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Influence of high temperatures on avian species: from physiological responses to ecological consequences

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GENERAL THESIS STRUCTURE

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Levillain, A., Mata, A., Massemin, S., Reichert, S. Physiological markers of avian dehydration: assessing the hyperthermia–dehydration trade-off. **In prep**.

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COMMUNICATIONS

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Levillain, A., Bleu, J., Reichert, S., Massemin, S. Contrasted effects of weather and timing on great tit (*Parus major*) breeding success in a forest and urban environment. **Talk**. 18/11/2024. Paris (France).

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Detailed table of content

GENERAL INTRODUCTION

The Dodo (*Raphus cucullatus*) is one of the most emblematic example of extinction due to anthropogenic pressure (Hume, 2006). Painting from Roelandt Savery (1626).

1. Climate change and biodiversity erosion

1.1. Biodiversity erosion

Human activity has been reported to be an important driver of extinction rates since prehistoric times (Bergman et al., 2023), and the extinction rates have increased considerably since the Industrial Revolution, with recent estimations drastically exceeding prehistorical rates (circa 1750; Figure 1; Ceballos et al., 2015; Pimm et al., 2014; Rounsevell et al., 2020). Approximately 25% of species are currently estimated to be threatened by extinction, although the risk of extinction varies considerably between taxa (IPBES, 2019; IUCN, 2023). Such estimates have led to the popularization of the concepts of "6th extinction" and "Anthropocene" (Barnosky et al., 2011; Kaiho, 2022). Growing awareness on the current biodiversity erosion eventually led to the writing of the convention on biological diversity (CBD) in 1993, which is currently ratified by 196 nations, and represents a legal frame for biodiversity conservation. The term biodiversity, i.e. "biological diversity", represents the variability of life and consequently encompasses many concepts. According to the IPBES (Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services), biodiversity includes variation in genetic, phenotypic, phylogenetic, and functional attributes, as well as changes in abundance and distribution over time and space within and among species, biological communities and ecosystems (Díaz and Malhi, 2022). Biodiversity erosion encapsulates the notions of habitat and species loss, habitat degradation, habitat fragmentation, and can thus be measured using a variety of indicators (Borges et al., 2019). Despite the increasing research and conservation effort is the past decades, biodiversity loss has continued to accelerate (Caldwell et al., 2024). Main drivers of biodiversity erosion are habitat changes, direct exploitation, climate change, pollution, and the introduction of invasive species (Butchart et al., 2010; Díaz and Malhi, 2022; Jaureguiberry et al., 2022; Maxwell et al., 2016; Urban, 2015). In this PhD thesis, we focus on climate change. However, it is important to note that it is currently not the only nor the main driver of biodiversity erosion for most species, and that effects of climate change are likely to add up with effects of other drivers.

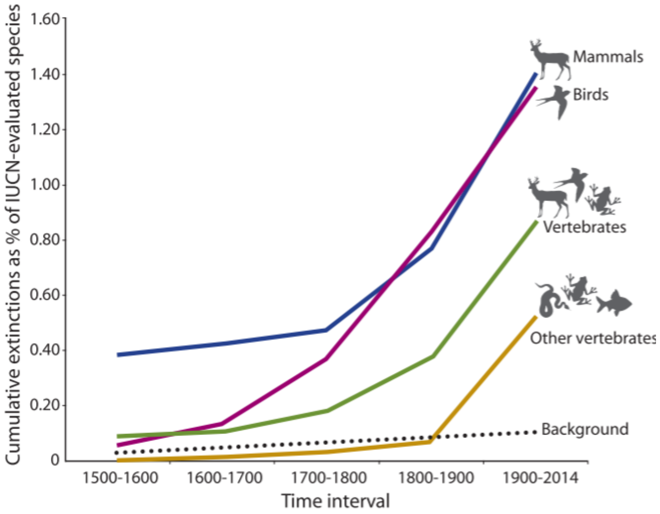

Figure 1. Cumulative vertebrate species recorded as extinct in the wild by the IUCN (2012). Dashed black curve represents the number of extinctions expected under a constant standard background rate. Adapted from Ceballos et al., 2015.

