the parent bird dies, any dependent brood dies, too. When the brood reaches the maximum age $a = a_{max}$ the brood becomes independent. Newly independent young are assumed to have no experience (e = 0) and mean levels of reserves and health ($f_{indep} = 0.5$).

3.3.2.5 MIGRATION

Migration may occur between two locations, differing in temporal food supply, and takes three weeks for both bird types. Once migration is started, it must be completed until the other location is reached. However, it may occur at any time of the year. The dynamics of reserves during migration are described by

$$x_{t+1} = x_t - (p_{act}c_{act} + (1 - p_{act})c_{pas})(1 + 0.001x^2),$$

where p_{act} is the probability of active flight, c_{act} is the energetic cost of active and c_{pas} of passive flight. The term $0.001x^2$ causes flight costs to increase with body reserves (Alerstam, 1991). The average health condition y_{t+1} of a bird after having migrated for one week is:

$$y_{t+1} = y_t - (p_{act}h_{act} + (1 - p_{act})h_{pas}),$$

where y_t represents the state of health in the previous week and h_{act} and h_{pas} are the health costs of active and passive flight.

Mortality $M_{migr}(x)$ during migration is assumed to be an accelerating function of body reserves, incorporating a behaviour-independent background mortality M_{bgmigr} :

$$M_{migr}(x) = M_{bgmigr}(1 + 0.01\frac{x}{x_{max}}).$$

3.3.2.6 SOURCES OF MORTALITY

There are three sources of mortality: starvation, disease and predation. Starvation occurs when reserve levels fall to zero. Disease risk increases with decreasing health condition. It includes a constant weekly disease risk M_{bgdis} associated to the maximum life expectancy of the modelled bird type, such that a bird in top condition throughout its life will live for $1/(M_{bgdis} * 52)$ years, on average. The weekly probability of death due to disease $D(y)$ is given by:

$$D(y) = M_{bgdis} + \left(1 - M_{bgdis}\right) * (1 - \frac{y}{y_{max}})^8.$$

Predation risk $M_{pred}(x, o, u)$ for a non-migrating bird depends on its location, foraging activity and body reserves. It increases with activity and reserve levels and comprises a location-specific background predation $M_{bgpred}(o)$ which is independent of behaviour:

$$M_{pred}(x, o, u) = M_{bgpred}(o) * u^2 * (1 + 0.01 * (\frac{x}{x_{max}})^2).$$

3.3.2.7 COMPUTING THE OPTIMAL STRATEGY AND EXPECTED BEHAVIOUR

The optimal behavioural strategy defines the probability of a bird to perform a specific action (start breeding, incubate, care for brood, migrate), depending on its state and week of the year. The optimal strategy maximizes fitness in terms of long-term reproduction success and is computed by stochastic dynamic programming, iterating backwards from a future target year until convergence (mathematical details in Appendix Section 6.2.2; Schaefer et al. 2018).

Subsequently, the realized behaviour within a large population adopting the optimal strategy in a given environment is determined by following it forward in time. Hereby, for each week t, the new distribution of states at week $t + 1$ is computed based on the old distribution of states at week t and the associated behavioural action as given by the optimal strategy. The iteration is started with a large cohort of newly independent young and stopped when the distribution of expected states and behaviour settles down at an equilibrium pattern, which only depends on state and time of the year but not the year itself (Houston and McNamara, 1999).

3.3.3 Indicator of plasticity

For each weak of year t, we aimed to assess the behavioural plasticity provided by the optimal strategy. To this end, we developed a simple indicator that measures the variation of potential behaviours that could be exhibited (are optimal) in week t when considering all possible states of the individuals. Specifically, the indicator quantifies the deviation of the optimal behavioural strategy from a strategy in which optimal behavioural activities are evenly distributed among states. In particular, for each week:

$$I_{plasticity,t} = \frac{|\left(\sum_{action}\left|\frac{N_{action}}{N_{total}} - \frac{1}{4}\right|\right) - 1.5|}{1.5}$$

where N_{action} is the number of states for which a certain behavioural action from the set of actions $\{subsist, start, care, migrate\}$ is optimal and N_{total} is the total number of around 2 million state combinations. The summation runs over all four potential actions. The value of 1.5 represents the summed deviation from a uniform distribution of actions among state combinations when only one behavioural option is optimal for all states. The indicator of the strategy's mean plasticity for the complete year then is

$$I_{plasticity,y} = \underset{t}{\mathrm{mean}}(I_{plasticity,t}).$$

Consequently, smaller indicator values represent lower plasticity in behaviour than higher values. A uniform distribution of actions among state combinations throughout the year will result in an indicator value of 1, while a value of 0 arises when always the same single behavioural action is optimal.

3.3.4 Global change scenarios

We explore population response and population phenology for six environmental change scenarios and two behavioural scenarios.

3.3.4.1 ENVIRONMENTAL SCENARIOS

For each bird type, we consider four food scenarios (Figure 3-1, Appendix Section 6.2.2) inspired by current assessments and predictions of global change in Europe and Africa (IPCC, 2013):

F1. Baseline. Environmental food supply varies sinusoidal over the year with the same yearly average in both locations but higher seasonality in the breeding location (Figure 3-1 a).

F2. Shorter winter associated with improved winter food availability in the breeding habitat. This scenario represents milder and shorter winters due to climate change and intensified winter agriculture, likely increasing availability and accessibility of food resources in the Northern location (Figure 3-1 b).

F3. Shorter winter with improved food supply but also a lower summer food peak in the breeding habitat. This scenario is based on the assumption that Northern summer become hotter and drier with an increasing number of droughts that can be expected to decrease food supply (Figure 3-1 c).

F4. Maximum change: F3 + lower overall food supply in the overwintering habitat. Predictions of hotter, drier climate with severe droughts also exist for the African overwintering habitat where, additionally, natural land is converted and degraded (Jayne et al., 2014). Thus, yearly food supply is assumed to decrease.

Additionally, the magnitude of F2-F4 is varied by setting the onset of spring and autumn in the breeding grounds (scenario F2-F4) to two and four weeks.

3.3.4.2 BEHAVIOURAL SCENARIOS

We test global change effects for two distinct behavioural scenarios: B1) The population is evolutionary adapted to historic environmental conditions and continues following the once optimal life-history strategy that has become outdated with environmental change. This scenario corresponds to the short-term behavioural response. B2) The population has adapted a new optimal life-history strategy in response to a new environmental equilibrium. This scenario corresponds to the long-term behavioural response.

3.4 Results

Model species migrate to the European breeding grounds in spring, initiate breeding there soon after arrival and start migrating to the African wintering grounds from late summer to mid-autumn. Breeding only occurs in the summer grounds.

3.4.1 Suboptimal behaviour in a new environment

3.4.1.1 POPULATION AND STATE DYNAMICS

Under the old optimal behavioural strategy (B1), higher winter food availability in the breeding grounds (F2) leads to a slight population increase in both model species if the resource peak in summer remains constant (Table 3.2). By contrast, if the peak food supply during the breeding period is decreasing (F3-F4), the populations decline. This decline is stronger when overall food supply in the wintering grounds decreases (F4). Hereby, even a small reduction of food supply by 5 % in the overwintering location has major impacts on population trends (Table 3.2), resulting in population declines of up to 23 % in the model (e.g. T1-B1-F4).

For both functional bird types, mean reserves and health condition increase when food supply solely changes in the breeding habitat (F2-F3, Table 3.3). However, in the F3 scenario, this is accompanied by strong population declines, so that the remaining population will have a higher mean state than prior to environmental change. The increase in health condition is larger for the stork functional type than for the falcon type (T1: 4-7 %, T2: 1-2 %). Again, deteriorating food conditions in the overwintering habitat (F4) have severe effects, reducing the population's mean energy reserves and, for the stork type (T1), also health condition.

3.4.1.2 TIMING OF BEHAVIOUR

The modelled stork (T1) population following the baseline strategy (F1) is strongly time-constrained and fixed in its behaviour (Figure 3-2 B1a-b, Table 3.2). Sole changes of food availability in the breeding habitat (F2, F3) do not result in notable shifts in their timing of spring migration or breeding. Food scenario F4 leads to a mean delay of spring arrival by three days and of autumn departure by one to two days.

Table 3.2: Development of population size and the timing of migration for both studied bird types when they follow the old optimal behavioural strategy under the given scenarios of food availability F1-F4 (B1) or when they follow the new optimal behavioural strategy (B2), whereby the food scenarios are (F1) the old baseline scenario, (F2) a shorter and better winter in the breeding grounds, (F3) additionally a worse summer in the breeding grounds, (F4) an additionally overall lower food availability in the wintering grounds, and whereby the strength of change is 5 % in the wintering grounds and 10 % in the breeding grounds with the onset of spring being two (four) weeks earlier than in the baseline model. Blue cells mark a positive change, red a negative and grey no change. Differing trends between sub-scenarios are in yellow.

Bird type	Assumed strategy	Food scenario	Change in population size over years, %	Change in mean timing of migration, days		Change in mean start of breeding, days
				Spring arrival	Autumn departure	

Stork	*Baseline*	*F1*	*0.0*	*Week 13*	*Week 32*	*Week 13*
(T1)	Old strategy (B1)	F2	+0.5 (+0.9)	0.0 (0.0)	-0.1 (-0.3)	0.0 (0.0)
		F3	-5.5 (-2.7)	0.0 (0.0)	+0.9 (+0.7)	0.0 (0.0)
		F4	-22.5 (-16.8)	+2.7 (+2.7)	+1.5 (+1.3)	+2.6 (+2.6)
	New strategy (B2)	F2	0.0 (0.0)	-9.3 (-10.8)	-1.5 (-0.3)	-8.7 (-11.1)
		F3	0.0 (0.0)	-6.9 (-10.9)	-1.0 (-0.5)	-6.4 (-11.2)
		F4	0.0 (0.0)	-4.3 (-8.1)	-6.5 (-7.7)	-4.2 (-8.3)
Falcon	*Baseline*	*F1*	*0.0*	*Week 13*	*Week 32*	*Week 15*
(T2)	Old strategy (B1)	F2	+1.3 (+2.0)	-0.3 (-0.4)	-2.6 (-4.5)	-0.7 (-1.3)
		F3	-11.4 (-0.5)	0.0 (-0.3)	+0.9 (-1.5)	-0.6 (-1.2)
		F4	-24.6 (-20.5)	+17.6 (+17.3)	+8.2 (+5.9)	+8.4 (+8.0)
	New strategy (B2)	F2	0.0 (0.0)	-9.8 (-18.9)	+1.5 (+43.3)	-6.6 (-1.0)
		F3	0.0 (0.0)	-9.6 (-19.7)	+0.2 (+31.9)	-5.0 (-2.9)
		F4	0.0 (0.0)	+4.2 (-2.7)	-2.6 (-0.6)	+2.2 (-2.8)

The falcon (T2) type advances spring arrival and breeding activities by less than a day, on average, when food availability is altered in the breeding habitat only (Figure 3-2 B1c-d, Table 3.2). Autumn migration is slightly advanced under the scenario of overall higher food availability in the breeding habitat (F2), whereby lower summer food peaks (F3) lead to mixed results. A notable delay of migration and breeding activities is predicted for scenario F4 (Figure 3-2 B1c-d), when food availability in the overwintering habitat decreases. Hereby, spring arrival is delayed more than breeding activities with 18 versus 8 days, respectively, such that the time interval between both activities decreases (Table 3.2).

Generally, the modelled falcon population shows higher variation in the timing of migration and breeding under equilibrium environment (baseline) and under the different food scenarios (Figure 3-2).

Table 3.3: Development of mean energy reserves and health condition for both studied bird types when they follow the old optimal behavioural strategy under the given scenarios of food availability F1-F4 (B1) or when they follow the new optimal behavioural strategy (B2), whereby the food scenarios are (F1) the old baseline scenario, (F2) a shorter and better winter in the breeding grounds, (F3) additionally a worse summer in the breeding grounds, (F4) an additionally overall lower food availability in the wintering grounds, and whereby the strength of change is 5 % in the wintering grounds and 10 % in the breeding grounds with the onset of spring being two (four) weeks earlier than in the baseline model. Blue cells mark a positive change, red a negative and grey no change. Differing trends between sub-scenarios are in yellow.

Assumed strategy	**Food scenario**	**Change in population's annual mean reserves, %**	**Change in population's annual mean health, %**

		Type Stork (T1)	**Type Falcon (T2)**	**Type Stork (T1)**	**Type Falcon (T2)**
Baseline	*F1*	*6.3* U_{res}	*6.4* U_{res}	*8.9* U_{health}	*7.8* U_{health}
Old strategy (P1)	F2	+3.2 (+6.0)	+3.2 (+5.9)	+0.5 (+0.8)	+1.5 (+2.4)
	F3	+2.3 (+5.0)	+1.6 (+4.3)	+4.2 (+7.0)	+1.2 (+2.2)
	F4	-3.5 (-0.6)	-3.3 (-1.1)	-0.4 (-0.1)	+0.2 (+1.1)
New strategy (P2)	F2	+1.1 (+3.4)	+1.0 (+1.5)	-0.5 (+0.6)	+1.0 (+0.7)
	F3	+2.4 (+4.2)	+1.1 (+1.4)	-0.9 (-0.2)	+0.5 (+0.6)
	F4	+2.4 (+4.3)	-0.1 (+0.7)	-1.2 (-0.9)	-1.0 (+0.1)

3.4.2 Developing a new strategy for the altered environment

3.4.2.1 POPULATION AND STATE DYNAMICS

Any population following its new optimal strategy for a particular altered environment will have a stable size by default. For white storks, the new environments lead to higher mean levels of energy reserves compared to the baseline environment, while mean health condition is marginally reduced by approx. 1 % (Table 3.2). The new mean levels of energy reserves and health condition within the falcon population lie slightly above the baseline values (F1) for food scenarios F2 and F3. For simultaneous changes of food supply in the overwintering grounds, the results are ambiguous and depend on the particular assumptions for the breeding grounds.

3.4.2.2 TIMING OF BEHAVIOUR

The white stork population advances both migration and breeding (Figure 3-2, Table 3.2). On average, individuals arrive in the breeding grounds and start breeding 6 – 11 days earlier. Autumn migration is only advanced by one day, when southern food availability does not decrease (F2-F3). By contrast, if the wintering grounds show overall lower food resources (F4), the advance in spring arrival is less pronounced while advance in autumn migration is more pronounced. Leaving their breeding location earlier in autumn allows more time for building up reserves and health condition in the overwintering location without compromising arrival time in the breeding location.

Advanced spring arrival and initiation of breeding under the new strategy is also observed for the falcon type when food availability only changes in the breeding habitat (Table 3.2, F2-F3). By contrast, autumn departure is delayed in these scenarios. If food availability decreases in the overwintering habitat (F4), the potential time shifts of migration are less clear and inconsistent between different magnitudes of spring advance and autumn delay. For example, the falcon spring migration is delayed when spring is advanced by two weeks in the breeding habitat but migration is advanced by three days when spring is advanced by four weeks. The scale of spring and autumn onset (2 vs. 4 weeks) strongly affects the strength of reaction in food scenarios F2 and F3, prolonging the birds' period of residence in the breeding habitat for over a month when the onset is 4 weeks. In food scenario F4, autumn migration is consistently shifted by one to three days earlier.

3.4.2.3 BEHAVIOURAL PLASTICITY UNDER THE OPTIMAL STRATEGY

The indicator of plasticity is consistently higher for the optimal behavioural strategy of the falcon functional type (T2) compared to the stork type (T1). For T1, indicator values range from 0.17 to 0.18, while for T2 they range from 0.20 to 0.21 in food environments F1-F4.

To identify major determinants of reduced plasticity in white storks, we ran a sensitivity analysis by systematically exchanging stork parameters (T1) by falcon parameters (T2) and re-computing the optimal behavioural strategy and its plasticity index for these new parameters sets. Age of independence proved to be the most

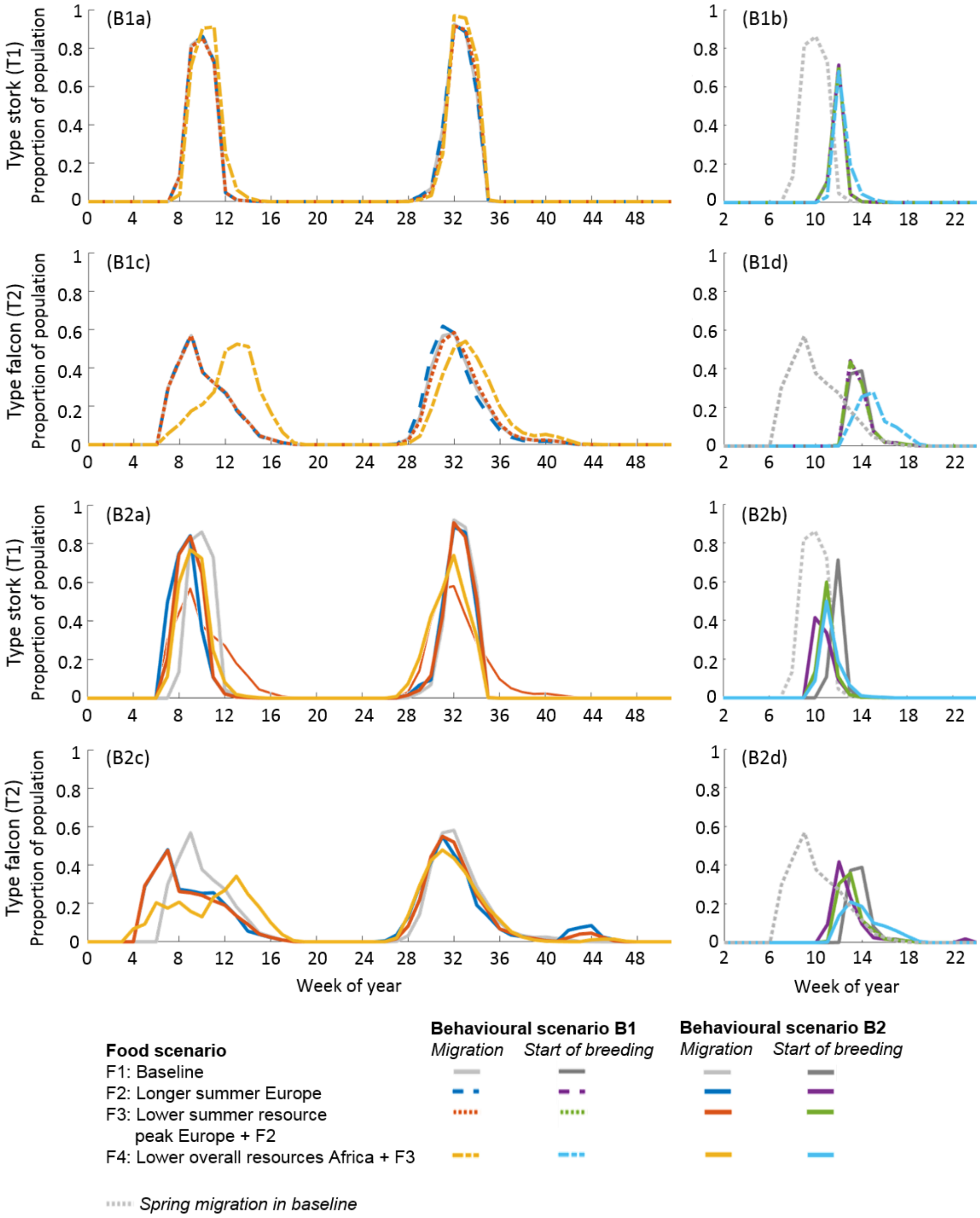

Figure 3-2: Timing of behaviour using the old optimal behavioural strategy in the new environment (B1a-d) and using the new optimal behavioural strategy in the new environment (B2a-d). Shown is the proportion of a population of the stork (a-b) and falcon (c-d) functional types migrating (a, c) and initiating breeding activities (b, d) at each week of the yearly cycle for four different food scenarios F1-F4 under the old optimal behavioural strategy. Food scenarios are (F1) baseline scenario, (F2) a shorter and better winter in the breeding grounds, (F3) additionally a worse summer in the breeding grounds, and (F4) an additionally overall lower food availability in the wintering grounds. The strength of change is 5 % in the wintering grounds and 10 % in the breeding grounds with the onset of spring being two weeks earlier than in the baseline model. The timing of behaviour changes notably only under scenario F4 of maximum change.

sensitive parameter, changing plasticity by over 20 % and highlighting time constraints in the schedule of the stork (T2) type and their influence on the strategy's plasticity. The effect of the other parameters was 3 % for altered basal metabolism, predation risk and migration costs, 5 % for altered lifespan and 7 % for altered brood care costs. Patterns were largely robust against different wind conditions. Longer availability of thermals for bird functional type T1, and thus a lower probability of active flight, did not change the overall migration and breeding pattern though the optimal timing of migration is slightly shifted (Appendix Section 6.2.3, Figure S 6.2-1).

3.5 Discussion

Here, we use theoretical models to study the effect of behavioural plasticity and adaptation in the phenological and population response of migratory birds to global environmental changes. In particular, we employed an optimal annual routine model (Schaefer et al. 2018) to explore the relationship between expected anthropogenic changes in food supply and the behavioural strategy and population dynamics of two long-distance migratory bird types that typically breed in Central Europe. Better understanding the role and mechanisms of behavioural plasticity in migratory birds to environmental change is vital for assessing the vulnerability of various migratory bird populations. Since migratory birds further serve as mobile linkers between ecosystems, changes in their large-scale movement patterns can have cascading effects onto local biodiversity (Jeltsch et al., 2013) and should be anticipated for biodiversity conservation.

A key finding of our research was that stable populations of the analysed bird functional types show an advanced spring migration and breeding phenology for nearly all analysed scenarios of altered food supply under global change (Figure 3-2 B2). This is in line with widely reported recent advances of spring migration and breeding in many migratory bird populations (Knudsen et al., 2011; Rubolini et al., 2007). Further, our scenarios of suboptimal behaviour under global change indicate that phenotypic plasticity alone cannot explain the observed advance of spring arrival. Our model results thus support the assumption that reported advances in the behavioural spring phenology of migratory birds (Lehikoinen et al., 2004; Rubolini et al., 2007) are adaptive and reflect the development of a new optimal behavioural strategy under changing environmental conditions.

Overall, the potential of plastic responses to altered food supply (under the suboptimal behavioural strategy) was comparably low in the model. The stork functional type (T1) did not adapt spring migration or breeding phenology at all in food scenarios F2 and F3. Thus, short-term behavioural responses due to behavioural plasticity were insufficient for preventing population declines of these large soaring migrants under the chosen environmental scenarios. Generally, plasticity could even lead to the opposite phenological response than would be required to keep the population size stable. For example, a shorter winter and decreased summer resource peaks in the breeding habitat resulted in delayed autumn departure of the falcon functional type (T2) under the old strategy (B1), which proved suboptimal as indicated by the new strategy (B2). Also additionally deteriorated overwintering food supply shifted behavioural timing under the old behavioural strategy (B1) into the opposite direction as would be required for keeping population size stable (B2).