1.2. Climate change as a driver of biodiversity erosion

Anthropic activity and especially increases in greenhouse gas emissions since the beginning of the Industrial Revolution has led to changes in the global climate. This phenomenon is commonly referred to as "climate change". Climate change is characterized by an increase in the global atmospheric and ocean temperatures, changes in precipitation, decrease in snow and sea-ice coverage, increase in ocean level and acidification of the ocean (Figure 2A; IPCC, 2014). Increases in global temperature are commonly referred to as "climate warming". However, variation in extreme weather events has also been related with climate change, such as changes in extreme temperature events, extreme precipitation-related events (i.e. floods, drought), or other climate hazards (e.g. storms, wildfire) in multiple regions across the globe. Heatwaves more specifically have been predicted to increase in frequency, duration and intensity (Figure 2.B; Diffenbaugh and Field, 2013; IPCC, 2014; Simolo and Corti, 2022). Since anthropic emissions of greenhouse gases have been continuously rising, and because their levels and effects on climate are predicted to be persistent, the impact of climate change on natural system is likely to increase with time (Solomon et al., 2020; IPCC, 2023).

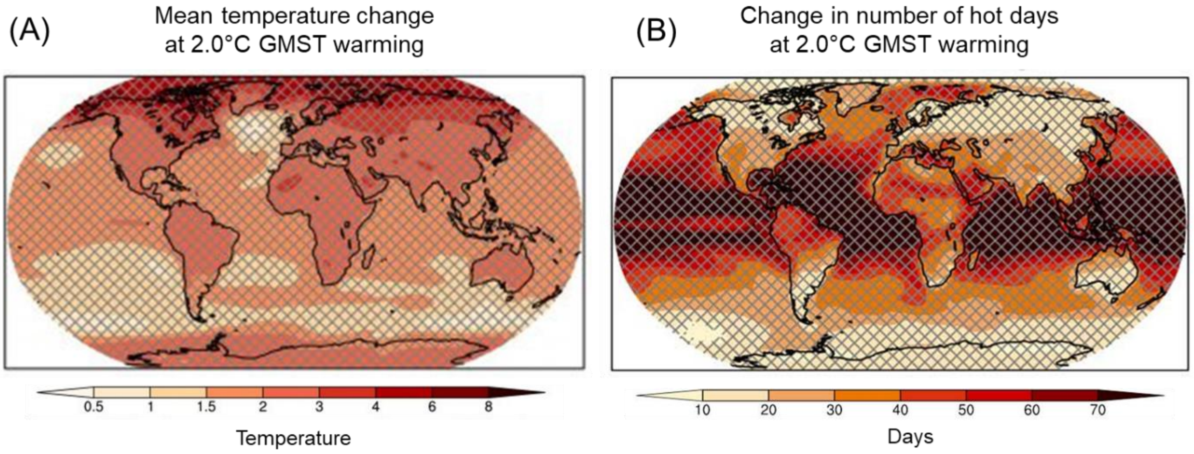

Figure 2. Projected changes in (A) mean temperature (B) the number of hot days per year (10th percentile of hottest days) at 2°C of global warming compared to the pre-industrial period (1861-1880). GMST: global mean surface temperature. Adapted from IPCC 2014.

Assessing biodiversity response to climate change must be evaluated across several biological scales, from the individual level, to population, community, and ecosystem (Figure 3; Bellard et al., 2012). At the individual level, physiological and behavioral responses are critical in determining fitness under changing environmental conditions (Spicer et al., 2019; Urban et al., 2016). Individual responses shape population traits such as changes in spatiotemporal distribution (Cohen et al., 2018; Menzel et al., 2006; Piao et al., 2019; Platts et al., 2019), population dynamic, and contraction or expansion of their range of distribution (Engelhardt et al., 2022; Stephens et al., 2016; Suggitt et al., 2023). Populations are expected to track climate change by shifting their range of distribution and phenology, and species response to climate change may be related to their ability to track optimal conditions in space and time (Macgregor 2019; Ralston., 2017). While phenology seems to advance with climate warming in most cases, phenological responses may not match with weather changes (Saino et al., 2011). Moreover, rate of advancement may differ between population, taxa and trophic levels, which is likely to have consequences on species interactions, community composition and structure (Figure 4; Kharouba and Wolkovich, 2020; Loughnan et al., 2024; Nakazawa and Doi, 2012; Thackeray et al., 2016; Vitasse et al., 2021). Finally, climate change is likely to influence ecosystem structure and function, potentially influencing the ecosystem capacity to buffer and recover from environmental challenges (Figure 5; Antão et al., 2022; Mahecha et al., 2024; Smith, 2011).

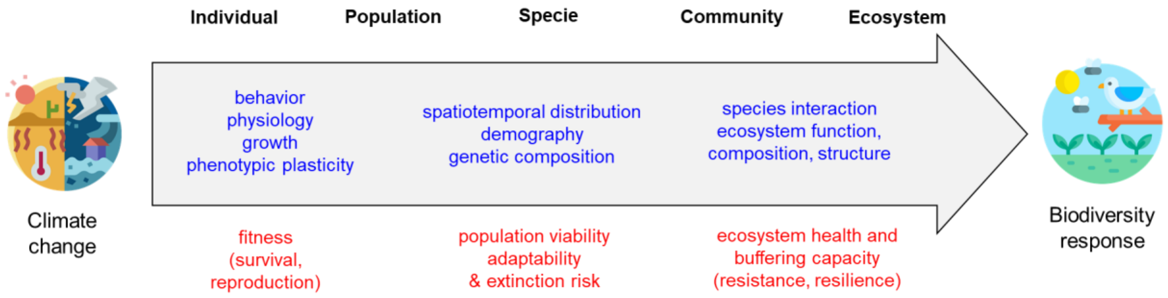

Figure 3. Hypothetical influence of climate change on biodiversity from individual responses to the ecosystemic level. We illustrate the potential effect of climate change on biodiversity via a non-exhaustive list of biological traits (in blue), or evolutionary and ecological consequences (in red).

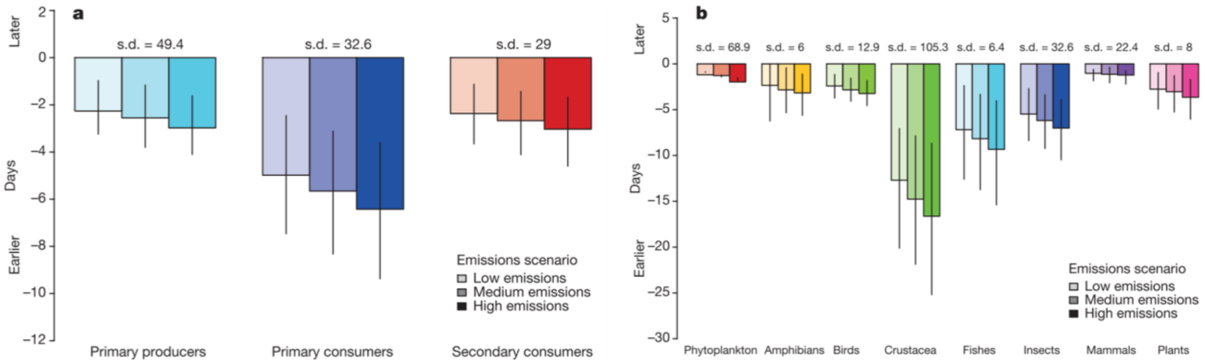

Figure 4. Estimated phenological shifts by the 2050s. Modelled responses to projected temperature and precipitation change, assuming contemporary climate sensitivity, for trophic levels (A) and taxonomic groups (B). Adapted from Thackeray et al., 2016.