These results concord with recent findings on the well-studied Eastern white stork populations (Kaatz 2004, Rotics et al. 2016, Kaatz et al. (eds.) 2017), which seem not to advance spring phenology (Gordo et al., 2013) and exhibited only marginal population increases between the international census in 2004/2005 and 2014/2015. These increases are thought to reflect natural fluctuations associated to the general overwintering situation in Eastern Africa (Thomsen, 2017). Similarly, several falcon populations like red-footed falcon and Eurasian kestrel have been declining over recent decades (Burfield, 2008) and Eurasian kestrels delayed autumn passage in the Western Pyrenees (Filippi-Codaccioni et al., 2010), indicating limitations in adaptation to novel conditions.

Still, observed changes in the timing of breeding and migration of birds are generally interpreted as being mostly plastic (Charmantier and Gienapp, 2014). Western white stork populations continue to rise after strong historic declines and arrive increasingly earlier at the breeding grounds (Thomsen, 2017). Also, populations of Eurasian hobby have been slightly increasing for several decades (Sanderson et al., 2006) and seem to advance autumn migration (Filippi-Codaccioni et al., 2010). This implies two important questions. First, why do some empirical results suggest higher behavioural plasticity than our model? Second, is the role of microevolution and new behavioural strategies underestimated?

Regarding the first question, new feeding opportunities on open Iberian landfills allow Western white storks to shorten migration and arrive earlier at the breeding grounds (Flack et al., 2016; Rotics et al., 2017), a feature not included in our model. This does not apply to Eurasian hobbies, though. Interestingly, both modelled bird functional types differed in the plasticity of their behavioural strategy, suggesting that a species or even population-specific assessment of vulnerability will be required for accurate predictions of their fate under global change and migratory bird conservation. Nearly all analysed traits of the falcon (T2) functional type enhanced plasticity of its behavioural strategy compared to the stork (T1) type. When phenotypic plasticity shifts timing of behaviour into the optimal direction as in scenario T2-F3 or potentially in Eurasian hobbies, it may act as buffer against negative global change effects (cf. Visser 2008). The major determinant of reduced plasticity in the stork (T1) functional type was the long nestling period. This trait might be difficult to modify short-term but might come with other benefits like higher offspring survival or advanced learning capabilities, which facilitates social learning as adaptive mechanism. Also, if the differences between the old behavioural strategy (B1) and the required new one (B2) are large, genetic adaptation might not act fast enough to prevent extinction. Overall, our study emphasises the need for research designed to disentangle the role and value of phenotypic plasticity and microevolution in observed behavioural changes.

Another mechanism that could facilitate the development and spread of a new adaptive behavioural strategy might be social learning. This is especially true for highly social birds like many falcon species or long-lived birds with high learning capabilities like the white stork that also flock together during migration, allowing information transfer. Social migratory bird species employing this mechanism might be less vulnerable to negative global change effects than species that are living more solitary. Indeed, we are still at the beginning of comprehending the effects of social learning and social behaviour on migratory bird populations and their response to global change (cf. Flack, Nagy, Fiedler, Couzin, & Wikelski, 2018). We thus advocate intensified research in this direction and propose to test sociality as an additional predictor of vulnerability, e.g. in statistical analyses of behavioural changes and population dynamics of migratory birds with respect to environmental change. Further, since adaptive social learning works much faster than microevolution, it should be facilitated through a network of sufficiently large and undisturbed habitat and stop-over sites promoting positive social interaction between birds as a conservation strategy.

Another trait of migratory birds that could improve future predictive frameworks might be flight mode, since the stork as soaring bird type experienced lower declines in the same food scenarios than the falcon type as active flier. However, though the overall pattern of results did not change under an extended favourable wind period, wind conditions were implemented quite crudely in the model and on a theoretical basis so that a further in-depth study is recommended including more realistic soaring conditions for the two species throughout the year. For example, falcons also use flap-glide mode despite being mainly active fliers (Nir et al., 2014).

Another important finding of our study is the influence of food abundance not only during the breeding phase but also in the overwintering location on population dynamics and behavioural timing. Higher winter food supply and shorter winters in the breeding location (F2) led to short-term population increases in both modelled bird types, suggesting that these could benefit from milder winters and advanced spring under global warming (Table 3.2). Accordingly, slightly increasing populations could be expected in the early stages of climate change, given that habitat loss is prevented. This is in accordance with international census data of growing white stork populations in the near past (Boere et al., 2006), a phase of intensive white stork conservation efforts and climate warming.

However, lower summer food peaks in the breeding location (F3-F4) and decreases in overall food supply (F4) in the overwintering location strongly counteracted population growth resulting from higher winter food supply in the breeding habitat. Such a reduction in food supply could be caused by land-use change and unsuitable farming practices and would induce the formerly synanthropic species to be paying for human-wildlife coexistence with declining populations.

Since the effect size of food shortenings during the breeding period was much stronger than of winter improvements in the breeding location, sufficient future food supply and quality needs to be ensured in the breeding habitat of migratory birds. Additionally, reduced food supply in the overwintering location (P1- F4) led to similarly severe reductions in population size of both modelled bird types as lowered food supply during the breeding season. This is in accordance with results from Dallinga and Schoenmakers (1987) and Schaub et al. (2005) who found that breeding success of Northern and Western white storks positively correlates with previous rainfall in the African overwintering habitat as an indicator of food abundance there. It highlights a need for intensified research, data collection and conservation efforts in the overwintering habitats of migratory birds, for which ecological information often is quite scarce.

3.6 Conclusion

The modelled bird functional types varied in their optimal behavioural strategy, their plasticity and their vulnerability to environmental change. Studying behavioural strategies of individual migratory bird populations in depth will thus be important for identifying risk levels and buffering capacities against environmental change and for designing effective conservation measures. This comprises not only improving our understanding of behavioural legacies but also of the behavioural routines to be expected or required in a changed world. The OAR modelling approach allows analysing both and could be a valuable tool for reaching a deeper and more mechanistic understanding of global change impacts on migratory birds. Besides pointing to worthwhile avenues of future research, it can help to predict future behavioural timing and the strength of future positive or negative impacts on focal migratory birds.

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3.8 Authors´ contributions

MS, DZ, SM and FJ conceived the ideas and designed methodology; SR, AF, WF, MK, UE, NS, RN and MW provided biological and environmental data and discussion; MS led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

4 Carry-over effects threaten migratory species beyond direct mortality under global change

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4.1 Abstract

Background: Many migratory bird populations are threatened by global change. Yet, predicting future population dynamics is challenging because of the seasonal movements across countries and continents, which expose the migrants to global change effects in different parts of the world. It is thus difficult to isolate overwintering effects on population dynamics from effects of environmental conditions during breeding phases.

Methods: Here, we used mechanistic state-based modeling to analyze how altered food supply in the overwintering range may affect the viability of white stork populations in their breeding range.

Results: Under decreased food supply during overwintering, breeding was delayed, fewer birds started a brood and they had lower energetic reserves at breeding start. The intensity of such carry-over effects depended on the timing, duration and strength of resource scenarios. Here, the phase directly after autumn and directly before spring migration turned out to be particularly important. Additionally, food shortenings directly decreased energetic winter reserves and increased mortality rates later in winter. Equivalent food surplus had opposing effects.

Conclusions: Our findings show that overwintering conditions can have profound impacts on phenology and demography of migratory birds, which depend on fine-scale resource dynamics. Modeling survival and behavior as patterns emerging from underlying biological processes allowed a deeper understanding how changing resource regimes during winter carry over to the breeding season and affect migration and breeding phenology as well as survival rates of migrants. Dynamic state-based modeling thus provides a promising approach for analyzing such complex seasonal interactions and may not only help to assess consequences from negative carry-over effects but also to understand effectiveness of conservation measures in different phases of the annual cycle of migrants.

4.2 Background

Migratory birds feature unique annual behavioral cycles, undertaking regular seasonal movements between their distant breeding and overwintering habitats (Berthold, 2012). Often, it is difficult to isolate how events and processes experienced in the breeding or overwintering habitats or during migration affect the breeding population dynamics. For example, food shortage or surplus will not only have immediate consequences for migratory birds such as reduced or increased energy reserves. Instead, also the bird's future state, performance and reproductive output might be affected through non-lethal 'carry-over effects' (COEs) that influence fitness in later seasons (Harrison et al., 2011; O'Connor et al., 2014). For instance, droughts in the overwintering area can lead to immediate reductions in population size through food shortage but also alter the timing and success of the following spring migration and breeding activities (Dallinga and Schoenmakers, 1987; Sæther et al., 2005).

COEs have the potential to accumulate or be buffered over time. For example, the autumn migration of collared flycatchers (*Ficedula albicollis)* got delayed with higher parental efforts, while the following spring migration advanced (Briedis et al., 2018). Breeding efforts in one year may further impair breeding options in the following year (Inger et al., 2010; Low et al., 2015). Thus, COEs may profoundly impact population dynamics of migratory birds but cannot be understood by studying seasons in isolation. Rather, they result from complex seasonal interactions, meaning that events affecting the non-breeding individuals and population may have repercussions on the breeding population (Harrison et al., 2011).

With ongoing global change, many migratory birds are threatened (Zurell et al., 2018) and will likely experience increased food shortages in the near future. Especially in their overwintering ranges including major parts of Africa, the climate is predicted to become hotter and drier with intensified droughts (IPCC, 2013). Further, land is converted and degrading rapidly, which represents a major driver of population declines in migratory birds (Bairlein, 2016; Vickery et al., 2014). Droughts but also major land conversions pose special challenges to organisms since they lead to unpredictable and abrupt food shortenings, making it difficult to adequately respond in time. Such environmental disturbances have event character rather than acting gradually as e.g. continuously rising global mean temperatures. Events and particularly extreme events are characterized by statistical extremity and have large effects on the life cycle of individuals up to whole ecosystems despite their short duration (Jentsch et al., 2007; Parmesan et al., 2000), e.g. by increasing direct mortality or reducing reproductive success through COEs due to arising food scarcity (Albon et al., 2017; Gardner et al., 2017).

Carry-over effects in migratory birds have been investigated with field data (Briedis et al., 2018; Marra et al., 1998; Norris et al., 2004) and theoretical models (McNamara et al., 2011; Norris and Taylor, 2006; Souchay et al., 2018). While most field studies identify COEs from the non-breeding to the breeding season (Harrison et al., 2011; López-Calderón et al., 2017), the overwintering phase seems to serve as a buffer in Hudsonian godwits (Senner et al., 2014), red-backed shrikes (Pedersen et al., 2016) and collared flycatchers (Briedis et al., 2018). Despite these valuable insights, field studies are limited because it is difficult to isolate effects of various influencing factors and of different time periods and to relate them to population dynamics (Norris, 2005). It also remains challenging to follow individuals up to populations throughout the annual cycle (McKinnon et al., 2015), to monitor relevant habitat features and to determine their effect on the inner state of the birds.

A density-dependent theoretical model with two seasons and pre-estimated COEs, was used by Norris (Norris, 2005) to predict how the population size of migratory birds changes with habitat loss and degradation in the overwintering area. Further variants of the model addressed more applied questions or had four seasons (Norris and Taylor, 2006; Sheehy et al., 2011, 2010). Runge and Marra (Runge and Marra, 2005) found that COEs among other factors strongly affected the population dynamics of migratory birds. In their two-season matrix model, the population was structured by sex and habitat quality and the breeding and wintering season were coupled by a migratory period. Using statistical modeling, Saino et al. (Saino et al., 2017) found that 65-70 % of variation in female fecundity of female barn swallows (*Hirundo rustica*) during spring could be explained by a combination of overwintering NDVI and migration timing. Similarly, Souchay et al. (Souchay et al., 2018) was able to explain 75 % of observed variance in breeding success by individual quality, breeding conditions and migration timing with structural equation modeling.

However, in none of the above models, COEs emerged from the underlying biological and ecological processes. In particular, external factors were directly linked to high-level variables of interest such as the size or breeding success of a population without considering the mechanistic pathways through which they act, such as changes in body condition or behavior. These models are thus limited in their suitability to fully understand the cause-effect links of COEs and to predict population dynamics in new environments. The density-dependent models mentioned above further treated individuals as identical and neglected stochasticity. Finally, time was usually aggregated to seasons so that it was impossible to study the effect of different spatiotemporal patterns onto population dynamics and behavioral patterns. Accordingly, it remains an open question how the timing and intensity of food surplus or shortenings in the overwintering habitat influence the occurrence, strength and persistence of COEs between the overwintering and the breeding season in migratory birds.

Optimal annual routine (OAR) modeling has been suggested to be particularly suited for investigating carry-over effects (Feró et al., 2008; Harrison et al., 2011; McNamara and Houston, 2008; Schaefer et al., 2018), but has not been employed for this specific purpose yet. OAR models are dynamic state-based full annual cycle models that allow to determine the optimal behavioral strategy for an organism within a given cyclic environment and to simulate behavior, internal state and population dynamics under a given behavioral strategy and environment (Clark and Mangel, 2000; Houston and McNamara, 1999). Hereby, the optimal behavioral strategy is the decision-rule governing which behavior is performed when and in which state so that a population following it maximizes its long-term reproductive success (Houston and McNamara, 1999). Since OAR models are based on first principles of energetic and evolutionary theory, they allow a mechanistic understanding of studied phenomena like COEs. Another advantage of OAR models is that they account for individual variation within a population (Houston and McNamara, 1999). OARs have been used to study the optimal timing of reproduction and migration (McNamara et al., 1998) and optimal molt strategies (Barta et al., 2008) in migratory birds, but also to investigate the influence of environmental variability on gonad regulation in non-migratory birds (Tökölyi et al., 2012).

Here, we aim to narrow the gap in our understanding of COEs in the annual cycle of migratory birds by theoretically exploring the effects of different resource dynamics during the overwintering phase up to the following breeding season in a long-distance migratory bird (Figure 4-1). To this end, we adapted an OAR model (*sOAR* by Schaefer et al. (Schaefer et al., 2018)) to first determine the optimal behavioral strategy of a model population of white storks (*Ciconia ciconia*) breeding in Central Europe and overwintering in Eastern Africa. Then, we simulated the dynamics of a population following this strategy under various scenarios of changing food availability in the overwintering season. By doing so, we are able to assess how differences in overwintering food supply (timing of resource pulse, intensity, overall food surplus or shortening) affect the breeding population and breeding phenology. Since changes in winter population size arising from such altered food supply can lead to seasonal compensation effects during the breeding period, we also looked at the overwintering dynamics of the population. We predict that (P1) COEs exist from the overwintering to the breeding season, (P2) post- and pre-migration represent a particularly vulnerable period for migratory birds since they might be exhausted from and need to prepare for the strenuous journey, and thus food events occurring in that time result in stronger COEs than mid-winter events, (P3) short but severe food deprivations may be compensated for until spring migration while longer but milder food shortenings carry-over to the breeding phase. We further assessed the suitability of state-based optimal annual routine modeling for predicting population dynamics of animals under global change.

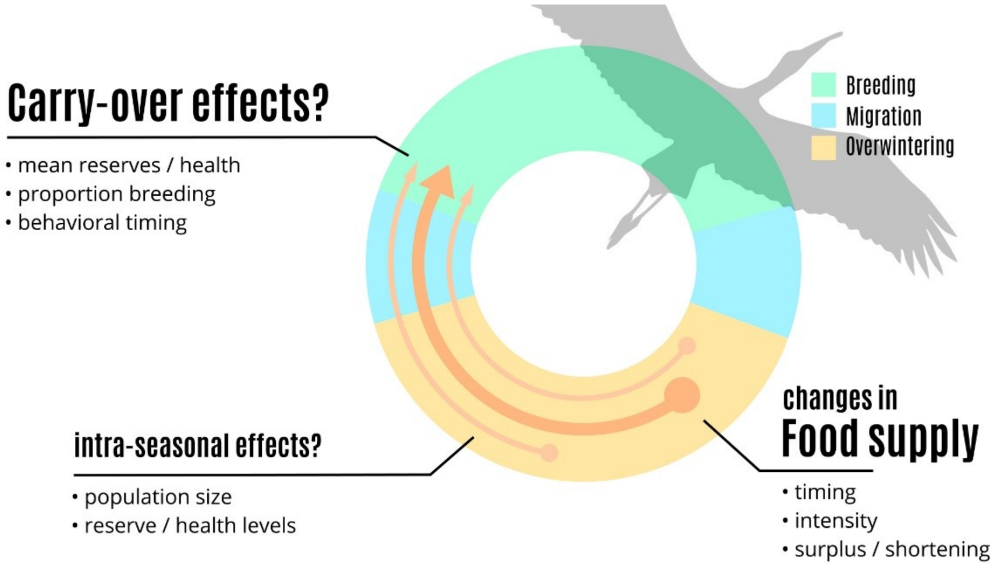

Figure 4-1: Conceptual model for exploring carry-over effects between overwintering food supply and early breeding season in migratory birds. The focus of this study are immediate and proximate effects of overwintering food surplus or shortening, both varying in their timing and intensity, on a modelled white stork population. We also look at intra-seasonal effects within the overwintering period since changes in population size arising from such changes in food supply can lead to seasonal compensation effects during the breeding period.

4.3 Methods

4.3.1 The model

White stork behaviour and population dynamics are modelled with the new open source software *sOAR* (Schaefer et al. 2018). For simplicity, only female birds and their long-term number of descendants are considered. They are characterized by the following state variables: energy reserves *x*, health condition *y*, experience *e*, breeding status *a*, location *o* and migratory state *s*. Using *sOAR*, we first determine the optimal behavioural strategy for a population of modelled white storks breeding in Central Europe and overwintering in Eastern Africa. The strategy is computed for an annual cycle that is divided into *T=52* weeks. At the beginning of each week, birds take a decision regarding their foraging intensity and potential migratory or reproductive activities. Migration can occur between two locations. The optimal strategy depends on the birds' internal state and week t and is computed using stochastic dynamic programming (Houston and McNamara, 1999; Schaefer et al., 2018). Environmental conditions, i.e. food supply and thermal conditions, vary with time of the year but are periodic between years. Second, a cohort of individuals employing the optimal strategy in the given environment is followed forward in time until its population dynamics settle down at an equilibrium pattern (baseline). Then, the equilibrium population is subjected to a year with temporal food shortage or surplus in the overwintering location. The population is tracked further in time, and the emergent population dynamics, behaviour and distribution of states within the population are analysed and compared to the baseline scenario of unaltered food conditions.

4.3.1.1 ENVIRONMENT

Model birds were constrained by food availability and thermal conditions. Environmental food supply *g(o,t)* varied sinusoidal over the year but with higher seasonality and a distinct resource peak during summer in the breeding location. Thermal availability, on which white storks depend during migration, was reflected in the weekly probability of active flight. This probability was zero in the African overwintering location but varied seasonally in the breeding location.

4.3.1.2 DYNAMICS OF ENERGY RESERVES

Energetic intake

Environmental food supply $g(o,t)$, a bird's increasing experience e and its selected foraging intensity $u \in [0,1]$ determined the bird's energetic intake $\gamma(e,o,u,t)$ in a given location o at a particular week t in the following way:

$$\gamma(e,o,u,t) = \theta^{e_{max}-e} * g(o,t) * u.$$

Hereby, gross energetic intake and experience were coupled via a parameter θ with $0 < \theta < 1$ that implicitly quantified the effect of density dependence acting on the foraging success of juveniles (see Houston and McNamara (Houston and McNamara, 1999)). In particular, more experience resulted in higher energetic gains from foraging. The value of the parameter θ was calibrated during computations such that the population following the computed optimal behavioral strategy would be of stable size (cf. (Houston and McNamara, 1999)).

Energetic expenditure

The energetic expenditure $c_{subsist}(u,x)$ of a subsisting bird was a function of its foraging intensity u, body reserves x and basal metabolism c_b:

$$c_{subsist}(u,x) = (c_b + 6u^2) * \left(1 + \left(0.01\frac{x}{x_{max}}\right)^2\right)$$

Additional energetic costs (c_{action}) arose from demanding behavioral activities, namely from initiating breeding (c_{start}), incubation (c_{incub}), brood care (c_{care}) and migration (c_{migr}). The average level of energy reserves at the beginning of next week $t+1$ then was

$$x_{t+1} = x_t + \gamma(e,o,u,t) - c_{subsist}(u,x) - c_{action},$$

where c_{action} was either any of the extra demanding activities or zero when the bird chose to subsist only. For migrating birds, $c_{subsist}$ technically equaled zero since it was accounted for in the constant energetic migratory costs c_{migr}. A bird that had dependent young must forage with sufficient intensity $u_{crit}(t) \leq u \leq 1$ to ensure their survival. Otherwise, the brood was abandoned and died.

4.3.1.3 DYNAMICS OF HEALTH CONDITION

Health condition was reduced by activity but improves when activity and thus metabolic expenditure was low. The average health condition of a bird at week $t+1$ was

$$y_{t+1} = y_t - h_{action} + (1 - 0.2c_{subsist}(u,x) - 0.01(c_{subsist}(u,x))^2,$$

where $c_{subsist}(u,x)$ was the metabolic expenditure of subsistence and h_{action} represented potential extra health costs ($h_{start}, h_{migrate}$) for initiating breeding or migrating during time t to $t+1$.

4.3.1.4 REPRODUCTION

Birds that had no brood ($a=-1$) and were not migrating ($s=-1$) could start a brood any time of the year with the outlined costs, changing the breeding status to $a=0$ at the next time step $t+1$. Then, each week of voluntary brood care increased the brood's age until $a=a_{max}$, upon which the brood became independent. If the parent could not gain sufficient energy $\gamma(e,o,u_{crit},t)$ from foraging to supply its young, the brood died while the parent bird's breeding status was reset to $a=-1$. If the parent bird died, any dependent brood died, too. Newly independent young were assumed to have no experience (*e = 0*) and mean levels of reserves and health ($f_{indep} = 0.5$).

4.3.1.5 MIGRATION

Migration took three weeks and was free to occur any time of the year, but had to be completed once started. Migratory reserve dynamics were described by:

$$x_{t+1} = x_t - (p_{act}c_{act} + (1 - p_{act})c_{pas})(1 + 0.001x^2),$$

where p_{act} was the probability of active flight, c_{act} was the energetic cost of active and c_{pas} of passive flight. The term $0.001x^2$ caused flight costs to increase with body reserves (Alerstam, 1990). The average health condition y_{t+1} after each week *t* of migration was:

$$y_{t+1} = y_t - (p_{act}h_{act} + (1 - p_{act})h_{pas}),$$

where y_t represented health levels in the previous week and h_{act} and h_{pas} were the health costs of active and passive flight. Mortality $M_{migr}(x)$ during migration was an accelerating function of body reserves and incorporated the background mortality M_{bgmigr} :

$$M_{migr}(x) = M_{bgmigr}(1 + 0.01\frac{x}{x_{max}}).$$

4.3.1.6 MORTALITY

Starvation occured when reserve levels hit zero. The weekly probability of death due to disease $D(y)$ increased with low health and was given by:

$$D(y) = M_{bgdis} + \left(1 - M_{bgdis}\right) * (1 - \frac{y}{y_{max}})^8,$$

whereby M_{bgdis} reflected the maximum life expectancy of white storks. Predation risk $M_{pred}(x, o, u)$ for a non-migrating bird depended on its location and increased with foraging activity and fat depots:

$$M_{pred}(x, o, u) = M_{bgpred}(o) * u^2 * (1 + 0.01 * (\frac{x}{x_{max}})^2),$$

whereby $M_{bgpred}(o)$ was the location-specific background predation.

4.3.2 Computing the optimal strategy and expected behaviour

The optimal behavioural strategy defines the probability of a bird to perform a specific action (start breeding, incubate, care for brood, migrate), depending on its state and week of the year. The optimal strategy maximizes fitness in terms of long-term reproduction success and is computed by stochastic dynamic programming, iterating backwards from a future target year until convergence. Further details on the computational routine to determine the optimal behavioural strategy can be found in Houston and McNamara (1999) and Schaefer et al. (2018). All parameters are listed in Table S 6.3-1, including selected values and relevant literature. After determining the optimal behavioural strategy, behaviour and population dynamics are modelled through forward iteration by simulating how individuals select their optimal behavioural option each week based on their current state. Simulations were run until equilibrium. Once a stable population was reached, we could apply different scenarios of global change and explore how these affected the population dynamics.

4.3.3 Food resource scenarios

We were especially interested how global change-induced alteration in food availability could affect migratory birds. To this end, we tested scenarios of food shortenings (-) and of food surplus (+) in the overwintering location, and compared these to the baseline scenario with its cyclic sinusoidal food supply. Specifically, food supply was varied in strength (-/+ 10/20/40/80 %) and duration (1/2/4/8/16 weeks) between scenarios. Two lines of scenarios were run: a) constant intensity (i.e. strength x duration) of food surplus or shortening over the overwintering season, whereby the strength (magnitude) and duration (number of weeks) of food change varied but the product thereof was kept constant b) increasing intensity of winter food shortening, whereby the duration of altered food supply increased while its strength was kept constant. In the latter line of scenarios, only food shortage was tested since detrimental droughts are expected to intensify in the African overwintering habitats (cf. IPCC, 2014).

4.4 Results

4.4.1 Baseline scenario

The modelled population of white storks showed a distinct temporal pattern of energy reserves and health condition during the overwintering period in the baseline scenario without alterations in environmental food supply (Figure 4-2). Mean energy reserves had a midwinter low (Figure 4-2 A) because the proportion of modelled birds with low reserve levels was increasing (Figure 4-2 C). At the same time, the mean health condition increased continuously during the overwintering period (Figure 4-2 B) as birds that arrived in bad condition were building up their health status (Figure 4-2 D).

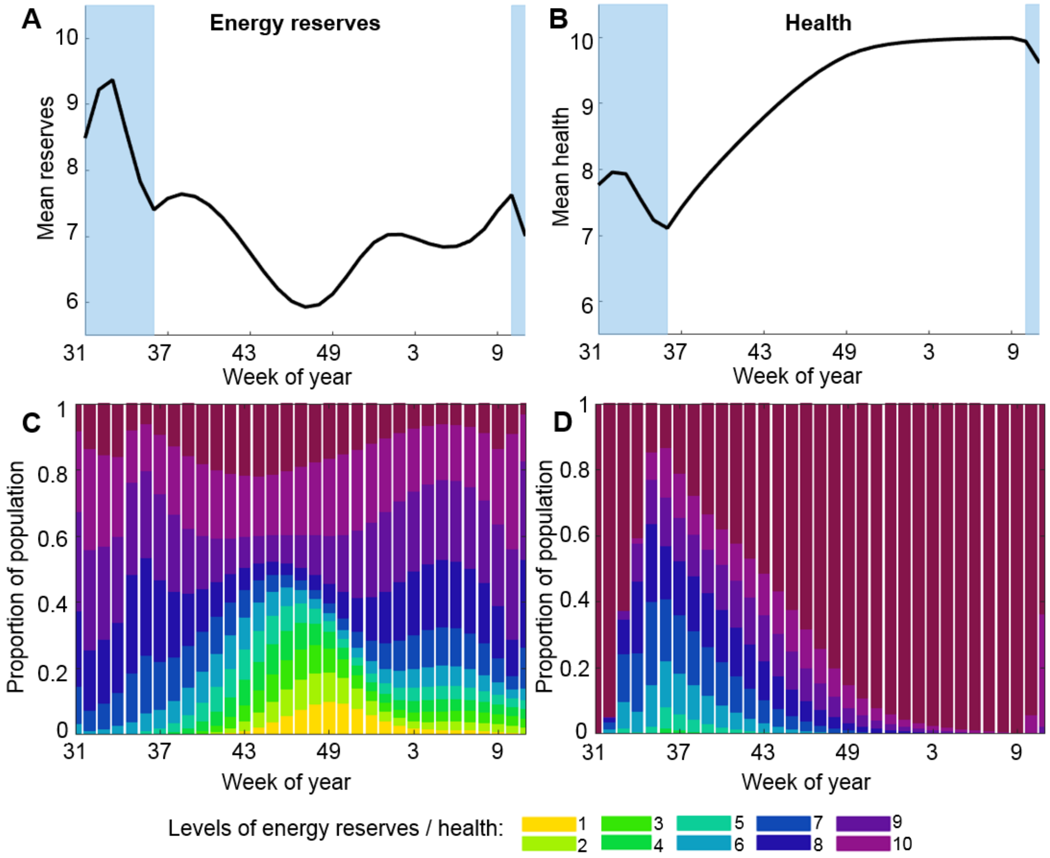

Figure 4-2: Development of energetic reserves and health condition over time in the baseline scenario. (A) Mean reserves (B) mean health condition (C) weekly distribution of reserve levels (D) weekly distribution of health levels.

4.4.2 Constant intensity of food surplus/shortening

Food shortenings during overwintering led to up to 16 % lower mean levels of reserves among birds that started breeding and a delayed start of migration and subsequent breeding activities of up to 5 days (Figure 4-3 A,B,C and Figure S 6.3-1). Nevertheless, the proportion of individuals starting a brood did not change much, decreasing only by up to 1.4 %. Food surplus during overwintering had opposing effects. Mean reserves were up to 22 % higher in birds starting to breed, and migration and breeding activities started around 1-4 days earlier compared to the baseline scenario (Figure 4-3 A,B,C; Appendix Section 6.3.3 Figure S 4.4-1). Again, the proportion of birds starting to breed changed little with increases of 0.5-1 %. In both food surplus and food shortening scenarios, health levels varied much less than energy reserves since health dynamics are only indirectly affected by food supply and have slower dynamics than the energetic reserves in the model (Appendix Section 6.3.3 Figure S 4.4-2 and Appendix Section 6.3.5 Figure S 4.4-3).

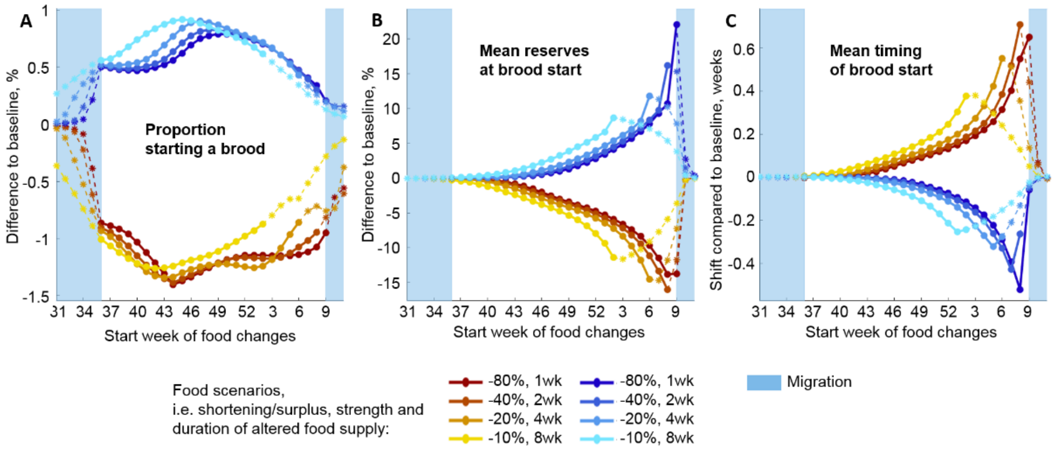

Figure 4-3: Carry-over effects from the overwintering to the beginning of following breeding period for various scenarios of food surplus (blue) and food shortenings (red) in the overwintering location. Effect on A) the proportion of the population starting a brood B) the level of mean reserves of parental birds when starting a brood C) mean timing of when the brood is initiated. The absolute change in food supply relative to baseline food supply was the same in all scenarios, meaning its intensity was constant. However, the duration and relative strength of food surplus or shortening was varied between +/-80 % change in food supply over only one week to +/-10 % change in food supply over 8 weeks, i.e. the population experienced short but strong changes in food supply (darker in colour) versus long but small changes in food supply (lighter in colour). Dashed lines represent the effect of altered resource dynamics that did not affect the complete population equally since they fell into the migratory period. The migratory period is depicted by light blue bars. The breeding period starts in week 11.

The effects on mean energy reserves and the timing of breeding (Figure 4-3 B,C) were larger in magnitude the later the food surplus/shortening occurred during the overwintering season, meaning the closer food alterations occurred towards the breeding period. The same applied for health condition and spring migration (Appendix Section 6.3.3 Figure S 4.4-4). Late breeders were particularly strongly affected by such food shortenings (Appendix Section 6.3.5 Figure S 4.4-5). These effects arise because the individuals need a certain time to build up their reserves. Considering only food shortenings occurring (and ceasing) before the onset of spring migration, longer-lasting mild food reductions impacted the level of energy reserves in spring and the timing of breeding more than short and heavy events around the same time (Figure 4-3 B,C; Figure 4-4 B,C). These differences between food shortenings that are of constant intensity but vary in duration became more pronounced for higher levels of overall food shortenings (Figure 4-4, green versus pink graphs).

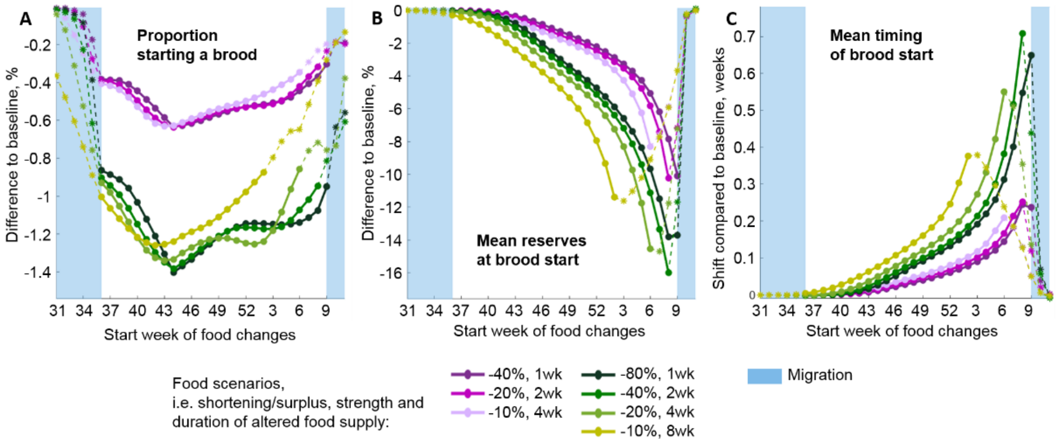

Figure 4-4: Dynamics in reserve levels and population size during the overwintering period when food shortening was initiated in five different weeks of the overwintering period. (A) Weekly mean reserve levels and (B) population size. Food shortening of -80 % was initiated in five different weeks (circles) and lasted only one week. The lines indicate the corresponding temporal development of mean reserves and population size after the event up to the following breeding season compared to the baseline scenario. The migratory period is depicted by light blue bars. The breeding period starts in week 13.

Figure 4-5 exemplarily shows the temporal development of mean reserve levels and population size relative to the baseline scenario when food shortening of -80 % lasting one week was initiated at different times during winter. Food shortening led to a direct reduction of mean reserve levels (Figure 4-5 A) between the week of food shortage and the following week. Hereby, food shortening directly after autumn arrival (week 36, blue) and just before spring migration (week 8, green) produced the largest direct effect on mean energetic reserves (Figure 4-5 A). Further, our model indicated a time lag between food shortage and increased mortality rates with shorter time lags the later the food shortage occurred during winter (Figure 4-5 B).

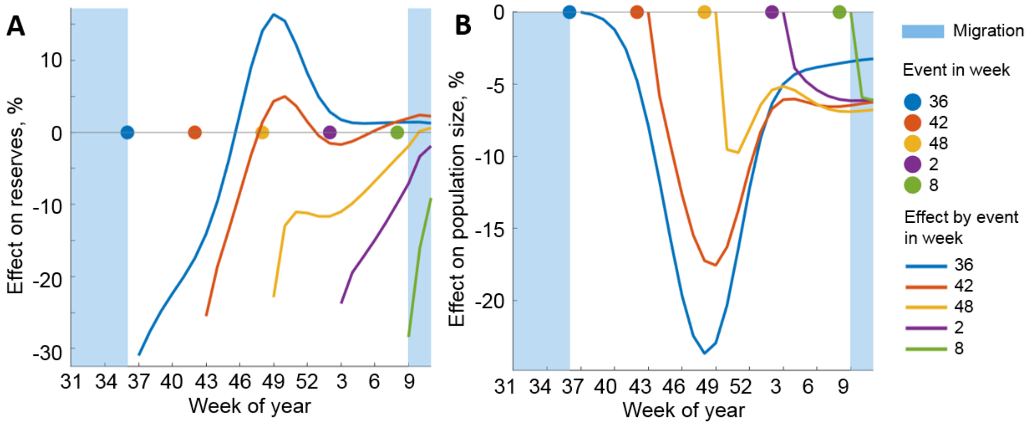

Figure 4-5: Dynamics in reserve levels and population size during the overwintering period when food shortening was initiated in five different weeks of the overwintering period. (A) Weekly mean reserve levels and (B) population size. Food shortening of -80% was initiated in five different weeks

(circles) and lasted only one week. The lines indicate the corresponding temporal development of mean reserves and population size after the event up to the following breeding season compared to the baseline scenario. The migratory period is depicted by light blue bars. The breeding period starts in week 13.

4.4.3 Increasing intensity of food surplus/shortening

When the duration and thus the intensity of food shortening increases, the proportion of breeding birds can decrease substantially (Figure 4-8). Specifically, in an extreme scenario in which per-week food supply was reduced by 20 % for 16 weeks during overwintering, the proportion of birds starting to breed decreased by one third (Figure 4-8 A). The largest effect on the number of birds initiating a brood was observed when food shortening occurred during midwinter (Figure 4-6 A and Figure 4-8 A), since reserve levels were comparatively low during this time (Figure 4-2).

Generally, longer food deprivations during winter reduced the mean reserve levels of parental birds in spring and delayed initiation of breeding more than shorter adverse periods of the same strength (Figure 4-8 B,C and Figure 4-7 B,C). When the period of food shortening in the overwintering location lasted into spring, however, the negative impact was smaller because the birds left the overwintering location by end of winter. The mean reserves of birds initiating a brood was slightly lower than those of the total population in early spring (not shown).

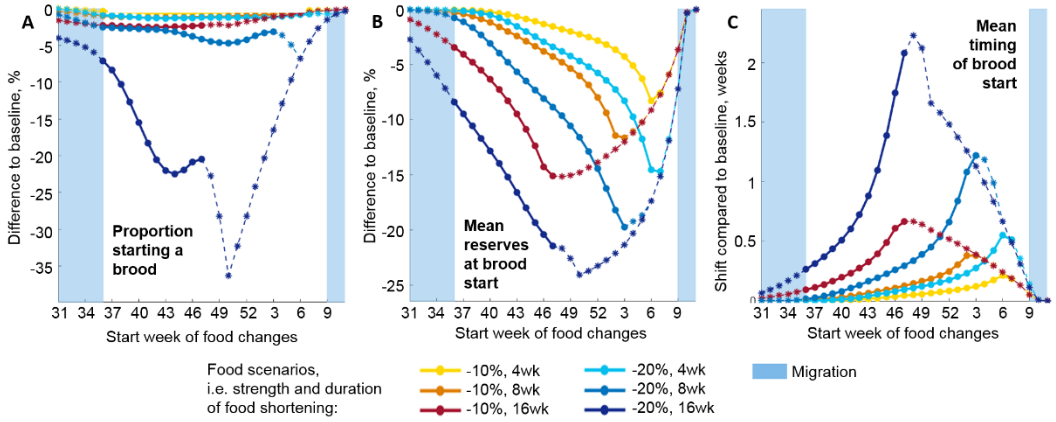

Figure 4-8: Carry-over effects under increasing duration of food shortages during the overwintering period. Shown are effects of prolonged food shortages on (A) the number of birds starting a brood (B) their mean reserve levels (C) delays in starting a brood. Food shortenings of 20 % per week over durations of 4-16 weeks are depicted in light to dark blue, while food shortenings of 10 % per week over durations of 4-16 weeks are shown in yellow to red. Dashed lines represent the effect of altered resource dynamics that did not affect the complete population equally since they fell into the migratory period. The migratory period is represented by light blue bars. The breeding period starts in week 13.

4.5 Discussion

Here, we explored carry-over effects in migratory birds resulting from changes in food supply during the overwintering season based on an optimal annual routine model (Schaefer et al., 2018). Since the frequency and strength of adverse events (e.g. the occurrence and intensity of droughts) can be expected to increase under global change, it is important to gain a better understanding of the long-term effects of such events on vulnerable migratory bird populations. Our results indicate that changes in food supply during overwintering can strongly affect breeding population sizes and timing of breeding as well as pre-breeding energy reserves with potentially strong effects on subsequent breeding success. Thereby, the timing of changes in food supply played a crucial role with food shortening in late winter showing the most detrimental effects. Food surplus resulted in corresponding positive effects, which might be interesting for designing conservation measures, though these effects were less pronounced except when occurring directly before spring migration.

Generally, optimal annual routine modeling proved to be a valuable tool for analyzing the effects of altered resource distributions on migratory birds. Using *sOAR* (Schaefer et al., 2018), it was not only possible to study the relative magnitude of carry-over effects on different aspects of the individual state and the population state but also to study how the timing of changing food supply affects the magnitude of the carry-over effects. Thus, we were able to explore whether short but strong food shortening is less or more detrimental then long but relatively small food shortening, and whether some kind of "tipping points" could be observed when the duration of food shortage increased. Due to *sOAR*'s mechanistic foundation based on energy- and health budgets, the timing of events and survival patterns emerged from the implemented ecological processes rather than being imposed on the modelled birds. Thus, simulated animal behavior and population dynamics responded flexibly to assumed changes in food supply, which is an important step forward for improving the predictive ability of models that are designed to capture global change impacts on animals.

Our findings are in line with evidence that survival rates of western white storks migrating to western Africa are positively correlated with yearly amount of rainfall in the African overwintering region, which is an indicator for African food supply in form of large insects (Dallinga and Schoenmakers, 1987; Kanyamibwa et al., 1990). Although Kanyamibwa et al. (Kanyamibwa et al., 1993) found no correlation between rainfall and population size for eastern white storks migrating to eastern and southern Africa, Sæther et al. (Sæther et al., 2005) detected time- and region-dependent effects for them. Survival rates of eastern white storks seem to further increase with primary production in the overwintering habitat (Schaub et al., 2005). Also, reproductive investment of Polish white storks is higher following rainier African winters (Tobolka et al., 2018). Dallinga & Schoenmakers (Dallinga and Schoenmakers, 1987) found that western white storks arrived earlier at their breeding grounds and that the number of pairs with a nest and their breeding success was higher in years with high winter rainfall and locust plagues in African wintering areas, which corroborates the importance of carry-over effects on population dynamics.

In the model, birds arriving at the breeding grounds in low physical condition were typically late breeders. These were particularly affected by food shortenings so that the mean level of reserves of birds initiating a brood was slightly lower than mean reserve levels of the total population under food shortenings. This indicates that carry-over effects might accumulate over time and that negative maternal effects might arise here with the parent's low body condition directly influencing the success of its young (Blount et al., 2006; Clausen et al., 2015; Verhulst and Nilsson, 2008). At the same time, a disproportionately negative effect of food shortenings on birds that are already in bad shape should drive the evolution of compensation measures like skipping a breeding period, prelaying adjustment of clutch size, partial or total destruction of eggs (ovicide) and killing of offspring (filial infanticide) including filial cannibalism, which have been observed in white storks (Kaatz et al., 2017).

Concordant with expectations, COEs from the overwintering to the breeding phase became stronger the closer the food shortening occurred to spring migration (Figure 4-3). In these cases, the time before the strenuous migratory journey was not sufficient for compensating any negative effects on body condition. Thus, late winter can be seen as the most vulnerable phase for white stork populations in terms of overwintering COEs affecting breeding. At the same time, food surplus directly before spring migration improved the analyzed breeding parameters.

At the beginning of the overwintering period, individuals were particularly sensitive to food reductions that led to the largest immediate decrease of energy reserves and caused mid-winter population declines. After the strenuous breeding phase and autumn migration reserves are typically reduced, and overwintering food supply, which is overall lower than summer supply in the breeding grounds, is not sufficient to replenish reserves of all birds. At the same time, however, the resulting COE on the breeding seasons was lower and relative population size decreases were smaller when food shortening occurred early. This indicates that the length of the overwintering season is crucial for the ability of individuals to buffer negative effects, corroborating findings from Briedis et al. (Briedis et al., 2018) where the overwintering phase allowed compensating for experimentally increased brood size in collared flycatchers. Here, our temporally highly resolved simulations help understanding transient dynamics, and with that the complex consequences related to timing and magnitude of carry-over effects.