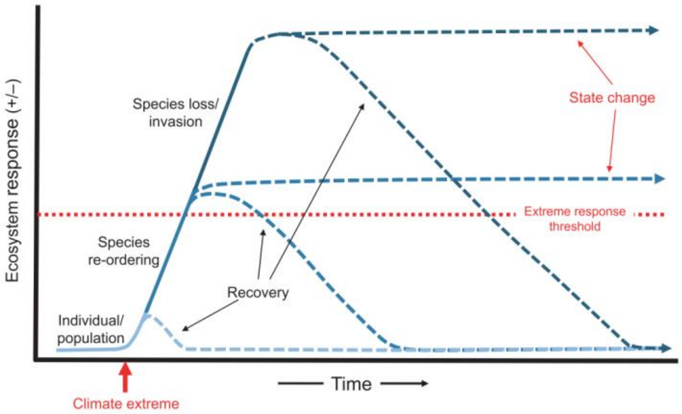

Figure 5. A mechanistic framework for assessing ecosystem response to climate extremes. Climate extremes may alter ecosystem structure and/or function outside the bounds of what is considered typical or normal variability, as a consequence of crossing an extreme response threshold (dotted red line) in which individual-level effects cascade to higher hierarchical levels to result in significant changes in community structure and large ecosystem impacts. These alterations may be characterized by prolonged recovery, or may even lead to persistent state changes. Adapted from Smith, 2011.

2. Birds in a warming climate

2.1. Birds as sentinels of climate change

Documenting, preventing, and eventually reversing biodiversity loss necessitate tools to assess ecosystem health and trajectory. To do so, research has been mainly focused on ‘sentinel species’, i.e. species that integrate environmental and ecosystem changes (Clark-Wolf et al., 2024). Birds have historically been strongly associated with the concept of ‘sentinel of the environment’, most notably since the publication of ‘Silent spring’ (Carson, 1962). Use of persistent pesticides led to population decline of several birds, revealing the effects of these compounds on the environment (Cade et al., 1988; Hickey, 1969). These compounds were eventually banned, and populations recovered during the next decades, highlighting the importance of long-term monitoring programs and the relevance of birds as sentinels (Ambrose et al., 2016). Birds are highly represented among sentinel species, mainly due to their abundance, large distribution, trophic position and ability to integrate environmental changes in a detectable manner (e.g. behavior, physiology, reproduction, population dynamic; Clark-Wolf et al., 2024; Goldsmith, 1991; Hazen et al., 2019).

Numerous bird populations are decreasing across the globe, and extinction risks are predicted to increase (Cooke et al., 2023; IUCN, 2023; Lees et al., 2022). Climate change seems to have an effect on many bird populations, from the individual level to the structure of avian communities (Chen and Khanna, 2024; Dunn and Møller, 2019; Ma et al., 2023). At the individual scale, climate change is predicted to influence avian behavior and physiology, potentially impacting turn individual fitness and in turn population dynamics (Andreasson et al., 2020c; Cunningham et al., 2021; Mainwaring et al., 2016; Radchuk et al., 2019; Ruuskanen et al., 2021; Sauve et al., 2021). Changes in populations traits have been associated with climate change, such as phenotypical variation, spatiotemporal distribution, contraction or expansion of their range of distribution and demographic rates (Figure 6; Cohen et al., 2018; Cotton, 2003; Dunn and Møller, 2014; Hällfors et al., 2020; Halupka et al., 2023; Neate-Clegg et al., 2024). Changes in migration or breeding phenology are likely to have consequences on trophic interactions, and asymmetric phenological response to climate change may lead to a mismatch between energy-requirements and food availability, or predation rate (Borgmann et al., 2013; Charmantier and Gienapp, 2014; Kharouba and Wolkovich, 2020; Saino et al., 2011). Overall, climate change is likely to have a direct effect on bird populations through changes in the thermal environment, but also indirect effects through changes in phenology, trophic interactions and abiotic factors (e.g. drought, snow or sea-ice coverage; Conrey et al., 2016; Iverson et al., 2014; Londe et al., 2021; Mallory et al., 2010; Viollat et al., 2024). Increase exposure to extreme events such as heatwaves or drought are predicted to threaten some populations (Maxwell et al., 2019; Moreno and Pape Møller, 2011; Stillman, 2019). In more alarming cases, some population may rapidly go extinct in a climate warming scenario (Pattinson et al., 2022; Ridley et al., 2021a).