We have to caution that although our model allows valuable insights into the complexity of COEs, it is still an abstraction of reality and makes several simplifying assumptions. For example, the mid-winter level of energy reserves was unexpectedly low in the model (Figure 4-2 and Appendix Section 6.3.6 Figure S 4.5-1), resulting in high impacts of midwinter food changes on population size and the number of breeding at the beginning of the following breeding season (Figure 4-9 A). Although Sæther et al. (Sæther et al., 2005) found large effects of midwinter rainfall in East-Africa on the population size of white storks in spring, Berthold et al. (Berthold et al., 2001) report that body mass and subcutaneous fat depots of white storks overwintering in captivity was very high and that corresponding anecdotal evidence exists from wild white storks overwintering in Africa. Thus, current empirical evidence indicates that mid-winter energetic levels in the model were too low, which could have two reasons. First, the applied optimal behavioral strategy had been computed for a predictable cyclic environment without additional stochasticity in the food resource trajectory. Accordingly, there was no need for spare reserves during winter. Secondly, in the model there is an inherent trade-off between building up energetic reserves through foraging activity versus building up health condition, which increases under rest and requires more time. Since quite high levels of both reserves and health are required in order to master the strenuous subsequent spring migration and breeding period, the previously determined optimal behavioral strategy thus favored investment into the immune system before fat stores (cf. Appendix Section 6.3.6 Figure S 4.5-2).

Tökölyi et al. (Tökölyi et al., 2012) found that non-migratory birds kept a certain degree of physiological preparedness for unfavorable periods, when food availability was variable in their OAR model focusing on the activation of gonads for reproduction in unpredictable environments. Since the modelled white storks showed no such adaptation in their energetics despite experimental indication, the food availability in their African overwintering grounds likely is more unpredictable than we assumed – even for an opportunistic and very mobile feeder like the white stork (Kaatz et al., 2017). However, the severity of immediate effects of mid-winter food shortages on the overwintering population in our model setting indicates that there exists a strong selective pressure for physiological or behavioral adaptations for white storks in a more variable environment. Potential adaptations could involve selection for higher energy acquisition during mid-winter, as found by Berthold et al. (Berthold et al., 2001) for captured white storks, or selection for a more nomadic lifestyle in the African overwintering grounds (Kaatz et al., 2017) especially as movement costs in Africa are cheap for soaring birds like the white stork due to high thermal availability. Overall, our findings highlight the importance of implementing unpredictable food regimes together with energy-budget driven mechanisms for non-tropical African overwintering sites in mechanistic models of bird migration, especially for long-lived birds.

With respect to the impact of short but severe versus longer but milder food events (P3), notable differences in the impact only arose for food events of high intensity. So, events of 40 % intensity differed little in their effects, while for 80 % intensity the temporal pattern of the event mattered (Figure 4-4). In particular, enduring events affected breeding parameters stronger than short-term events of equivalent intensity – if the event fell completely within the overwintering period. Consequently, it is crucial to consider spatiotemporal environmental patterns resulting from global change when predicting impacts on migratory birds under severer global change scenarios. A first step in this direction has been performed by La Sorte et al. (La Sorte et al., 2017) who matched the weekly distributional dynamics of Neotropical migratory forest birds with predicted spatiotemporal patterns of altered land use and climate in order to characterize their vulnerability to global change.

4.6 Conclusions

In summary, global changes in the wintering grounds may affect both demography and breeding phenology of migratory birds through carry-over. However, dynamic state-based modeling and optimal annual routine modeling in particular improve our understanding of carry-over effects within the annual cycle of migratory birds and represent a valuable tool for global change ecology. Furthermore, they not only allow studying potentially negative carry-over effects but also assessing the effectiveness of conservation measures in different parts of the annual cycle. In the future, our model could be extended to study how COEs affect population dynamics over several consecutive breeding seasons.

4.7 List of abbreviations

COEs: Carry-over effects; OAR: Optimal annual routine.

4.8 Declarations

4.8.1 Ethics approval and consent to participate

Not applicable.

4.8.2 Consent for publication

Not applicable.

4.8.3 Availability of data and materials

The extended sOAR version and configuration files are available upon request from the authors.

4.8.4 Competing interests

The authors declare that they have no competing interests.

4.8.5 Funding

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4.8.6 Author’s Contributions

MS, DZ and FJ conceived the idea and designed methodology. MS performed the computations and analyses and led the writing of the manuscript. All authors discussed the work and contributed critically to the final manuscript.

4.8.7 Acknowledgement

We wish to thank Wolfgang Fiedler, Andrea Flack, Michael Kaatz, Ran Nathan, Shay Rotich and Martin Wikelski for insightful discussions on bird migration and the biology of white storks.

5 Synthesis

In the three studies presented in this thesis, I investigated how global change impacts the behaviour, state and population dynamics of long-distance migratory birds (Chapter 3, 4) and developed the first open-source optimal annual routine model (Chapter 2) to this end (Figure 5-1). Generally, my findings demonstrate the importance of reaching a deeper mechanistic understanding of global change effects on migratory birds and the need for good predictive models that can assist conservation efforts. In particular, I found that altered food supply, as it can be expected under global change, will have mostly negative effects on the behaviour and population dynamics of the studied migratory stork and falcon bird types, which are not only population specific but act across different temporal scales.

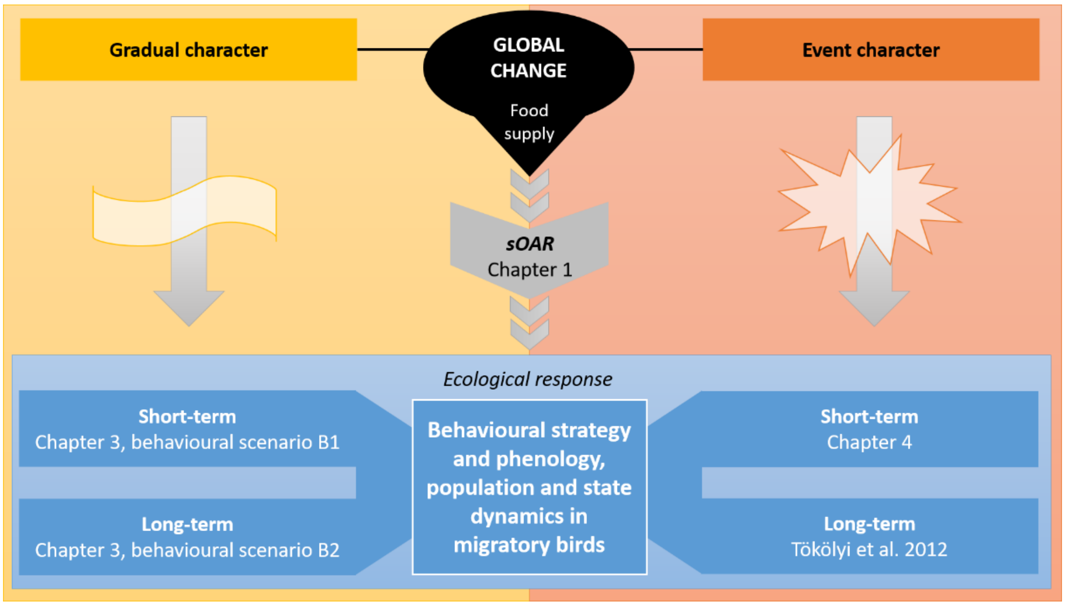

Figure 5-1: Performed research on the impacts of global change on migratory birds as presented in this thesis. Two temporal characteristics of global change (yellow and orange box) are considered, while global change is abstracted to changes in environmental food availability (black). The expected ecological responses of migratory birds (blue boxes) are determined across two temporal scales (short- and long-term) using the software sOAR (broad grey arrow) that was developed for this thesis.

From the short-term perspective, many birds might not be able to adjust in time to altered environmental conditions and generally decreasing food supply will likely further reduce the population size of many migratory birds (Section 3.4.1). Intensifying extreme events like food shortenings from increasing droughts (IPCC, 2013) will add to this development, not only directly reducing population sizes through starvation of individuals but also leading to negative carry-over effects (Section 4.4). In the long-term, long-distance migratory birds will need to update their behavioural strategy in order to persist, e.g. by advancing spring migration and breeding phenology next to adjusting the timing of autumn migration (Section 3.4.2). Whether and how fast a population is able to adapt its behavioural strategy to the new environmental situation will determine its vulnerability. The scope of required adjustments, which varied with the analysed bird type and assumed environmental scenario (Section 3.4.2), could serve as an indicator of the experienced evolutionary pressure and thus the vulnerability of a population of migratory birds. For example, the new optimal timing of migration in the falcon type requires larger time shifts of behaviour than in the stork type (Section 3.4.2). In the following, I discuss my work and major findings including their relevance in a wider scientific context. In particular, I assess the value and challenges of employing OAR modelling for global change research (Section 5.1) before discussing the modelled short- and long-term effects of global change on the behaviour, population and state dynamics of migratory birds in relation to scientific literature (Section 5.2). Then, I will broaden the discussion to look at the ecological implications of my work, considering also animal migration in general (Section 5.3). Finally, I suggest how to advance the movement ecology framework (Section 5.4) and how to develop a new indicator of vulnerability for migratory birds based on my research (Section 5.5), before ending with worthwhile future directions of research (Section 5.6).

5.1 OAR modelling for global change research

Optimal annual routine (OAR) modelling, which I heavily employed for this thesis, proved to be a powerful tool for modelling potential impacts of global change on migratory birds. Indeed, the OAR approach is suited for a much wider range of ecological questions and taxa, and deserves to be applied more frequently in global change, behavioural, evolutionary and movement ecology. In Chapter 2, I therefore introduced *sOAR*, the first open source OAR implementation (Schaefer et al., 2018). *sOAR* is based on the well-known OAR framework by Houston and McNamara (1999) and was designed as a user-friendly application for computing optimal animal life-history strategies in cyclic environments and for simulating the emerging behaviour and population dynamics under such a strategy. It shall help to open up the excellent but complicated and thus frequently used OAR technique (Feró et al., 2008) to a wider user circle.

Generally, animal movement under global change can be studied in a more holistic sense considering the causes, constraints and consequences of movement as envisioned by Nathan et al. (2008) using the excellent OAR modelling approach. OAR modelling theoretically works over large temporal, spatial and entity scales that would be difficult to tackle experimentally. It not only allows to better understand the spatial-temporal patterns observed in animal behaviour and the resulting population dynamics of the focal species (cf. Chapters 2, 3, 4). But, it additionally helps to analyse how complex movement and behavioural patterns evolve in animals, how their behavioural decisions including the timing of migration are constrained by internal and external factors and how natural selection shapes trade-offs in animal behaviour within cyclic environments. Such knowledge is crucial for anticipating potential species' response to global environmental change. Consequently, and especially evidenced in Chapters 3 and 4, OAR modelling possesses high potential for research in movement ecology, particularly within the context of global change.

sOAR is particularly suitable for investigating bird migration since I extended the original OAR framework with important features such as differentiation of active vs. passive flight costs in response to periodic time- and location-dependent wind conditions. Recent studies suggest that migratory birds optimize migratory decisions with respect to prevailing wind conditions (Kranstauber et al., 2015; Vansteelant et al., 2017). Figure S 6.2-1 confirms this view because the optimal migration timing of the studied stork functional type got shifted when the period of high thermal availability was prolonged, even though the overall pattern of results did not change. Therefore, wind conditions need to be considered when predicting global change impacts on migratory birds, as it is now possible with *sOAR*. Data on large-scale atmospheric patterns become increasingly available as well as high-resolution remote sensing data, improving the parametrization of thermal and food availability. Also tracking data is increasingly available at high spatial and temporal resolution and for more and more populations (e.g. at www.movebank.org), benefitting model validation. Blending such data with empirical and theoretical approaches like *sOAR* in order to resolve outstanding research questions regarding how global change will affect migratory animals in seasonal environments is highly promising, as highlighted by the results presented in Chapters 3 and 4.

My work shows that *sOAR's* main characteristics are major advantages when modelling global change impacts on migratory birds – namely that it is a mechanistic, dynamic, state-based model covering the full annual cycle and incorporating behavioural decision-making within the evolutionary sound framework of life-history theory (cf. Section 1.3.1). As argued in Chapter 1, mechanistic modelling is needed to understand and project species responses to global change. The mechanistic basis of *sOAR* which included life-history considerations allowed for making predictions for an altered future environment. This would be difficult with statistical modelling because historic correlations between the focal animal and the environment might not hold anymore under global change. Mechanistic modelling ensured that computed patterns emerged from underlying ecological processes instead of being imposed on the modelled birds. Thus, simulated bird behaviour and population dynamics responded flexibly to the assumed changes in food availability, which is important for improving the predictive capacity of models for projecting ecological impacts of global change. To capture the temporal patterns in the seasonal life-style of migratory birds, dynamics were required, which might be a favourable model property whenever time-dependent behaviour including movement is involved. Indeed, one major benefit of using *sOAR* is that one can not only study how strongly environmental change affects the state of the individual and the population, but also how the specific timing of change influences the occurrence and magnitude of effects (cf. Chapter 4). By working with internal states, the immediate motivation driving behaviour was included in the model and it was accounted for how individuals vary within a population. Both of these factors have been recognized as being important in ecology. To capture the role of different seasons in the life of migratory birds and resulting interdependencies with their behaviour, as addressed in Chapter 4, a full annual cycle approach was necessary. Finally, the focus on behavioural decision-making and underlying behavioural strategies allowed studying how behavioural responses to global change leads to the observed declines in bird populations worldwide. Indeed, behavioural changes could serve as early-warning signals to anticipate population declines. It is possible that the model properties presented in this paragraph are actually the core ingredients of any realistic model to accurately predicting global change impacts on mobile animals, suggesting that highly complex models such as *sOAR* are needed in the future.

Nevertheless, *sOAR* would profit from two optional extensions: explicit density-dependence and a more detailed breeding process. The former integrates the effect of population size on food availability into the model, which should be important for populations whose size is close to the carrying capacity of their habitat. Explicit density-dependence could be reached by a circular computational process as it has been suggested by Houston and McNamara (1999) and been employed by Barta et al. (2006) and Barta et al. (2008) to analyse molt patterns in non-migratory and migratory birds. Here, the optimal behavioural strategy depends on food availability, which in turn is influenced by the population size that emerges when the computed behavioural strategy is followed by a model population. Usually, this iterative procedure converges towards the strategy that is the best response to itself given the environmental food supply, i.e. an evolutionary stable strategy (ESS) (Barta et al., 2008, 2006; Houston and McNamara, 1999). More realism in the modelled breeding process, e.g. including partial brood abandonment, would expand *sOAR*'s range of applications because population dynamics could realistically be simulated across breeding seasons, allowing to even follow the complete life-history of an animal.

Complex models pose various challenges with respect to their parametrization, implementation, validation, application, documentation and transfer, though (Grimm et al., 2010).

One effective approach to reduce parametrization efforts for complex mechanistic models is to revert to functional groups of organisms (as done in Chapter 3) instead of trying to calibrate the model for each existing species, which will be impossible. In plant ecology, there already exist rich databases of plant functional traits to classify functional types (e.g. Kattge et al., 2011; Kleyer et al., 2008; Poschlod et al., 2003), which are widely used and have successfully been employed in various mechanistic models (Giacomini et al., 2013; Jeltsch et al., 2008; May et al., 2009; Reeg et al., 2017). Also animal functional types are increasingly used in mechanistic ecological modelling (Kearney et al., 2010; Scherer et al., 2016; Teckentrup et al., 2018). Though it can be difficult to derive the relevant animal functional traits and groups (Blaum et al., 2011; Buchmann et al., 2012, 2011), modelling studies might also help solving this challenge since they can be used to identify the influencing factors in ecological processes and to test and validate our assumptions (Railsback and Grimm, 2012).

Certain implementation as well as parametrization and validation challenges could be met by strengthening interdisciplinary collaborations between ecologists and computer scientists. For example, digital ecological data can be distributed in bits and pieces, be difficult to access and process, and profit from automatization that allows research of larger scale. Here, productive collaboration between ecologists and people with high IT competency could not only take place within research projects and in education but also through new collaborative approaches like hackatons or data challenge events, where participants from various backgrounds come together for some hours to days to intensely and collaboratively work on a certain problem.

Another challenge arising from the demand for large and complex models is that we need to develop and establish appropriate routines to document such models, maximizing transparency of the modelling process. For individual- and agent-based modelling, there exist the ODD and ODD+D protocols to standardize model descriptions in order to reveal their theoretical foundations and to make them better understandable and complete (Grimm et al., 2010, 2006; Müller et al., 2013). Acknowledging their success, they could serve as a template for a more general documentation scheme that is also suited for OARs among other types of complex mechanistic models.

At the same time, the applicability and user-friendliness of complex models need to be ensured, which includes being easily adjustable to specific research questions. Publishing *sOAR* (Schaefer et al., 2018) as a modular ready-to-use standalone and an open source binary distribution including an extensive documentation in form of a user manual represents a first fundamental step in this direction. Another nice prototype for improving the user-friendliness of ecological models is given by the simulation platform *RangeShifter* by Bocedi et al. (2014), which allows modelling and visualizing species' responses to environmental changes considering spatial eco-evolutionary dynamics via a graphical user interface (GUI). Still, the value of *sOAR* lies in automatized large-scale computations that are better performed via shell/batch scripting than via GUI and should profit from existing big data solutions.

5.2 Predicted global change impacts on migratory birds

5.2.1 Short-term effects of global change

5.2.1.1 POPULATION DEVELOPMENT

In the short term, my results mostly predicted declining populations for the studied stork and falcon bird functional type when food supply was altered according to likely global change scenarios (Sections 3.3.4 and 4.3.3). This finding concurs with statistical analyses of field data showing that the populations of several smaller falcon species such as the red-footed falcon and the Eurasian kestrel are declining in size (Burfield, 2008). Also Eastern white storks seem to strongly depend on and decline with overwintering food supply since the size of white stork populations from all over Central and Eastern Europe fluctuate synchronously (Thomsen, 2017). Though their populations are currently still stable, lasting population declines can be expected from my results (Section 3.4.1) in the near future when the impacts of global change on their food supply are becoming more severe.

Further, cross-sectional analyses of field data show that migratory birds in general are particularly threatened by global change (Bairlein, 2016; BirdLife International, 2018; Sanderson et al., 2006). In Germany, 45 % of migratory bird populations declined over the years 1998-2008, compared to 28 % for partial migratory and 17 % for non-migratory bird species, for example (Wahl et al., 2015). Long-distance migrants like those used as model birds for this thesis, were found to be particularly threatened by global change (Zurell et al., 2018) and show stronger population declines than short-distance migrants or resident birds (Berthold et al., 1998; Both et al., 2009). Likely, they are particularly sensitive to global change, performing regular strenuous journeys and depending on the well-functioning of various ecosystems (Bauer and Hoye, 2014). Luckily, conservation measures and options to shorten the migration can benefit long-distance migrants at times, as growing white stork populations in Western Europe demonstrate. Here, white storks were re-introduced and benefited from intensive conservation measures, while they were additionally able to shorten their migration route feeding on open land-fills in Spain in recent years (Barbraud et al., 1999; Kaatz et al., 2017; Schaub et al., 2004).

5.2.1.2 BEHAVIOURAL TIMING

Regarding changes in the timing of major life-history events such as breeding and migration, both studied bird functional types showed only minor responses to gradual global change in the short-term (Section 3.4.1.2). Likewise, real Eastern white storks have not adjusted their behavioural timing (Gordo et al., 2013), while declining Eurasian kestrels are delaying their autumn passage into the Western Pyrenees (Filippi-Codaccioni et al., 2010), both indicating limitations in adaptation to novel conditions according to my results (Table 3.2).

Such non-adaptive responses – whether simulated or observed – can be treated as early-warning signal of global change since observed advanced spring migration and egg laying dates have been interpreted as an adaptive response to climate change (Usui, Butchart, and Phillimore, 2017; Knudsen et al., 2011). Indeed, species that notably advanced their spring migration during the years 1990-2000 were stable, while migratory bird species with declining populations did not adjust their migratory timing over the same time period (Møller, Rubolini, and Lehikoinen, 2008). Moreover, modelled stable populations that followed the new optimal strategy in the altered environment migrated earlier to the breeding location and also advanced breeding (Section 3.4.2 and Table 3.2).

The temporal shifts of autumn migration depended strongly on the specific scenario of food supply in the model and did not show a consistent pattern (Section 3.4). In field studies, autumn phenology is tackled less than spring phenology due to methodological complexities among other reasons, so that it was termed ’the neglected season in climate change research’ (Gallinat et al., 2015). For example, it is often less obvious when birds are departing for their overwintering grounds than when they are arriving at the breeding grounds (Gallinat et al., 2015; Lehikoinen et al., 2004). Therefore, it is currently still difficult to validate modelled projections of autumn migration timing in migratory birds.

Many but not all migratory bird species displayed changes in behavioural timing in recent decades, which are generally interpreted as a response to climate change (Knudsen et al., 2011; Lehikoinen et al., 2004; Rubolini et al., 2007; Usui et al., 2017). The observed responses differ among taxa and populations, just like for the modelled stork and falcon type (Section 3.4). The challenge is to explain the observed variation and to identify vulnerable populations for conservation. Some of the variation in observed responses could be explained by migratory distance, body mass, general timing of migration and phylogeny in the latest and most comprehensive meta-analysis to date considering data sets of >400 bird species across 5 continents covering >=15 years (Usui et al., 2017). Still, the authors concluded that a substantial part of the existing variation in how migratory birds alter their behavioural timing in response to climate warming remains largely unexplained. Therefore, additional useful predictors of phenological responses are needed. Since the modelled bird types not only responded differently to altered food supply but also differed significantly in their migratory flight costs, flight mode might be one such potential predictor of vulnerability to global change (Section 3.5, also see Section 5.2.3 on the influence of wind conditions). Flight mode, particularly use of active versus passive flight, indicates how costly flight and migration are with respect to energy expenditure. Another useful predictor could be sociality (Section 3.5), as predicted phenotypic plasticity in the behavioural strategy and thus the adaptive potential was generally low in the model (Section 3.4.2.3). Sociality facilitates the spread of new adaptive behaviour within a population and could thus reduce the vulnerability to global change, as also discussed in Section 5.2.2.

5.2.1.3 CARRY-OVER EFFECTS

Predicted climate change and land conversion in the southern overwintering grounds of many migratory birds (IPCC, 2014, 2013) give reason to expect overwintering food shortenings in the near future. As shown in Chapter 4, food shortenings threaten migratory birds beyond direct mortality from starvation. Rather, food shortenings will also induce notable carry-over effects (COEs) according to my results (Section 4.4), which likely impair breeding success and negatively affect the offspring with consequences for long-term population dynamics. For example, when spring migration and breeding were delayed in the model, less birds started breeding and these were overall in worse condition than without the assumed food changes. Similar COEs from the overwintering to the breeding season were noted experimentally for other species (Harrison et al., 2011; López-Calderón et al., 2017), whereas in studied Hudsonian godwits (Senner et al., 2014), red-backed shrikes (Pedersen et al., 2016) and collared flycatchers (Briedis et al., 2018) the overwintering period buffered carry-over effects from the breeding phase.

Critically, *sOAR* allowed to investigate fine-scale temporal effects for the first time, demonstrating that whether and how strongly COEs come into effect, is not only determined by the magnitude of food change but also by its timing and duration. For example, longer food deprivations during winter had larger negative carry-over effects on parental birds in spring than shorter adverse periods of the same strength (Figure 4-8 and Figure 4-3 B, C). Also, birds were particularly sensitive to food changes in the pre- and post-migratory phase. Although food shortening during this time led to severe COEs and population declines, food surplus especially before spring migration had positive effects. This suggests that supplemental feeding before migration and on arrival might be an appropriate conservation measure (Robb et al., 2008). In conclusion, OAR modelling provides a valuable tool for isolating effects of altered food supply from other influencing factors and for analysing temporal effects, which remains challenging in experimental studies (McKinnon et al., 2015).

Further, OAR models allow to anticipate potential effects of extreme events on the population dynamics of migratory birds. This is especially important since extreme events are not only expected to intensify under climate change (IPCC, 2013), but by their very nature they are unpredictable and have disproportionately large effects compared to their short duration (Jentsch et al., 2007). In the study in Chapter 4, unexpected extreme food shortenings enduring over nearly the complete overwintering season reduced the share of model birds initiating a brood by one third (Figure 4-8 A), which would have major consequences for population dynamics in the following years. But also minor events can have lasting negative effects in a population, according to my results, whereby these effects increase nonlinearly with increasing duration and strength of the event (Section 4.4). My results are supported by field data studies of lower temporal resolution, which show that survival data of white storks positively correlates with yearly rainfall in the African Sahel zone (Kanyamibwa et al. 1990 and Dallinga and Schoenmakers 1987). Further, increasing droughts and desertification in Northern Africa have been made responsible for observed declines in Afro-Palaearctic migratory birds (Newton, 2004; Sanderson et al., 2006). Here, sophisticated modelling techniques like *sOAR* and advanced remote sensing and tracking technologies can be expected to generate new research insights on the overwintering situation of migratory birds in the upcoming years, which is still mostly unknown, especially for remote African or tropical regions.

Generally, my short-term predictions (Section 3.4.1, Section 4.4) confirm that migratory birds are highly vulnerable to global change and that further population declines can be expected under global change even if specific populations still seem to be stable. The negative effects of altered food supply, such as declining populations (Section 3.4.1) and negative carry-over effects (Section 4.4), represent the cost of non-adaptation to global change because the simulated behavioural plasticity was quite low in the model, so that this potential mechanism for buffering negative effects of environmental change could not become effective. Thus, my research results emphasize the need for targeted conservation measures.

5.2.2 Long-term effects of global change

In the long-term, evolution should select for an advanced spring phenology in migratory birds according to my results. In particular, modelled spring migration and breeding occurred earlier in the year under the new optimal behavioural strategy in both analysed bird functional types (Section 3.4.2). Accordingly, and assuming they are able to adapt their strategy to the new environment, migratory birds can be expected to return earlier to their breeding ground. My work thus theoretically underpins that observed advances in the spring phenology of migratory birds (Lehikoinen et al., 2004; Rubolini et al., 2007; Usui et al., 2017) represent an optimal response to climate change. Since such beneficial responses have been witnessed over the period of only a few decades or generations in some populations, they can occur faster than previously assumed (Pulido and Berthold, 2004). Interestingly, the relative role of microevolution versus phenotypic plasticity in this context is still debated. As of 2019, observed changes in the timing of breeding and migration of birds are generally interpreted as being mostly plastic because they frequently correlate with climatic variables and also occur during the lifetime of individual birds (Charmantier and Gienapp, 2014; Merilä and Hendry, 2014).

The generally assumed strong role of behavioural plasticity in recent changes of behavioural timing in migratory birds (Charmantier and Gienapp, 2014; Merilä and Hendry, 2014) contradicts my finding of low plasticity in the behavioural strategy for the stork and falcon functional type. In my model, behavioural plasticity stems from variance in energy reserves and health condition. Environmental change or altered food supply, respectively, changes the distribution of these state variables within the population. Accordingly, behaviour should change in my model if the underlying strategy would involve plasticity. Plasticity hereby means that, under the same strategy, different behavioural activities should be performed at a certain time of the year in state combinations that were formerly unlikely but are reached under environmental change. This is not the case, though, so that behavioural plasticity was comparatively low, especially for the stork functional type. The main determinant of lower plasticity in the stork type compared to the falcon type was the longer nestling phase. Inferring, long-distance migratory birds and in particular long-lived species are generally limited by time constraints that make their adaptation to environmental change more difficult than for resident birds. This could explain why migratory bird populations are over-proportionately declining compared to non-migratory birds (cf. Chapter 1).

Returning to the role of evolutionary versus plastic responses, my results raise the vital question whether other adaptive mechanisms have been missed and underrepresented in previous research. Indeed, we observe comparatively rapid behavioural changes in some migratory bird species like the European Blackcaps (*Sylvia atricapilla*) (Bearhop et al., 2005; Berthold et al., 1992) although behavioural plasticity might be lower than previously assumed (cf. Chapter 3) and the evolutionary rate in vertebrates was assessed to be low (Gienapp et al., 2008). Therefore, a key suggestion of my research is that other important mechanisms to spread a new behavioural strategy within a population might have been overlooked.

One such adaptive mechanism could be social learning, especially for highly social birds like many falcon species or long-lived birds like the white stork which also flock together during migration allowing information transfer. In the model, the required magnitude of behavioural change would remain the same under social learning but if such additional adaptive mechanisms existed, they would have sped up the birds` adjustment to change. In that case, also a new set of potential indicators to assess the vulnerability of a species to global change, such as sociality, would become necessary and should be tested for their suitability. Mechanisms like social learning act much faster than evolution but are far from being understood (Flack et al., 2018). Nevertheless, they might be supported by appropriate conservation measures such as undisturbed gathering sites of sufficient size and quality to provide for larger flocks of birds. My results (Section 3.4) stimulate the discussion on the mechanisms underlying the observed advances in the behavioural phenology of birds and promote the idea that studying sociality and social learning is a worthwhile point of departure for future research in this context. Disentangling the role of various mechanisms including social learning in observed responses to environmental change will additionally improve future predictive frameworks, also for other taxa and systems.

Migratory birds that are not able to adapt will likely experience severe population declines and potentially go extinct (Section 3.4.1.1). Unfortunately, migratory birds face specific challenges in adapting their behavioural timing to climate change as it would be required according to my results (Section 3.4.2.2). In particular, migratory birds need to predict the phenology of their food resources from hundreds to thousands of kilometres away so that different suitable cues triggering migration have evolved under natural selection (Berthold, 2012). Adapting the migratory strategy to ongoing climate change now involves updating whether and how strongly to react to certain cues triggering migration (Winkler et al., 2014). Since global warming acts unevenly around the globe, however, migratory birds seem to be particularly threatened by climate change when the rate of warming in their breeding habitat surpasses the one in their overwintering habitat so that correct cueing is interrupted (Tim and Will, 2009).

5.2.3 The influence of wind conditions

Due to their flying movement mode, migration timing and energetic flight costs strongly depend on atmospheric circulation patterns, which are also expected to be impacted by climate change. Though confidence in the predictions regarding how they will change in the near future is still low (IPCC, 2013), it is reasonable to assume that the period of thermal availability will lengthen and thermals become stronger with global warming. Then, larger passive fliers like the white stork or various vultures might experience longer windows of opportunity with cheap flight costs. Accordingly, they might be less vulnerable to climate change in this respect than smaller birds that mainly employ active flight and save less energy from soaring/gliding due to different flight energetics (cf. Pennycuick, 1972). This argument is not only supported by findings that population declines in migratory birds correlate negatively with body mass (Usui et al., 2017) but also by my finding that the modelled active flyer (falcon) showed stronger population declines than the modelled passive flyer (stork) for the same food scenarios (Table 3.2).

The influence of wind conditions on migratory patterns has only recently come into the scientific focus, despite excellent theoretical considerations on wind as a selective force for migratory birds (Alerstam, 1979) and experimental approaches to determine the flight mechanics and dynamics of birds (e.g Pennycuick, 1972). Kranstauber et al. (2015) used 21 years of available global wind data to compute the optimal flight route with respect to wind support between any two locations in the world. Following these wind-optimized routes would save birds around 27 % of travelling time compared to the shortest route, with likely consequences for survival (Kranstauber et al., 2015). Many known migratory flyways (cf. Figure 1-2) overlap with the computed routes so that they likely represent energetically cheap aerial highways to which migratory birds adapted at the population level (Kranstauber et al., 2015). Meanwhile, it was shown that Honey Buzzards, which are large soaring migrants, make seasonal detours to exploit predictable favourable wind patterns further down the route (Vansteelant et al., 2017). Even nocturnally migrating songbirds in the USA could benefit from altered wind regimes under climate change as projected future wind patterns were theoretically found to assist them during their migration (La Sorte et al., 2018).

Generally, it seems vital to re-address pending questions regarding how wind conditions affect migratory bird population for improving predictions regarding the impacts of global change on migratory birds. Now, in the era of advanced tracking technology, high-performance computing and big data, we also have the tools for doing so and can model wind effects more explicitly, as it is possible with *sOAR*, for example, and has been done in Chapters 3 and 4.

5.3 Ecological consequences of declining migrants

In the following, I will set my findings into the bigger ecological picture, considering their wider ecological consequences and also other migratory animal populations. Besides migratory birds, also other migratory animals have notably decreased in population size over recent decades (Wilcove and Wikelski, 2008). For example, the migratory Mongolian antelope (*Saiga tatarica mongolica*) has dropped from over one million to less than 50,000 individuals within 20 years, which is equivalent to a population decline of over 95 % (Berger, Young, and Berger, 2008). Similarly, scientists estimated that the biomass of salmon returning to the Pacific Northwest of the USA for reproduction is only 5-9 % of the biomass of salmons that reached this area prior to European settlement (Gresh et al., 2000). Accordingly, Wilcove and Wikelski (2008) warned that migratory animals and the phenomenon of animal migration could disappear altogether under global change, with major consequences for whole ecosystems.

At the individual level, the changes in temporal patterns of resource supply induced by global change will require the adjustment of the timing of life-history events by migratory birds. Otherwise, ecological mismatches between the bird's resource demand and available supply might incur negative fitness consequences throughout its lifecycle (Both et al., 2009; Møller et al., 2008; Thomas et al., 2001). Accordingly, modelled populations that kept following the outdated behavioural strategy in the new environment had mostly declining populations (Section 3.4.1).

The potential for detrimental resource mismatches under climate change also applies to other taxa and can be expected to alter species interactions and potentially shift community compositions (Both et al., 2009).

Keeping pace with the advancing phenology of food resources and utilizing new feeding opportunities, migration distances might decrease or migration be given up at all (Knudsen et al., 2011). Though the affected populations will be saving the energy spent for migration, it was shown that migratory populations also suffer from reduced migration, potentially accelerating their decline. Typically, migratory animals are assumed to encounter more diverse parasites and pathogens than sedentary animals and to experience temporary high infection risks (Bauer and Hoye, 2014; Satterfield et al., 2015), e.g. during flocking on departure. However, migration also allows to escape contaminated regions, kills off infected individuals during the strenuous journeys, and can lead to pathogen loss along the route (Krkošek et al., 2007; Satterfield et al., 2015). Accordingly, migration positively affected disease dynamics for the host species in several recent studies on wild animals (Bartel et al., 2011; Daversa et al., 2018; Krkošek et al., 2007). For example, the infection rate of American monarch butterflies (*Danaus plexippus*) with a certain pathogen is much lower in migratory populations than in populations that have become sedentary, although the pathogen virulence was similar in both populations (Satterfield et al., 2015).

At higher systematic levels, migratory animals form part of biodiversity - meaning that declining populations of migratory birds and other migratory animals down to extinctions will directly reduce biodiversity. Therefore, not only species richness will be negatively affected but also other important components of biodiversity such as the genetic, functional, phenotypic and phylogenetic diversity (CBD, 2014; Díaz et al., 2013; Pereira et al., 2013). Generally, the population declines predicted for the modelled bird functional types in Chapter 3 are in line with the current scientific view that the biotic world is becoming more homogeneous globally (Primack et al., 2018; Thuiller et al., 2011).

Finally, population declines and corresponding changes in biodiversity have consequences at the ecosystem-level. Migratory birds are mobile links that connect ecosystems and perform various ecosystem services such as controlling insects, dispersing seeds, serving as energetic prey and redistributing nutrients among others (Bauer and Hoye, 2014; Şekercioğlu, 2006; Şekercioğlu et al., 2004). Decreasing population sizes will threaten such services. For example, in an experimental study on a Jamaican coffee farm, coffee shrubs were infested 40 % - 58 % more by the major insect pest in coffee when they were experimentally excluded from foraging by birds (Johnson et al., 2010). Here, migratory birds constituted 26 % - 41 % of detected birds on the coffee farm (Johnson et al., 2010). The corresponding ecosystem service of pest control provided freely to humanity by the birds was estimated to be worth 12 % of total crop value, which would need to be substituted by harmful pesticides (Johnson et al., 2010). Additionally, positive ecosystem properties can be expected to suffer from population declines in migratory birds. For instance, given the observed magnitude of predation in the example above, the birds in the coffee farm should have strong top-down effects on the prey insect communities, potentially altering competitive interactions therein (cf. Chase et al., 2002). From an ecosystem perspective, noted and predicted declines in migratory bird populations might thus decrease the stability and resilience of ecosystems (cf. Cardinale et al., 2012; Jiang and Pu, 2009; van der Plas, 2019).

Other migratory animals also serve such important wider ecological functions, which will be affected by their declining populations with far-reaching consequences. For instance, due to the huge decline of migratory salmon mentioned above, rivers in the American Northwest were estimated to receive only 6 % - 7 % of historic input of nitrogen and phosphorus from the sea (Gresh et al., 2000). These nutrients are typically spread by bears and other predators and scavengers of salmon from the rivers to the vicinity (Gende et al., 2007). There, they act as a fertilizer for plants (Hocking and Reynolds, 2011; Hurteau et al., 2016) and it was shown that these salmon-derived nutrient subsidies influence the abundance, species richness and community composition of plants which are present (Hocking and Reynolds, 2011; Hurteau et al., 2016). Accordingly, declining populations of migratory animals can be expected to significantly affect the ecosystems of their different habitats (Cardinale et al., 2012; Jiang and Pu, 2009; van der Plas, 2019; Wilcove and Wikelski, 2008).

Besides such ecosystem services, also ecosystem properties will be affected, when populations decline or go extinct since higher trophic levels in the food web depend on them. Some predators will switch prey when their favourite prey becomes less abundant (Chase et al., 2002), for example the modelled white stork which is an extremely opportunistic feeder (Kaatz et al., 2017). Though prey switching can act as a so-called stabilizing mechanism that maintains species coexistence (Chesson, 2000; Jeltsch et al., 2013), such mechanisms are not always sufficient to prevent biodiversity loss. For example, predators can still experience food scarcity when several focal prey species decline. Then, a chain of co-extinctions might be induced, in which predators decline or go extinct because their food sources have dwindled or disappeared (Strona and Bradshaw, 2018). Thus, because resource and consumer species are intertwined in complex hierarchical food webs, biodiversity loss might be amplified by co-extinction processes at higher trophic levels (Strona and Bradshaw, 2018).

5.4 Advancing the movement ecology framework

In the following, I will interpret my findings within the theoretical framework of movement ecology of Nathan et al. (2008), which has been introduced to facilitate a holistic understanding of movement processes and their consequences (cf. Section 1.3.2). I will highlight where my work fits into the framework but also make valuable suggestions on how it could be extended so that important findings of my research regarding global change impacts on migratory birds can be better captured by it (Figure 5-2). With these extensions, the framework would also work smoother across different time and entity scales.

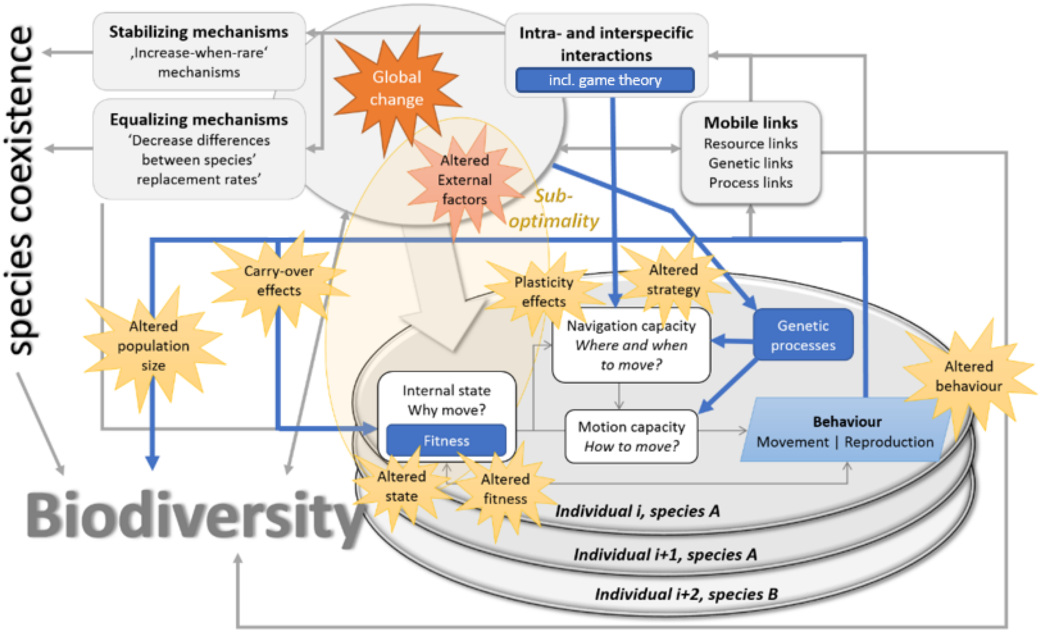

Figure 5-2: Suggested modifications (blue boxes and arrows) of the frameworks by Nathan et al. (2008) and Jeltsch et al. (2013) for studying movement ecology and its interplay with biodiversity, respectively. The modifications allow capturing the findings (yellow stars) of research presented in this thesis (Chapters 2,3,4) regarding global change (orange stars) impacts on migratory birds

Global change is equivalent to altering the external factors in the movement ecology framework. I abstracted global change to changes in food supply which can directly affect the internal state of an individual, leading to changes in the distribution of state variables within the population, e.g. in the level of energy reserves (Chapter 4). In view of my work, it makes sense to interpret death as a particular realization of the internal state. Death could be equivalent to zero or the minimum level of energy reserves, for example, as in my model. In this way, two major measures for the ecological fitness of an individual would be readily included in the movement ecology framework, namely energetic gains and survival. Additionally, it would provide an option to capture the loss of individuals within a population, which will become necessary when more wide-ranging consequences of movement on biodiversity shall be considered as it is possible with the extended framework by Jeltsch et al. (2013).

The immediate effects of global change on the motion or navigation capacity of an individual are not considered in my model though both can directly be affected by changes in the environment. For example, wind turbines that get installed to mitigate the impacts of climate change are frequently responsible for broken wings in raptors (Kirby et al., 2008) and night time light pollution leads to disorientation in birds among other animals (Gaston et al., 2013). Focusing on behavioural strategies under global change in my research, the navigation capacity nevertheless is the element of the movement ecology framework which connects most prominently to my work.

The navigation capacity encompasses the cognitive machinery enabling an individual to orient in time and space (Nathan et al., 2008) and is responsible for the optimal timing of breeding and migration in migratory birds. It thus includes the optimal behavioural strategy, which *sOAR* computed for the given environmental scenarios and which the model birds followed in the simulations. Even if an animal adheres to its traditional behavioural strategy, it might change its behaviour in the short-term under environmental change because the behavioural strategy can involve phenotypic plasticity. For example, when summer food supply decreases, birds could be in worse condition by autumn and thus migrate later than usual. Though phenotypic plasticity was low in my study (Section 3.4.2.3), it represents an important adaptive mechanism (Charmantier and Gienapp, 2014) that might not only invoke changes in observed movement patterns but, at least as importantly, in altered reproductive activities.

Successful reproduction produces additional individuals and thus naturally connects different entity and time scales. Additionally, long-term reproductive success represents the ultimate measure of fitness (Houston and McNamara, 1999; McNamara et al., 2001) and needs to be considered when mechanisms working at evolutionary time-scales shall be incorporated into the framework. I, therefore, recommend to substitute the 'movement path' in the movement ecology framework more generally by 'behaviour', which would then encompass both movement and reproduction activities that both feed back to the internal state of an individual.

Under global change, the optimality paradigm incorporated in the movement ecology framework would become invalid, at least for a transient period of time. In particular, the traditional timing of migration and reproduction in migratory birds will often be suboptimal with respect to maximizing long-term reproduction success under global change, as indicated by the results in Chapter 3. If migratory birds keep following the outdated behavioural strategy despite global change, their behaviour might not be the best possible response to the environment anymore and can lead to carry-over effects and notable declines at the population level (Chapter 3, 4). Though under favourable environmental changes, populations might also grow (Chapter 3, 4) until density-dependent mechanisms start to kick in.

The required long-term response to global change (Chapter 3) ensuring stable populations cannot be captured by the original movement ecology framework. Suboptimality between the environment, or external factors, and the internal state of the individual will provoke natural selection of better adapted individuals and thus the evolution of a new optimal behavioural strategy. My results showed that permanently altered food supply will not only have major short- but also such long-term consequences on migratory birds. In particular, birds should return earlier to the breeding grounds and start breeding earlier if they are able to adapt their behavioural strategy to the altered environment (Section 3.4.2), as it is also evidenced by earlier mean spring arrivals and earlier mean breeding dates in different bird populations (Lehikoinen et al., 2004; Rubolini et al., 2007; Usui et al., 2017).

To update the framework so that it works better over evolutionary time scales, it must include the individual-level genetic processes which cause individuals to vary in their navigation and motion capacity. These genetic processes would be another new element within the framework and act on both capacities, being able to create a new optimal behavioural strategy that again fulfils the optimality paradigm. The genetic processes could further be influenced by the external factors, e.g. when pollution increases mutation rates.

However, the new optimal behavioural strategy would still need to spread within a population. Here, it is appropriate to switch from the movement ecology framework to the framework of Jeltsch et al. (2013), which links movement ecology and biodiversity research. The latter explicitly incorporates intra- and interspecific actions that arise from the (movement) behaviour of individuals and, via various mechanisms, influence biodiversity including the focal individual. If evolutionary game dynamics (Maynard Smith, 1993) were to be integrated into the interactions in the framework at the population level, there would emerge a direct link from these interactions to the navigation and motion capacity of an individual because the individual’s capacity is strongly determined by the outcome of the evolutionary dynamic game. Generally, interactions between animals with different behavioural strategies can mathematically be treated as a dynamic game with multiple players (Maynard Smith, 1993). Then, the fitness consequences of a behavioural action depend on which behavioural strategy is pursued by other individuals involved in the game besides the focal player’s ones (Houston and McNamara, 1999; Maynard Smith, 1993). This can lead to evolutionary stable strategies of behaviour over evolutionary timescales (Hines, 1987; Houston and McNamara, 1999; Maynard Smith, 1993).

The framework by Jeltsch et al. (2013) also provides for the integration of social learning, which represents an important but overlooked mechanism for adapting to global change (Section 3.5). Social learning represents an alternative way to develop a new optimal behavioural strategy, apart from evolutionary adaptation. Working over ecological time scales, it could be involved in many rapid behavioural adaptations to global change, especially in long-lived and social animals like the studied stork and falcon bird functional types. In the framework by Jeltsch et al. (2013), social learning could be included in the element of intra- and interspecific interactions and link to the navigation capacity.

To conclude, building on the valuable theoretical frameworks of Nathan et al. (2008) and Jeltsch et al. (2013), my work highlighted significant advances which will improve their coherence across temporal and entity scales and expand their scope of application. Uncovering important adaptive response mechanisms and integrating them explicitly into the frameworks, I further improved their suitability for research questions within the context of global change.

5.5 Developing a new indicator of vulnerability to global change

The approach and findings presented in this thesis should not only be evaluated from the viewpoint of theoretical ecology but also be assessed with respect to their conservation value. In the following, I want to outline how OAR modelling could principally be used for conserving migratory birds under global change and in particular for determining the vulnerability of different migratory bird populations. Though extending *sOAR* might present one option in that direction, the presented considerations will also apply to alternative, appropriate mechanistic models.

Complementing traditional extinction risk assessments such as climate envelope modelling (Thuiller et al., 2005; Zurell et al., 2018), OAR modelling could be used for developing a mechanistic indicator of vulnerability to global change. This could happen within a hierarchic process that starts analysing the extinction threat at ecological time scales and broadens to include an evolutionary perspective. In the next paragraph, I outline potential steps of this hierarchic process. Generally, it should be reverted to bird functional types in order to cover a broad range of species.

In a first step and using OAR modelling, the historic behavioural strategy needs to be determined for model populations of various bird functional types. Following the approach in Chapter 3, model populations employing the computed optimal behavioural strategy should then be subjected to environmental change. This experiment provides the expected response at ecological time scales, assuming no adaptive mechanisms are at work. If populations are predicted to decline, the old behavioural strategy can be regarded as suboptimal and the population at risk of extinction. The magnitude of decline (cf. Chapter 3) and an analysis of arising carryover effects (cf. Chapter 4) provide a first proxy for how urgent conservation measures are. Thus, the approach helps to identify the most vulnerable functional types and to prioritise conservation measures accordingly.

In a second step, the new optimal behavioural strategy for the altered environment needs to be computed (cf. Chapter 3). If the difference between the old and the new optimal strategy is large, adaptation pressure likely is strong. This procedure further points out whether and to what degree the focal population might be able to adapt, at all. For example, no new optimal solution might be found within the given constraints, indicating that the focal population cannot survive in the expected new environment if major functions underlying biological processes such as metabolic functions do not change. Though it must be acknowledged that behavioural responses could be developed, too, this step provides critical additional information for conservation.

In a third step, phenotypic plasticity should be assessed because it may buffer simulated global change impacts and thus buy time for evolutionary adaptation. In particular, it needs to be determined, how much phenotypic plasticity is included in the outdated behavioural strategy and whether it acts towards the same direction as the new environment requires (cf. Chapter 3). The indicator proposed in Chapter 3 represents a first exemplary method for this purpose. Highly plastic strategies acting towards the optimal response might reduce the urgency of conservation measures, while the opposite might be true for rigid strategies or maladaptive plastic responses in behavioural timing. However, higher selective pressure in the latter case could also speed up evolutionary responses.

A reasonable fourth step is to analyse which factors determine a population's grade of plasticity (cf. Chapter 3). Some factors like migratory or brood care costs could be manipulated by conservation measures such as food provisioning, while others like metabolic constraints might only be tackled by microevolution.

Finally, the results should be complemented by an assessment of other factors that partly predict the vulnerability of a species to global change based on statistical analyses of field data. For example, body mass, phylogeny, migratory distance and the general timing of migration were found to correlate with changes in phenology (Usui et al., 2017). My work (Chapter 3) further suggests that flight mode could be such a predictive factor since the modelled bird functional types, employing either active or passive flight, differed notably in their response to altered food supply. I also came to the conclusion that social learning likely plays a larger role in adaptive responses of social or long-lived birds than previously acknowledged (Chapter 3) and might provide additional useful hints regarding species vulnerability.

Generally, migratory birds are threatened by multiple independent environmental factors under global change that act accumulatively (Zurell et al., 2018). My thesis reveals that there exist additional risks stemming from behavioural constraints and evolutionary limitations, which have not been included in vulnerability assessments. Hence, a major step forward in predicting the vulnerability of migratory bird populations will be to create a composite indicator of vulnerability for migratory birds, which integrates the results of highly developed statistical methods with the outcomes of advanced mechanistic modelling methods. This goal requires defining the scope of assessment, specifying relevant functional groups and identifying suitable model species for which there is enough data and process knowledge to parametrize the complex mechanistic models.

5.6 Quo vadis?

Achieving a complete understanding of the global change impacts on migratory bird populations and predicting their responses remains an open challenge. As was demonstrated throughout this thesis, optimal annual routine modelling represents a promising research avenue to approach this goal. With the first open-source OAR model *sOAR* that I presented in Chapter 2, there now exists an excellent basis to employ OAR modelling more frequently for research questions related to global change impacts and to refine the method. Here, I wish to outline meaningful next steps of research based on my work:

1. **Supplement model validation and further explore potential limitations** of *sOAR* and the OAR approach. In particular, perform a global sensitivity analysis of the complete parameter space of the model. Though this will require time and extensive computations, it would be very useful to thoroughly understand the model's sensitivity to each parameter and its constraints. So far, I have performed local sensitivity analyses around most parameters including e.g. food supply, metabolic costs, mortality. Additionally, where possible, model predictions regarding the timing of migration can be compared with increasingly available tracking and ringing data in more detail.
2. **Improve parameter estimations, particularly for uncertain or sensitive parameters and functions**. For example, overwintering food availability can have severe effects on the dynamics of migratory bird population (Chapter 3), which may carry over and affect fitness in subsequent seasons (Chapter 4). At the same time, assumptions of winter food supply are often highly uncertain due to a lack of data, especially for Eurasian long-distance migrants overwintering in Sub-Saharan Africa. To improve these estimates, we need to get a better understanding of the food availability in such remote regions of the world, e.g. by blending land use, NDVI and climate data from intensified data collection

efforts. Additionally, the birds' overwintering locations and movements need to be evaluated. Nomadic movements following available food sources are quite wide-spread in the overwintering habitats (Andersson, 1980; Dean, 2004; Runge et al., 2015), for instance. Chapter 4 suggests that the African overwintering food supply might be more unpredictable than assumed in the model. Generally, a better understanding of the overwintering conditions will also help tackle other important ecological questions such as whether the summer and winter niches of migratory birds overlap (Thorup et al., 2017).

3. **Reach a better understanding of differential behavioural patterns and the evolutionary shaped life-history of birds** by analysing modelled results from additional perspectives. For example, investigate how juveniles and adults differ in their behavioural timing, foraging and mortality patterns or how the reproductive value changes over time. Tentative analyses I have performed (not shown here) in this direction showed that departing a week before the adults represents an optimal response to the environment for juvenile white storks. It would be worthwhile to investigate which patterns of differential migration timing arise under which biological constraints and environmental conditions, especially as differential timing of behaviour also occurs in other species (Kjellén, 1992; Mueller et al., 2000). For this purpose, I recommend to make flight costs experience-dependent since juvenile white storks have been shown to spend more energy during their first migration than more experienced birds (Rotics et al., 2016). Importantly, the assumed share of employed active and passive flight must reflect the biology and typically experienced wind conditions of the focal population (cf. stork functional type in Chapter 3).
4. **Examine flight mode and sociality as additional predictors of a species' response and vulnerability to global change** (as suggested in Chapter 3). For a start, these parameters could be included as explanatory variables in existing statistical approaches for separating out the major determinants of a species vulnerability, such as the mixed effects meta-analytic approach by Usui et al. (2017). In the case of flight mode, the required data could be extracted from existing literature and databases or be derived from other morphological parameters such as wing shape (Blaum et al., 2011). The sociality factor will likely be more difficult to grasp and define since comparative studies on the social behaviour of migratory birds and its effects are still rare, except for research on flocking behaviour and flight formations (Flack et al., 2018). Apart from

that, it will be challenging to disentangle the social learning capabilities of a population from its social behaviour. For example, many short-lived song-birds are threatened and highly social but their social learning capabilities might be restricted compared to longer-lived species. In any case, it should be noted that both sociality and flight mode would be better represented by gradients rather than binary parameters.

5. **Seek to explain the evolution of different migration strategies for active and passive fliers**, performing additional computations with *sOAR*. To this end, evaluate how increasing flight costs affect emerging behavioural patterns. A nuanced but potentially important consideration is that in reality different flight costs are likely to be coupled to different metabolic and predation costs, e.g. larger birds experiencing higher energetic costs during active flight also have a different metabolism and predation risk than smaller birds. Additionally, rich databases for different bird species will be required for such a study.
6. **Assess the ecological role of reduced migration distances in the few observed population increases of migratory bird populations** including Western white storks. Here, *sOAR* could be adapted so that it is able to work with multiple stopover locations that are characterized by individual food supply and wind conditions. This would require a higher discretization of the location variable and implementing assumed connectivity between the individual locations (cf. Bauer et al., 2008).
7. **Study seasonal interactions including carry-over effects at the individual level**, extending *sOAR* by an individual-level Monte-Carlo simulation. In this case, the breeding process should be modelled in more detail, in order to analyse seasonal interactions and carry-over effects arising from a single event across multiple breeding seasons. Then, it would also be possible to simulate the complete life-history of an individual, including potential long-term effects of early life experiences. Such long-term studies are challenging to perform experimentally, especially in migratory birds with their distant breeding and overwintering ranges. Apart from that, there is scientific evidence that breeding events influence migratory behaviour (Low et al., 2015), that overwintering conditions carry over to affect later survival and breeding success (Chapter 4, Norris, 2005; Norris et al., 2004), and that carry-over effects arising from overwintering conditions vary with age and sex (López-Calderón et al., 2017).

8. **Improve the accuracy of the predicted annual routines** by extending *sOAR* to include explicit density dependence in the food availability as outlined in Section 5.1 and done by Barta et al. (2006) and Barta et al. (2008). Then, in an iterative process, the size of a population following a certain behavioural strategy in the given environment would be computed, its effect on food supply via density dependence determined, in turn influencing the optimal behavioural strategy. Ideally, these computations would converge and the resulting behavioural strategy would represent an evolutionary stable strategy (ESS) within life-history theory (Barta et al., 2006; Houston and McNamara, 1999).
9. **Model and analyse the larger ecological consequences of predicted population declines and altered behavioural timing** in migratory birds at the community-level. Given that migratory birds perform various ecosystem functions (Şekercioğlu, 2006; Şekercioğlu et al., 2004) and often represent a substantial share of the local avifauna (Somveille et al., 2013), such changes in their ecology can be expected to have notable effects on the whole ecosystem (cf. Chapter 1, Bauer and Hoye, 2014; Jeltsch et al., 2013). A suitable approach to tackle community-level effects induced by population-level changes in migratory behaviour might be network modelling. As of 2019, not only do there exist robust methods to analyse food webs and social networks, but scientists are also developing an increasing number of tools to assess the movement network of an individual as well as the interplay of movement and social networks (Jacoby and Freeman, 2016). Developing spatially explicit, individual based models (IBMs) (Railsback and Grimm, 2012) could also be ideal for simulating species interactions under decreasing population sizes or different behavioural strategies of migratory birds. Of course, sufficient biological data and ecological process knowledge would be required to parametrize such multi-species models. A promising IBM that spans multiple hierarchical levels from individual processes to consequences at the community level has been presented by Teckentrup et al. (2018) and works based on different body mass distributions.
10. **Verify life-history theory and the OAR approach for global change research**, e.g. by combining OAR modelling and experiments on micro-organisms or other suitable small animals with short generation cycles. This allows testing for which circumstances various optimality paradigms such as optimal foraging theory still hold. Moreover, the interplay between environmental changes, the inner state of an individual and behaviour can be explored under controlled

conditions and across temporal scales, ranging from instantaneous responses over the life-cycle of the individual to multiple generation times. In larger animals, the inner state can be tracked by utilising sensors tracking heart rates, motion, brain activity, body temperature etc. (Wilson et al., 2015). Since any sensor and device attached to or implanted in an animal can seriously impair its ecological fitness, it should be carefully assessed though whether the particular experiment is justified (McMahon et al., 2011).

5.7 Conclusion

Ongoing global biodiversity loss due to global change is exemplified by observed population declines in many migratory bird species. Recently noted changes in their behavioural timing have further been ascribed to anthropogenic climate change. Though individual populations vary in their response to global change, this variation including the underlying ecological mechanisms are not fully understood (Usui et al., 2017). It further remains unproven whether observed responses are actually adaptive in the long-term (Knudsen et al., 2011). Both aspects represent prerequisites for identifying vulnerable migratory bird populations and for designing effective conservation measures. Still, existing models for anticipating global change impacts on migratory birds are typically statistical models (e.g. Zurell et al., 2018), which limits their applicability to novel environmental conditions as they are developing under global change. Moreover, it is often neglected (Jentsch et al., 2007) that global change features two temporal characteristics, namely gradual versus punctuated changes, though these likely differ in their impact on natural populations.

In this thesis, I filled these gaps by developing an open-source software (*sOAR*) to determine the optimal behavioural strategy for animal populations in a given environment and to simulate the emerging behaviour and dynamics when the population is following the computed behavioural strategy. The software is a modular and extended implementation of the optimal annual routine framework by Houston and McNamara (Houston and McNamara, 1999) and is based on first principles, allowing to reach a process-based understanding of global change impacts on migratory birds. I applied an adapted version of the software to investigate how changes in food supply as they can be expected under global change will influence the population dynamics and behavioural timing of a migratory stork and falcon bird type in the short- and long-term. My findings theoretically underpin that advancing spring migration and breeding phenology is a required response under global change for keeping population sizes stable. They further highlight that severe population declines of migratory birds are to be expected in the near future, especially when environmental conditions in both the breeding and overwintering habitat change. Unfortunately, according to my results, long-distance migratory birds will face various constraints in adapting to environmental change, including major time-constraints. Further, unpredictable punctuated changes in the overwintering habitat, such as intensifying droughts, can lead to notable carry-over effects that have the potential to affect population dynamics across seasons and generations. Here, *sOAR* and OAR modelling in general proved to be a valuable tool for examining fine-scale temporal effects that would be challenging to tackle experimentally. Considering the temporal dimension at higher resolution suggested that there is a threshold at which the negative effects of short but intense food shortenings will surpass those of enduring milder food shortening. Furthermore, targeted conservation measures during the pre- and post-migratory phase, in which modelled birds were particularly vulnerable, might have overproportionately positive effects on the individual. Importantly, my research indicates that additional predictors of vulnerability such as flight mode and important mechanisms of adaptation such as social learning have been overlooked.

Overall, my results advance a mechanistic understanding of the impacts of global change on migratory birds across temporal scales. They further allow to refine predictive models for anticipating the responses of migratory birds to global change. In particular, they provide valuable insights and techniques for developing a new indicator of vulnerability that also accounts for the inherent constraints and trade-offs migratory birds face in adapting to global change. Finally, theoretical ecology could be advanced through my work, updating the excellent movement ecology framework (Nathan et al., 2008) and framework to integrate movement ecology and biodiversity research (Jeltsch et al., 2013). Now, empirical studies need to be designed that test and validate the model predictions and analyse their larger consequences for biodiversity.

6 Supporting information

6.1 Appendix to Chapter 2

6.1.1 Overview of stage and state variables in sOAR

Table S 6.1-1: Overview of stage and state variables in sOAR, including a characterization of variables and their allowed range of values. The grid of each discretized variable is equally spaced. For energy reserves and health condition non-integer values are possible.

Variable	**Characterization**	**Range of values**
Time, t	Stage variable/decision epoch: at each stage of time a behavioural decision must be made.	$t \in \{0,1, \dots t_{max}\}$
Energy reserves, x	State variable: level of energy reserves within defined range.	$x \in \{x_{min}, \dots, x_{max}\}$ with $0 \leq x_{min} < x_{max}$ and $x_i - x_{i-1} = const.$
Health condition, y	Optional state variable: state of the immune system.	$y \in \{y_{min}, \dots, y_{max}\}$ with $0 \leq y_{min} < y_{max}$ and $y_i - y_{i-1} = const.$
Age of offspring, a	State variable: existence and age of dependent offspring. A value of -1 indicates no offspring, a value of 0 newly born offspring and values >0 the age of dependent offspring in number of decision epochs. Offspring becomes independent at a_{max}.	$a \in \{-1,0,1, \dots, a_{max}\}$
Experience, e	State variable: foraging experience of individuals, e.g. newly independent young might be less efficient at finding resources.	$e \in \{0,1, \dots, e_{max}\}$
Location, o	State variable: location of the animal. When migration is enabled, o can take one of two values representing the two locations between which the animal can migrate.	$o = 1$ or $o \in \{1,2\}$
Migratory state, s	Optional state variable: indicating if and how long the animal has been migrating; the total duration of migration (in number of decision epochs) is user-defined.	$s = -1$ or $s \in \{-1, 0, \dots, s_{max}\}$

6.1.2 Parameter settings in illustrative example on optimal migration timing

Table S 6.1-2: Model parameters and their corresponding values or formulas as used in the example illustrating how the optimal timing of spring and autumn migration may vary with environmental food availability at a site. Where three values are given, these refer to the three simulated environmental scenarios. Extra costs of reproductive or migratory activities add to the cost of subsistence (details in the sOAR User Manual).

Parameter	Symbol	Value / Formula
State and stage variables:		
Range of energy reserves	x	$\in [0, 10], \in \mathbb{N}$
Range of health condition	y	$\in [0, 10], \in \mathbb{N}$
Range of experience	e	$\in [0, 2], \in \mathbb{N}$
Age of any offspring	a	$\in \left[-1, a_{incub} + a_{indep} + 2\right], \in \mathbb{Z}$
Location	o	$\in [1, n_{loc}], \in \mathbb{N}$
State of migration	s	$\in \left[-1, s_{migr} - 1\right], \in \mathbb{Z}$
Week of year	t	$\in [0, 51], \in \mathbb{N}$
General biology:		
Background mortality by disease	M_{bg}	0.0016
Basic metabolic cost	c_b	2.0
Foraging intensity	u	$\in [0, 1]$
Energetic cost of subsistence	$c_{subsist}$	$c_b(1 + 0.01(x/10)^2) + 6u^2(1 + 0.01(x/10)^2)$
Health cost of subsistence	$h_{subsist}$	$1 - 0.2c_{subsist} - 0.01{c_{subsist}}^2$
Environment:		
Number of locations	n_{loc}	2
Average food availability at site 1	$A_{food}(1)$	1.0
Average food availability at site 2	$A_{food}(2)$	1.0
Degree of seasonality of food at site 1	$\varepsilon(1)$	$0.1, 0.2, 0.3$
Degree of seasonality of food at site 2	$\varepsilon(2)$	0.7
Predation risk at location 1 and 2	M_{loc1}, M_{loc2}	$0.01u^2(1 + 0.01(x/10)^2)$
Probability of active flight	p_{act}	1.0
Reproduction:		
Duration of incubation in weeks	$a_{incub} = a_{max} - a_{indep} - 2$	4
Age of independence in weeks	$a_{indep} = a_{max} - a_{incub} - 2$	6

Energetic cost of starting a brood	c_{start}	0.5
Energetic cost of incubation	c_{incub}	1.5
Energetic cost of brood care	c_{care}	7.0
Health cost of starting a brood	h_{start}	1.0
Number of offspring	n_{brood}	2
Fitness of offspring at independence	f_{indep}	0.5
Computed equilibrium value for foraging efficiency of inexperienced bird ($e = 0$)	θ	$0.7165, 0.7581, 0.8123$
Probability of increasing experience	p_{exp}	0.02
Migration:		
Duration of migration in weeks	$s_{migr} = s_{max} + 1$	3
Energetic cost of active flight	c_{act}	2.0
Reserves change during migration	Dx_{migr}	$p_{act}c_{act}(1 + 0.001x^2)$
Health cost of active flight	h_{act}	1.0
Health change during migration	Dy_{migr}	$p_{act}h_{act}$
Predation risk during migration	M_{migr}	$0.01(1 + 0.01(x/10)^2)$

6.1.3 Parameter settings in illustrative example on optimal number of brood cycles

Table S 6.1-3: Model parameters and their corresponding values or formulas as used in the example illustrating how the optimal number of brood cycles may vary with environmental food availability. Where three values are given, these refer to the three simulated environmental scenarios. Extra costs of reproductive activities add to the cost of subsistence (details in the sOAR User Manual).

Parameter	Symbol	Value / Formula
State and stage variables:		
Range of energy reserves	$\boldsymbol{x}$	$\in [\mathbf{0}, \mathbf{10}], \in \mathbb{N}$
Range of health condition	$\boldsymbol{y}$	$\in [\mathbf{0}, \mathbf{10}], \in \mathbb{N}$
Range of experience	$\boldsymbol{e}$	$\in [\mathbf{0}, \mathbf{2}], \in \mathbb{N}$
Age of any offspring	$\boldsymbol{a}$	$\in [-\mathbf{1}, \boldsymbol{a_{incub}} + \boldsymbol{a_{indep}} + \mathbf{2}], \in \mathbb{Z}$
Location	$\boldsymbol{o}$	$\in [\mathbf{1}, \boldsymbol{n_{loc}}], \in \mathbb{N}$
State of migration	$\boldsymbol{s}$	$\in [-\mathbf{1}, -\mathbf{1}], \in \mathbb{Z}$
Week of year	$\boldsymbol{t}$	$\in [\mathbf{0}, \mathbf{51}], \in \mathbb{N}$
General biology:		
Basic metabolic cost	$\boldsymbol{c_b}$	$\mathbf{1.87}$
Foraging intensity	$\boldsymbol{u}$	$\in [\mathbf{0}, \mathbf{1}]$
Energetic cost of subsistence	$\boldsymbol{c_{subsist}}$	$\boldsymbol{c_b} + (\mathbf{2}\boldsymbol{u} + \mathbf{3}\boldsymbol{u}^2)$
Environment:		
Number of locations	$\boldsymbol{n_{loc}}$	$\mathbf{1}$
Average food availability	$\boldsymbol{A_{food}}(\mathbf{1})$	$\mathbf{1.1}$
Degree of seasonality of food	$\boldsymbol{\varepsilon}(\mathbf{1})$	$\mathbf{0.2}$
Predation risk at location	$\boldsymbol{M_{loc1}}$	$\mathbf{0.0019} + \mathbf{0.004}\boldsymbol{u}^2$
Reproduction:		
Duration of incubation in weeks	$\boldsymbol{a_{incub}} = \boldsymbol{a_{max}} - \boldsymbol{a_{indep}} - \mathbf{2}$	$\mathbf{2}$
Age of independence in weeks	$\boldsymbol{a_{indep}} = \boldsymbol{a_{max}} - \boldsymbol{a_{incub}} - \mathbf{2}$	$\mathbf{3}, \mathbf{4}, \mathbf{5}$
Energetic cost of starting a brood	$\boldsymbol{c_{start}}$	$\mathbf{0.5}$
Energetic cost of incubation	$\boldsymbol{c_{incub}}$	$\mathbf{2.3}$
Energetic cost of brood care	$\boldsymbol{c_{care}}$	$\mathbf{4.6}$
Number of offspring	$\boldsymbol{n_{brood}}$	$\mathbf{1}$
Fitness of offspring at independence	$\boldsymbol{f_{indep}}$	$\mathbf{0.5}$
Computed equilibrium value for foraging efficiency of inexperienced bird ($\boldsymbol{e} = \mathbf{0}$)	$\boldsymbol{\theta}$	$\mathbf{0.4998}, \mathbf{0.5133}, \mathbf{0.5260}$
Probability of increasing experience	$\boldsymbol{p_{exp}}$	$\mathbf{0.04}$

6.1.4 Environmental food availability

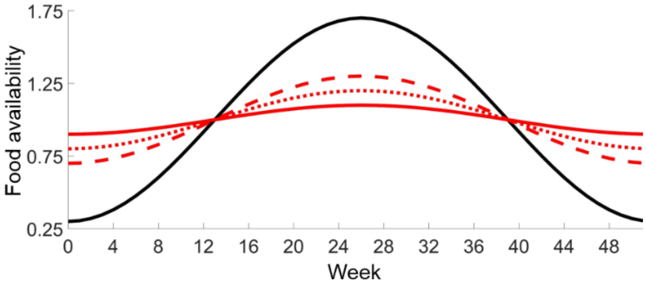

Figure S 6.1-1: Environmental food availability in the breeding (black) and wintering (red) habitat varying sinusoidal over the year. Average yearly food supply in both locations is the same but the degree of seasonality in the wintering habitat varies from low (solid, high tropics) to high (dashed, subtropics). Please note that the actual energetic gain of an animal further depends on foraging intensity and experience and is scaled according to the maximum possible energy level.

6.2 Appendix to Chapter 3

6.2.1 Derivation of parameter values

Parameter values for the stork functional type (T1) were derived from available literature on the white stork species, while the falcon functional type (T2) is based on literature on several small falcon species like red-footed falcon, lesser kestrel and Eurasian hobby. Though the values were determined carefully, we would like to note that parameter settings might be uncertain due to missing, inconsistent, uncertain or large variation in the underlying data, as it often is the case with biological data.

To set the energetic cost values, we converted all corresponding literature values to [kJ/week] and then translated them into model units using a bird-specific conversion factor. This factor was obtained by multiplying the range of individual reserves in the model species with the energetic value of fat, which is 37.4 kJ/g (Food and Agriculture Organization of the United Nations (FAO) 2003), and then dividing the result by the range of ten model units.

6.2.1.1 STORK FUNCTIONAL TYPE

General – The range of individual reserves for the stork functional type was computed using data by Mata et al. (2001), where the mean body mass of experimental white storks was 3322 g just before fasting and lean body mass was 2418 g. The associated range of reserves of 904 g multiplied with the outlined caloric value divided by ten model units results in a caloric worth of one model unit of ≈3381 kJ. We computed the basal metabolic cost c_b for an average experimental stork by taking the mean value from three approaches: the basal metabolic rate for birds as given by Bezzel and Prinzinger (1990) and by Aschoff and Pohl (1970), assuming

16 hours of activity and 8 hours of rest since storks are day active, and the basal metabolic rate for homeotherms as given by Peters (1983). The resulting weekly cost of ≈ 5733 kJ for basal metabolism (BMR) divided by the conversion factor of 3381 kJ amount to $c_b = 1.7$ model units. Activity increases metabolic costs (Glazier, 2008; Hammond and Diamond, 1997) and modelled metabolic expenditure under maximal sustained activity ($u = 1$) is the BMR plus six model units, scaled by reserve-dependent factor. Accordingly, maximal sustained energy expenditure is about 3.5 x BMR, or approximately three times the existence metabolic rate, and thus within the observed range for birds (Hammond and Diamond, 1997). Health costs $h_{subsist}$ increase with metabolic expenditure and, in the model, health levels fall from highest to lowest levels within about two months under maximum metabolic expenditure. Under minimum activity, it takes about four month to recover from lowest to highest health levels.

Mortality – The background mortality M_{bg} due to disease is set such that an individual in top shape throughout its life will die of disease after 35 years in the model. It thus reflects the maximum lifespan of white storks (Kaatz et al., 2017). The predation parameter includes collisions with man-made structures and human hunting. In the northern breeding habitat death cases are rare and mainly caused by collisions and electrocution (Haas et al., 2003; Hancock et al., 1992; Kaatz, 2004). In the African overwintering areas, white storks are also hunted and there are no laws for bird-friendly power line constructions. Accordingly, we assume that the predation risk M_{bgpred} in the overwintering location is twice as high as in the breeding location. The exact values are reasoned from modelled mortality and assessed causes of death (Barbraud et al., 1999; Haas et al., 2003; Kaatz, 2004; Ryslavy, 2011; Schaub et al., 2004). Predation risk further slightly increases with reserves (cf. Lima 1986; Gosler et al. 1995).

Reproduction – Energetic cost c_{start} of starting a brood are the converted mean value of known energy requirements of birds for producing eggs (Carey, 1996), i.e. basal metabolic costs multiplied by 0.9. Based on Monaghan and Nager (1997), modelled incubation costs c_{incub} equal one quarter of the existence metabolism, which is 1225 kJ/d for white storks in their breeding habitat (Profus, 1986). The field metabolic rate c_{fmr} of ground-foraging birds with nestlings can be estimated by $c_{fmr} = 7.76\, {m_{gram}}^{0.75}$ with m_{gram} being the bird's mass in gram (Nagy et al., 1999). The body mass of white storks can range from 2300 to $4400\ g$, theoretically resulting in field metabolic rates of $2577 - 4192\ kJ\ d^{-1}$ for parental white storks, and thus weekly costs for brood care of $3.6 - 7.0$ model units (excluding basal metabolic costs). However, mean body mass of adult white storks in different studies (Mata et al., 2001; Nir et al., 2014; Rotics et al., 2016) rather approximated $3.5\ kg$ (≈5.7 model units) and McNamara et al. (1998) worked with brood care costs of six model units within the same range of energy reserves. We thus assume energetic costs of brood care to be $c_{care} = 6$. The incubation period of white storks ranges from 24 to 34 days for a clutch (Kaatz et al., 2017), whereby incubation of the individual egg was 31-32 days in captivity (Bauer et al., 1987), so that an incubation period of four weeks is assumed in the model. Since nestlings fledge approximately 54 – 68 days after hatching (Creutz, 1985), the period of brood care (a_{indep}) is set to nine weeks in the model. The average clutch size of three to five eggs (Creutz, 1985) results in two offspring per successfully breeding parent, i.e. $n_{brood} = 2$. Clutch sizes of four eggs are also the ones most commonly observed (Profus, 1986). Experience of young grows with probability $p_{exp} = 0.01$ by one unit per week so that full experience is reached by the age of 3.8 years, on average, which corresponds to the age of 3–5 years at which white storks successfully start reproduction and are considered to be fully matured (Hancock et al., 1992). Health costs h_{start} of initiating a brood and the fitness f_{indep} of offspring at independence are oriented at McNamara et al. (McNamara et al., 1998) due to lack of data. However, it has been shown that reproductive effort impairs the immune system of breeding birds (Deerenberg et al., 1997; Lochmiller and Deerenberg, 2000; Norris and Evans, 2000).

Migration – Migration is assumed to take $s_{migr} = 3$ weeks in the model based on studies by Berthold et al. (Berthold et al., 2001) and Kaatz (2004). Modelled background predation M_{bgmigr} during migration is twice as high as in the northern breeding location due to increased electrocution and hunting risk en route (Haas et al., 2003; Hancock et al., 1992; Kaatz, 2004). In the employed OAR framework (Houston and McNamara, 1999; Schaefer et al., 2018) migratory energy and health costs are implemented as weekly constants, integrating any costs and gains during migration including stopovers. Thus, they can only be a rough estimate of the real costs, for which the data situation is scarce, too. We estimated the energetic cost of migration using passive flight as follows. First, we computed the energetic cost of soaring/gliding, resting, preening and foraging during migration. Hereby, the respective time share of each activity was extracted from Rotics et al. (2016) and multiplied by its assumed energetic cost in kJ before converting the result to weekly applying model units. Mean flight costs on a migration day were determined for a reference soaring and gliding white stork with morphometric parameters as in Eder et al. (2015) flying in air with density $\rho = 1.15$ km/m³, using the software *Flight 1.24* (Pennycuick, 2011). In particular, we assumed 8.2 h of flight per day for a reference stork of 3.53 kg with wing span 1.98 m and wing area 0.55 m², so that flight consumes 680.4 kJ/h. On-ground time is 15.8 h/d of which 56 % were assumed to be spent on resting at basal metabolic rate, 19 % on preening with existence metabolic rate (Profus, 1986) and 25 % on foraging with field metabolic rate. For the latter, we used the mean of the field metabolic rate for temperate meadow birds ($FMR = 18.7 * {m_{gram}}^{0.548}$) and for omnivore birds ($FMR = 9.36 * {m_{gram}}^{0.628}$) as given by Nagy et al. (1999) for the reference bird. This results in a daily energy expenditure for these activities of approximately 5583 kJ/d for flying, 300 kJ/d for resting, 153 kJ/d for preening and 270 kJ/d for foraging, summing up to a total energy expenditure of 6306 kJ/d on migratory days. Energy intake during migratory days is the product of foraging time and the maximum energy intake rate of 1330 kJ/h (Johst et al., 2001), resulting in 5350 kJ/d of energy uptake. The assumed time budget during stopover days differs since we assume only one hour of foraging flight based on the average movement of 44 km/d on stopover days found by Flack et al. (Flack et al., 2016) and an approximate gliding velocity of 0.75 km/min during foraging flights (Johst et al., 2001). The remaining time is spent on resting and preening as on migratory days, while the remaining time is used for foraging. However, not all individuals stopover during migration or spent a complete day at stopover sites (Kaatz, 2004; Rotics et al., 2016). Therefore, in the model, the weekly energetic cost of migration is the summed energetic cost of six migratory days plus one day for which the costs equal the weighted average of 30 % energetic gains during stopover and 70 % energetic losses during flight days. Then, the weekly energetic cost c_{pas} of migrating in passive flight mode is $6 * 956 + (0.3 * (-12014) + 0.7 * 956)$ kJ/wk, or 0.8 model units, respectively. According to flight theory, active flight is energetically more expensive than passive flight, especially for larger birds (Duriez et al., 2014; Hedenström, 1993; Pennycuick, 1972). Therefore, we here assume the energetic costs c_{act} of active flight to be five times the cost of passive flight, so that $c_{act} = 4$. In reality, these costs might even be higher (Pennycuick 1972). Still, with a migratory period of three weeks and a maximum level of energy reserves of 10 units, performing the complete migration in active flight will be not feasible in the model. For health costs, we also assume a ratio of 5:1 for those costs arising from active flight versus those from passive flight. Hereby, health costs of active flight for the white stork are assumed to be double as high as for the smaller falcon. Following Houston and McNamara (McNamara et al., 1998), energetic losses during migration are further scaled by a mass-dependent factor to account for the negative aerodynamic effect of heavier fuel burdens (Alerstam, 1991).

6.2.1.2 FALCON FUNCTIONAL TYPE

We consider a composite of the following falcon species: *Lesser kestrel* (*Falco naumanni*), *Red-footed falcon* (*Falco vespertinus*), *Merlin* (*Falco columbarius*), *Eurasian kestrel* (*Falco tinnunculus*) and *Eurasian hobby* (*Falco Subbuteo*). If not indicated otherwise, all biological information is taken from the respective species descriptions in Mebs and Schmidt (2014), including the average body mass of females that is used to compute many dependent parameters such as metabolic rates or the factor to convert caloric units to model units.

General – To compute the range of reserves, we assumed that energetic reserves of an average female can decrease or increase by 25 %. This results in a mean range of 99 g of fat reserves for the composite of the considered falcon species. In the model, the range of reserves is 10 model units. Assuming a caloric value of 37.4 kJ/g_{fat}, one model unit is thus worth 371 kJ for the modelled falcon functional type. To determine the costs of basal metabolism c_b, we compute the mean basal metabolic rate using the approaches by Aschoff and Pohl for nonpasserines (Aschoff and Pohl, 1970), for birds by Bezzel and Prinzinger (Bezzel and Prinzinger, 1990) and for homeotherms by (Peters, 1983), again. Then, we convert the resulting value of 112 kJ/d to model units, which apply per week. This results in approximate costs of $c_b = 2$ model units for basal metabolism in the falcon functional type. Maximum activity increases metabolic costs by 6 model units, which is again in the known range for birds and corresponds to 3 x BMR. Taking the same value as for the stork type eases model comparison and might make sense since falcons are less inert from their morphology than white storks. Similarly, we keep the relationship between health costs and metabolic expenditure that was outlined above.

Mortality – Except for the much longer-lived Eurasian kestrel, which has a maximum age of 21 years, the maximum lifespan of ringed individuals of the considered species lies between 9 and 15 years. Accordingly, we here set the background mortality M_{bg} due to disease such that on average, an individual in top shape throughout its life will die after 12 years. The background predation M_{bgpred} is set somewhat intuitively. Small falcons not only experience similar threats as the white stork, e.g. illegal hunting, traffic incidents, electrocution and collisions with man-made structures (Bauer et al., 2012). But they also seem to be more vulnerable to these and additionally have natural enemies, e.g. they are predated by larger raptors such as the Northern Goshawk and face stronger direct competition with other raptors (Bauer et al., 2012). Accordingly, we assume predation risk to be significantly higher for the falcon than the stork functional type and set $M_{bgpred} = 0.01$.

Reproduction – The considered falcon species mostly lay 3-5 eggs. Thus, the number of offspring per female is set to $n_{incub} = 2$. Incubation time in the falcon species ranges from 26 to 31 days, so that we assume an incubation period a_{incub} of four weeks. The modelled energy requirement for starting a brood c_{start} is based on the additional energetic expenditure of egg production of 29 % in hawks and owls, which are usually heavier and produce larger eggs than the modelled small falcons, and of 13-41 % for the smaller passerines (Carey, 1996). Under these assumptions, the energetic cost of starting a brood would lie somewhere in the range [0.3, 0.9], and we here set it to $c_{start} = 0.5$. The weekly energetic cost of incubation c_{incub} would equal around 0.7 model units for an averaged falcon if we again follow the general assumption that incubation increases energy expenditure by around 25 % (Monaghan & Nager 1997) and if we use the formula by Bezzel and Prinzinger (1990) to compute the existence metabolic rate of the model falcon. However, Masman et al. (Masman et al., 1988) measured a mean energy expenditure of 13.6 Watt/kg^{-1} in incubating female Eurasian kestrels which corresponds to 4.4 model units per week including basal metabolism or rather 2.4 model units on top of the assumed basal metabolism rate for Eurasian kestrels. We take the average of these two values for incubation costs in the model, which then becomes $c_{incub} = 1.5$. The nestling phase of the falcon species typically takes around four weeks. However, depending on the species, either both parents or only the male can continue provisioning their offspring with food up to four more weeks, which can be only supplementary as for example in Eurasian hobby. Here, we assume that the offspring becomes independent from its mother at an age a_{indep} of six weeks. As far as we know, the only direct estimation of brood care costs for falcons stems from measurements of field metabolic rates in male Eurasian kestrels that are provisioning for nestlings (Masman et al., 1989). These expended a total daily energy of 382 kJ/d, on average, which amounts to 6.2 model units. The more general equations for computing field metabolic rates during parental care that were used for the white stork would result in a total daily energy expenditure of around eight model units for an averaged falcon. However, female falcons are usually less involved in food provisioning than males (Masman et al., 1989; Mebs and Schmidt, 2014). In comparison to the white stork, we also would expect aerial hunters that rely more on flapping flight to have a higher energy expenditure during food provisioning than soaring white storks, which feed walking and picking. Taking all together, we set c_{care} to an approximate value of seven model units. The probability p_{exp} that experience grows by one unit is set to 0.02 so that modelled birds reach full experience at an age of around two years, which corresponds to the time when the majority of considered falcon species breeds for the first time. Due to lack of data, health costs h_{start} of initiating a brood and the fitness f_{indep} of offspring at independence are again taken from McNamara et al. (McNamara et al., 1998).

Migration – From the little that is known about the migration of the considered falcon species, they differ substantially in their migration pattern. Known maximum migration distances are 2700 km for Merlins from Northern Norway to Southern Italy (ring findings), 2000 to 6440 km for Eurasian kestrels from Germany and Sweden overwintering in Western Africa (ring findings), around 8000 km for Eurasian hobbies from Germany migrating at an average speed of around 180 km/d to their overwintering ranges in Southern Africa (Meyburg et al., 2011), over 10,000 km for Red-footed falcons from Kazakhstan overwintering in Southern Africa as determined by geolocator tracking (Katzner et al., 2016) and 2500 km for Lesser kestrels migrating from Portugal to the Savannah regions in Western Africa within 4-5 days found in a geolocator study by Catry et al. (2010). Thus, for simplicity and in order to ease comparison of modelling results between the falcon and the stork functional type, the duration s_{migr} of migration was set to 3 weeks. This time frame approximately matches how long some of these falcon species would need in order to cover a similar migratory distance as we assumed for the modelled white storks. Unfortunately, migration costs could be only estimated very roughly for the modelled falcon functional type. We employed the software *Flight 1.24* (Pennycuick, 2011) to compute mere flight costs for all considered falcon species, using a flight altitude of 754 m (Mateos-Rodríguez and Liechti, 2012) and body morphometrics as given by Agostini et al. (Agostini et al., 2015) and Mueller et al. (2002). The resulting chemical power requirement of each species

(3.7, 4.9, 9.1, 5.1, 7.2 W for Lesser kestrel, Red-footed falcon, Merlin, Eurasian kestrel and Eurasian hobby) was then converted to kJ/h before multiplying it with an assumed daily flight time of eight hours. Such, a species-specific daily energy requirement (106.3, 140.3, 262.4, 147.7, 207.9 kJ/d) for flight was obtained, which was then translated into species-specific model units (2.5, 3.2, 4.9, 2.4, 3.3). Finally, we computed the mean of these costs, resulting in average energetic flight costs of 3.3 model units per week. These occur on top of the usual costs of existence, which here amount to approximately another three model units. Actual migration costs will be lower though since the considered falcon species are known to feed regularly during migration and stopover for multiple days. Thus, we assume that the model falcon functional type is able to compensate for around 2/3 of its migratory costs and set $c_{act} = 2$. This is half of the migration costs the modelled stork functional type would experience in active flight. Assuming the same relationship for migratory health costs of falcon and stork type results in $h_{act} = 1$. This value also corresponds to the model settings in McNamara et al. (1998), which was parametrized for a small songbird that can be assumed to employ flapping flight.

6.2.2 Mathematical details

6.2.2.1 FOOD AVAILABILITY

The location-dependent environmental food availability over the year in the baseline scenario is described by:

$$g(o,t) = \left(\varepsilon(o) * \sin\left[\frac{2\pi(t-13)}{52}\right] + A_{food}(o)\right) * (x_{max} - x_{min}),$$

where $A_{food}(o)$ represents the yearly average and $\varepsilon(o)$ the seasonality of food supply at location o and x_{min}, x_{max} are the minimum and maximum level of energy reserves. Weekly food availability in the breeding habitat in scenarios F2-F4 were acquired by cubic spline interpolation with *Matlab R2017b* between the peak values in winter and summer and the onset of spring and autumn when food supply would be equal to that in the overwintering habitat. Hereby, food peaks were increased by 10% in winter (F2-F4) and decreased by 10% in summer (F3-F4) depending on the scenario. Additionally, food availability in the overwintering location was reduced by 5 % over the year in scenario F4 of maximum change.

6.2.2.2 WIND CONDITIONS

The exact weeks at which the probability of active flight start changing in the model were set based on a systematic series of test runs to ensure that the resulting behavioural timing of the model population is realistic, fitting that of real white stork populations in North-Eastern Germany. They were subsequently compared to the occurrence of thermals in that region, as retrieved for the period 1994-2004 via the *Env-DATA system* (Dodge et al., 2013) on *Movebank* (www.movebank.org), and found to differ only moderately. Still, we also run the baseline model with an extended period of passive flight to check if the quality of results would be affected.

6.2.2.3 DYNAMIC PROGRAMMING EQUATIONS

Let $V_n(x, a, e, a, o, s, t)$ denote the reproductive value of a bird in state (x, a, e, a, o, s, t) at the beginning of week t, n years before the target year, which forages with intensity u and has a survival probability of $S(y, o, s, t, u)$ during that week. We further define the criterion function for comparing the value of different behavioral options for the bird to be the reproductive payoff $H_{action}(u)$. Then, the expected reproductive payoff of subsistence is

$$H_{subsist}(u) = S(y, o, s, t, u)[(1 - p_{exp})V_n(x_{subsist}, y_{subsist}, e, -1, o, s, t + 1) + p_{exp}V_n(x_{subsist}, y_{subsist}, e', -1, o, s, t + 1],$$

of initiating a brood is

$$H_{start}(u) = S(y, o, s, t, u)[(1 - p_{exp})V_n(x_{start}, y_{start}, e, 0, o, s, t + 1) + p_{exp}V_n(x_{start}, y_{start}, e', 0, o, s, t + 1],$$

of caring for dependent brood is

$$H_{are}(u) = S(y, o, s, t, u)[(1 - p_{exp})V_n(x_{care}, y_{subsist}, e, a + 1, o, s, t + 1) + p_{exp}V_n(x_{care}, y_{subsist}, e', a + 1, o, s, t + 1]$$

and migrating results in the expected reproductive payoff

$$H_{migrate}(u) = S(y, o, s, t, u)[(1 - p_{exp})V_n(x_{migrate}, y_{migrate}, e, -1, o, s + 1, t + 1) + p_{exp}V_n(x_{migrate}, y_{migrate}, e', -1, o, s + 1, t + 1].$$

Hereby, $e' = \min(\mathrm{e} + 1, e_{max})$ represents the bird's experience at the next week $t + 1$ given it grows by one unit, which it does with probability p_{exp}.

To identify the best behavioural action for that bird for each week of the year, and thus retain the optimal behavioural strategy, we first compute the optimal foraging intensity u for each feasible behavioural action, except for the fixed payoff of migration. It maximizes expected long-term number of descendants under that action:

$$H^*_{action} = \max_{0 \le u \le 1} H_{action}(u),$$

$$H^*_{migrate} = H_{migrate}.$$

The available behavioural actions are state-dependent as follows:

if $\boldsymbol{a = -1}$ and $\boldsymbol{s = -1}$ (no brood, not migrating),	$\{\boldsymbol{subsist}, \boldsymbol{start}, \boldsymbol{migrate}\}$;
if $\boldsymbol{-1 < a < a_{max}}$ and $\boldsymbol{s = -1}$ (breeding, not migrating),	$\{\boldsymbol{subsist}, \boldsymbol{care}\}$;
if $\boldsymbol{a = a_{max}}$ and $\boldsymbol{s = -1}$ (brood of max. age, not migrating),	$\{\boldsymbol{subsist}\}$;
if $\boldsymbol{a = -1}$ and $\boldsymbol{-1 < s < s_{max}}$ (no brood, migrating),	$\{\boldsymbol{migrate}\}$;
if $\boldsymbol{a = -1}$ and $\boldsymbol{s = s_{max}}$ (no brood, reaching other location),	$\{\boldsymbol{subsist}\}$.

Then, the behavioural action with maximum reproductive payoff under the optimal foraging intensity from the set of feasible actions including migration is selected, i.e. the optimal behavioural decision resulting in the corresponding optimal reproductive value for the particular state-week combination. This results in the optimal payoff

$$V_n(x, y, e, a, o, s, t) = \max(H^*_{subsist}, H^*_{start}, H^*_{migrate})$$

for a bird that had neither been breeding nor migrating at the beginning of week t and

$$V_n(x, y, e, a, o, s, t) = \max(H^*_{subsist}, H^*_{care})$$

for a non-migrating but breeding bird. When the brood is turning independent and abandoned, the payoff for the parent includes the reproductive value of its young:

$$V_n(x,y,e,a,o,s,t) = H^*_{subsist} + n_{offspring} V_n(x_{indep}, y_{indep}, 0, -1, o, 0, t),$$

where $n_{offspring}$ is the number of offspring per brood, and x_{indep} and y_{indep} are the energy reserves and health condition levels of the newly independent young. Migrating birds that are not finishing migration until next week receive the payoff

$$V_n(x,y,e,a,o,s,t) = H^*_{migrate},$$

while those finishing migration and reaching the other location have an optimal payoff of

$$V_n(x,y,e,a,o,s,t) = H^*_{subsist}.$$

The payoff of birds which depleted their energy reserves, and thus die, is set to

$$V_n(0,y,e,a,o,s,t) = 0.$$

The computation of the optimal behavioural strategy, i.e. the optimal behavioural actions for all states and all weeks of the year, is started from the terminal reward

$$V_0(x,y,e,a,o,s,52) = 1$$

by backward iteration. Hereby, we use the wrap-around condition (cf. Houston and McNamara 1999)

$$V_n(x,y,e,a,o,s,52) = V_{n-1}(x,y,e,a,o,s,0)$$

to ensure temporal continuity from one yearly cycle to the next.

At the end of each year n, the convergence factor λ_n is computed for all state combinations which had a reproductive value $V_{n-1}(x,y,e,a,o,s,0) > 0$ in the previous year using

$$\lambda_n(x,y,e,a,o,s,t) = \frac{V_n(x,y,e,a,o,s,0)}{V_{n-1}(x,y,e,a,o,s,0)}.$$

When

$$\max_{(x,y,e,a,o,s,t)} |\lambda_n(x,y,e,a,o,s,0) - \lambda_{n-1}(x,y,e,a,o,s,0)| < 10^{-6}$$

computations are stopped.

6.2.3 Influence of assumed wind conditions

6.2.3.1 TIMING OF BEHAVIOUR

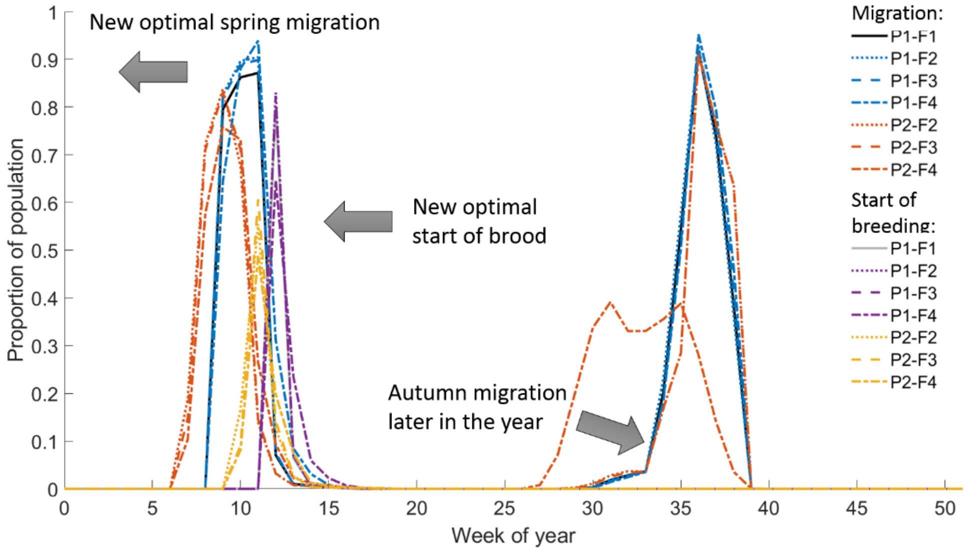

Figure S 6.2-1: Timing of behaviour in various food environments (F1-F4) assuming longer thermal availability for a population of bird functional type T1 (stork) following either the old (P1) or new (P2) optimal behavioural strategy.

6.3 Appendix to Chapter 4

6.3.1 Parameter settings

Table S 6.3-1: Selected values/formulas of model parameters used for the optimal annual routine model sOAR (Schaefer et al., 2018) in this study and relevant sources. Energetic values were computed from published data as described in Section 6.2.1.

Parameter	Symbol	Value / Formula	Background information
State and stage variables:			
Range of energy reserves	x	$\in [0,10], \in \mathbb{N}$	McNamara et al. (1998)
Range of health condition	y	$\in [0,10], \in \mathbb{N}$	McNamara et al. (1998)
Range of experience	e	$\in [0,2], \in \mathbb{N}$	McNamara et al. (1998)
Age of any offspring	a	$\in [-1, a_{incub} + a_{indep}], \in \mathbb{Z}$	Schaefer et al. (2018)
Location	o	$\in [1, n_{loc}], \in \mathbb{N}$	McNamara et al. (1998)
State of migration	s	$\in [-1, s_{migr} - 1], \in \mathbb{Z}$	Schaefer et al. (2018)
Week of year	t	$\in [0,51], \in \mathbb{N}$	McNamara et al. (1998)
General biology:			
Background mortality by disease	M_{bg}	0.00055	Reflecting a maximum lifespan of 35 years for white storks (Kaatz et al. 2017)

Basic metabolic cost	c_b	1.7	Mean from Aschoff and Pohl (1970), Bezzel and Prinzinger (1990), Peters (1983), assuming 16 h of activity and 8 h of rest.
Foraging intensity	u	$\in [0,1]$	McNamara et al. (1998)
Energetic cost of subsistence	$c_{subsist}$	$c_b(1 + 0.01(x/10)^2) + 6u^2(1 + 0.01(x/10)^2)$	Hammond and Diamond (1997)
Health cost of subsistence	$h_{subsist}$	$1 - 0.2c_{subsist} - 0.01{c_{subsist}}^2$	Assumption: four months to recover from lowest to full reserves under minimum activity, two months to deteriorate from highest to lowest reserves under maximum activity.
Environment:			
Number of locations	n_{loc}	2	Breeding and overwintering location
Average food availability at overwintering and breeding location (baseline)	A_{food}	$[1.0, 1.0]$	Same yearly average in both locations
Degree of seasonality of food at overwintering and breeding location (baseline)	ε	$[0.3, 0.7]$	Higher seasonality in the breeding location with higher summer but lower winter peak
Background predation for both locations	M_{bgpred}	$[0.004, 0.002]$	Twice as high in the overwintering location; derived from Barbraud et al. (1999), Haas et al. (2003), Kaatz (2004), Ryslavy (2011), Schaub et al. (2004)
Predation risk	M_{pred}	$M_{bgpred}\,(o)u^2(1 + 0.01(x/10)^2)$	Risk slightly increases with reserves (Gosler et al., 1995; Lima, 1986)
Probability of active flight	p_{act}	$p_{act}(o,t)$	Derived from real thermal availability along the migratory route in 1994-2004 (www.movebank.org, Dodge et al., 2013, Ákos et al., 2008) and several test runs to ensure realistic behaviour.
Reproduction:			
Duration of incubation in weeks	a_{incub}	4	Kaatz et al. (2017)
Age of independence in weeks	a_{indep}	9	Creutz (1985)

Energetic cost of starting a brood	c_{start}	1.53	Carey (1996)
Energetic cost of incubation	c_{incub}	0.63	Monaghan and Nager (1997); Profus (1986)
Energetic cost of brood care	c_{care}	6.0	McNamara et al. (1998); Nagy et al. (1999)
Health cost of starting a brood	h_{start}	1.0	Houston and McNamara (1999); McNamara et al. (1998)
Number of offspring	n_{brood}	2	Average clutch size (Creutz, 1985) allocated per parent
Fitness of offspring at independence	f_{indep}	0.5	Houston and McNamara (1999)
Computed equilibrium value for foraging efficiency of inexperienced young	θ	0.7381	Computational details in McNamara et al. (1998)
Probability of experience growth	p_{exp}	0.01	Full experience at the age of 3.8 years, on average; corresponds to the age of 3–5 years at which white storks successfully start reproduction (Hancock et al., 1992)
Migration:			
Duration of migration in weeks	s_{migr}	3	Berthold et al. (2001); Kaatz (2004)
Energetic cost of passive flight	c_{pas}	0.8	Eder et al. (2015); Flack et al. (2016); Johst et al. (2001); Kaatz (2004); Nagy et al. (1999); Pennycuick (2011); Profus (1986); Rotics et al. (2016)
Energetic cost of active flight	c_{act}	4.0	Assuming active flight is five times more costly than passive flight (Duriez et al., 2014; Hedenström, 1993; Pennycuick, 1972)
Reserves change during migration	Dx_{migr}	$(p_{act}c_{act} + (1-p_{act})c_{pas})(1 + 0.001x^2)$	Increasing with heavier fuel burdens (Alerstam, 1991)
Health cost of active flight	h_{act}	2.0	Assuming double the cost as McNamara et al. (1998) took for a small passerine
Health cost of passive flight	h_{pas}	0.4	Assuming a ratio of 5:1 for costs arising from active vs. passive flight
Health change during migration	Dy_{migr}	$p_{act}h_{act} + (1-p_{act})h_{pas}$	Schaefer et al. (2018)

Background predation during migration	M_{bgmigr}	0.004	Assumedly twice as high as in the breeding location based on Haas et al. (2003); Hancock et al. (1992); Kaatz (2004)
Predation risk during migration	M_{migr}	$M_{bgmigr}(1 + 0.01(x/10)^2)$	Increasing with reserves (Gosler et al., 1995; Lima, 1986)

6.3.2 Energetic conversion factor

Modelled energetic costs were computed from published energy costs using a conversion factor of 3381 kJ for 1 model unit. The factor is based on the weight difference between free-fed white storks and their lean body mass (Mata et al., 2001), the energetic value of fat and the range of 10 model units for reserve levels.

6.3.3 Carry-over effects regarding migration timing and health condition

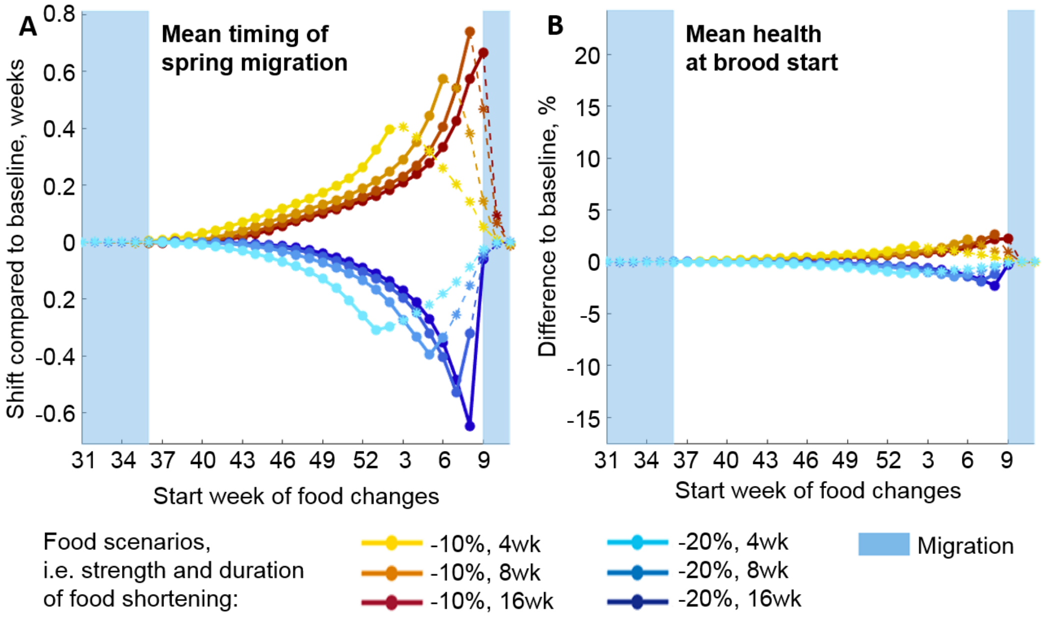

Figure S 6.3-1: Carry-over effects from the overwintering to the beginning of following breeding period for various scenarios of food surplus (blue) and food shortenings (red) in the overwintering location. Effect on A) the mean timing of spring migration B) the level of mean health of parental birds when starting a brood. The absolute change in food supply relative to baseline food supply was the same in all scenarios, meaning its intensity was constant. However, the duration and relative strength of food surplus or shortening was varied between +/-80 % change in food supply over only one week to +/-10 % change in food supply over 8 weeks, i.e. the population experienced short but strong changes in food supply (darker in colour) versus long but small changes in food supply (lighter in colour). Dashed lines represent the effect of altered resource dynamics that did not affect the complete population equally since they fell into the migratory period. The migratory period is depicted by light blue bars. The breeding period began in week 11.

6.3.4 Carry-over effects under different intensities of changes in food supply

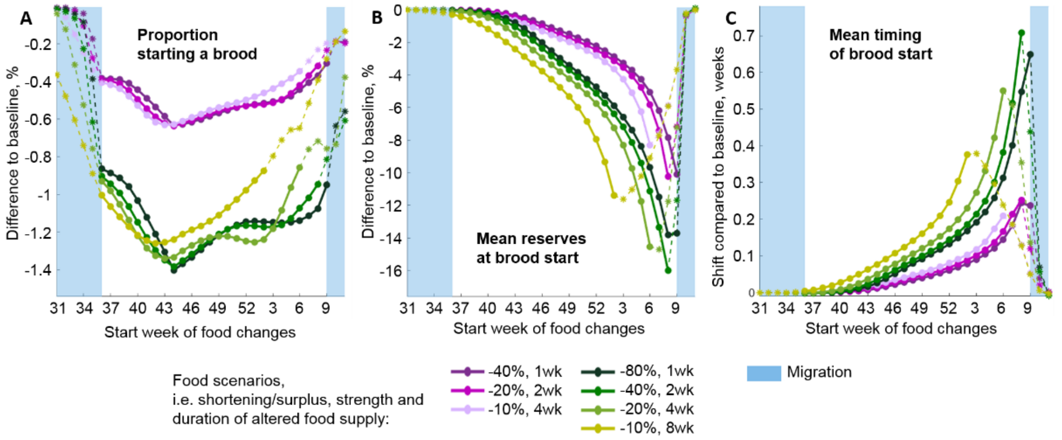

Figure S 6.3-2: Effect of different intensities (pink: -40%, green: -80%) of food events on breeding parameters in early spring, i.e. on (A) the proportion of the population starting a brood (B) mean reserves levels of parental birds when initiating their brood (C) mean timing of breeding activities. The intensity of an event depends on its strength and duration. Shorter and intense events are darker in colour, while longer but milder events are light-coloured. Dashed lines represent the effect of events that did not affect the complete population equally since the events fell into the migratory period. The migratory period is depicted by light blue bars.

6.3.5 Carry-over effects on mean reserves of early, medium and late breeders

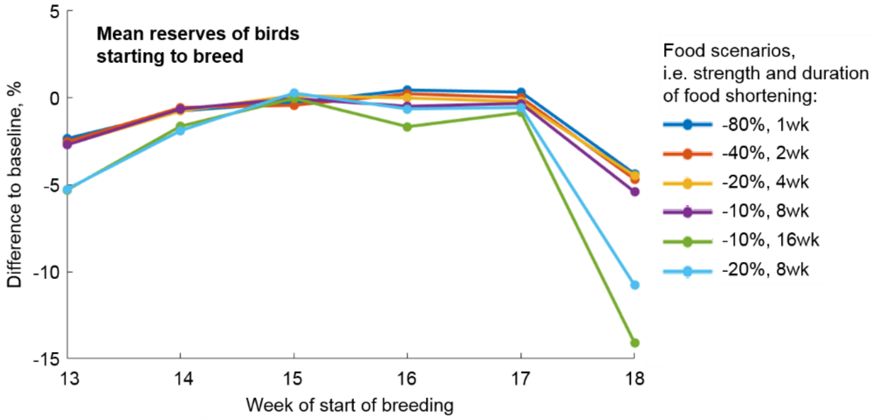

Figure S 6.3-3: Carry-over effects from the overwintering to the beginning of following breeding period on the level of mean reserves of parental birds starting a brood for various scenarios of food shortening in the overwintering location, differentiated by the week in which the brood is initiated. Particularly late breeders (week 18) had much lower reserves under food changes compared to the baseline scenario.

6.3.6 Distribution of reserves and health over time

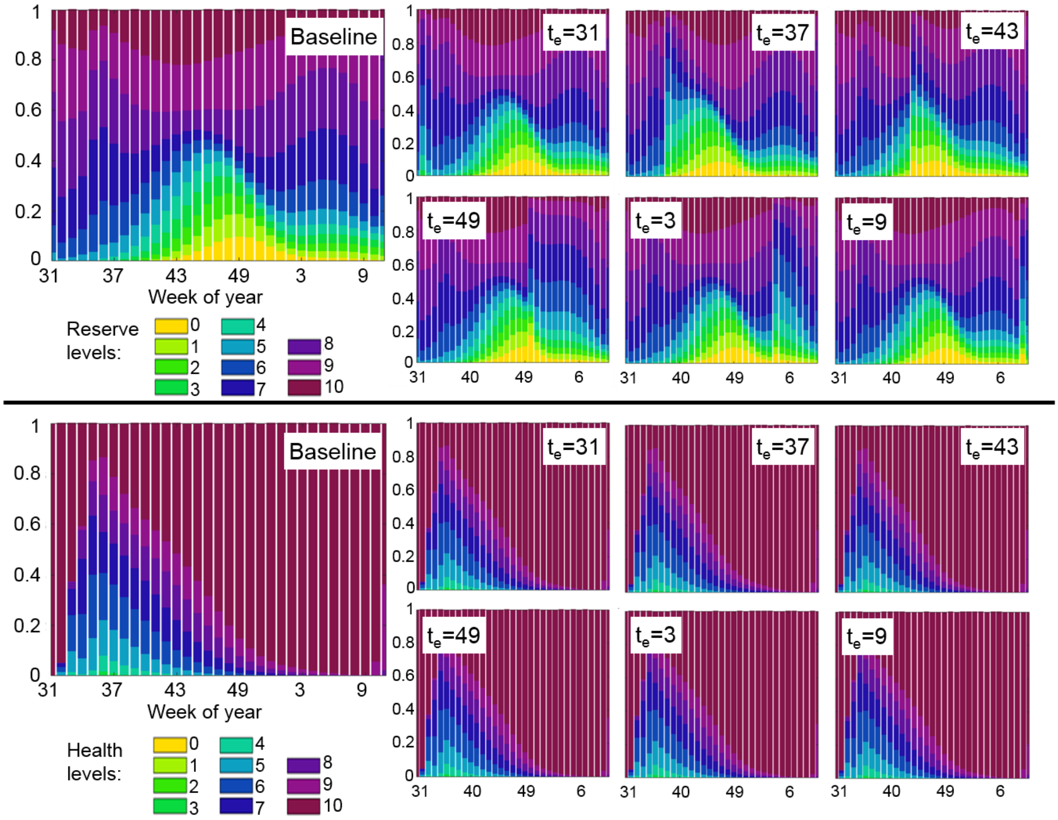

Figure S 6.3-4: Distribution of the levels of energy reserves (top) and health condition (bottom) over the analysed non-breeding season for the baseline scenario (large, left) and under various scenarios of altered food supply (small, right). The week of altered food supply is indicated by t_e, whereby the baseline food supply was reduced by 80 % for one week.

6.4 *sOAR* User Manual, software, code and configuration files

The open-source *sOAR* software including a User Manual (Version 1.0, 98 pages) and sample *Matlab* and *R* code to analyse the raw output of *sOAR* is publicly available in form of a source and binary distribution at < https://sourceforge.net/projects/soar-animal-behaviour >.

The *sOAR* User Manual, the sample *Matlab* and *R* code for analysing *sOAR*'s raw output as well as the sample configuration files used for Chapter 2 have further been published by *Ecography* (Schaefer et al., 2018, Supplementary material Appendix ECOG-03328, 1–5) and can also be downloaded at < www.ecography.org/appendix/ecog-03328 >.

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Declaration of Authorship

This work was done wholly or mainly while in candidature for a research degree at this University.

Where any part of this thesis has previously been submitted for a degree or any other qualification at this University or any other institution, this has been clearly stated.

Where I have consulted the published work of others, this is always clearly attributed.

Where I have quoted from the work of others, the source is always given. With the exception of such quotations, this thesis is entirely my own work.

I have acknowledged all main sources of help.

Where the thesis is based on work done by myself jointly with others, I have made clear exactly what was done by others and what I have contributed myself.

Signed:

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