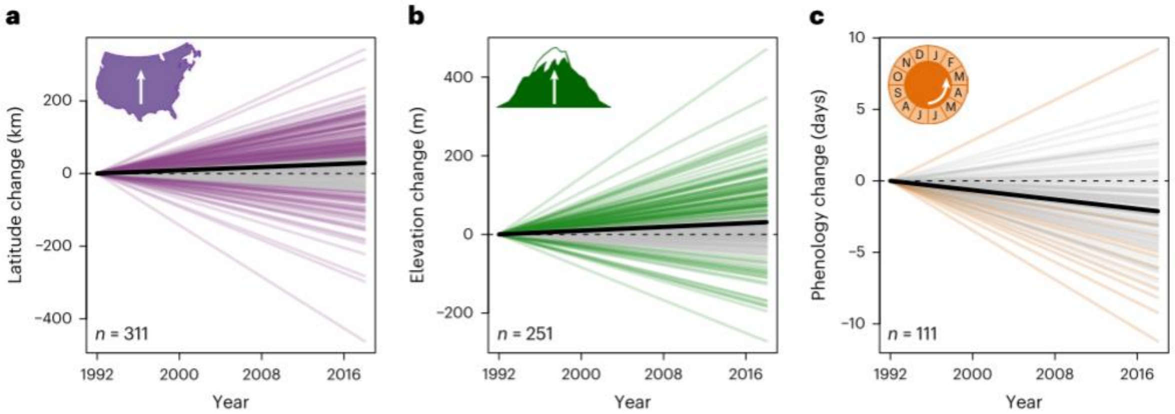

Figure 6. North American landbirds are shifting poleward, upslope and earlier in their breeding phenology. Cross-species trend lines (thick black lines) represent the average change inbreeding latitude (A), elevation (B) and phenology (C) since 1992, whereas species-specific trends (couloured

lines) show shifts relative to the no-change line (dashed). Species trends with 95% confidence interval overlapping 0 are depicted in grey. The combination of different datasets resulted in variable number of species (n) evaluated for shifts in each dimension. Adapted from Neate-Clegg et al., 2024.

Improving our ability to predict climate change impact on biodiversity and bird population necessitate to develop mechanistic models on key parameters driving population sensibility to environmental change and viability (e.g. physiology, demography; Urban et al., 2016). Assessment and prediction of population viability necessitates to invest research effort into long-term monitoring programs, allowing the estimation of demographic parameters, population size, structure and spatio-temporal distribution (Tian and Hua, 2023). Thermal environment is an important key driver of avian reproduction, and plays consequently and important role in shaping population dynamics (Figure 7; Andreasson et al., 2020; DuRant et al., 2019; Nord and Giroud, 2020; Sauve et al., 2021). In the following section, we explore the effects of the thermal environment on incubation, offspring development and parental investment.

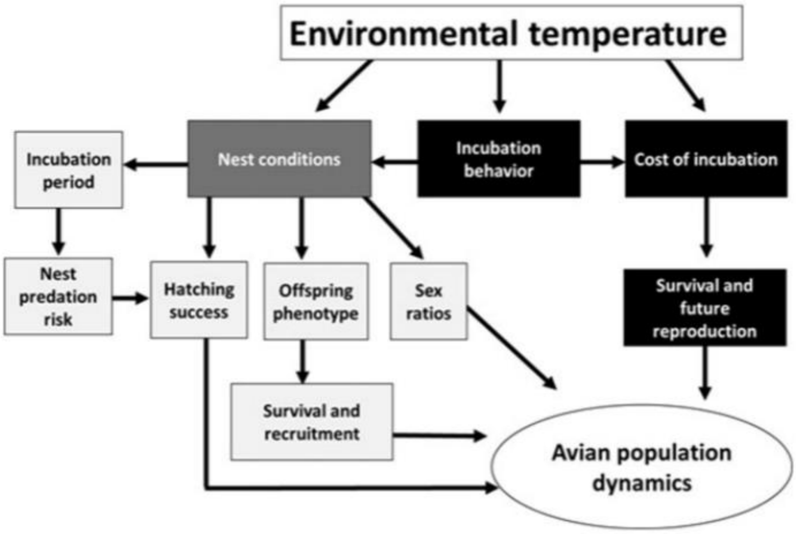

Figure 7. Pathways through which environmental temperatures can shape avian population dynamics, such as via effects on incubation behavior, cost of incubation, and thermal conditions experience by the embryos. Black boxes represent effect on parental endpoints, and light gray boxes represent effects on offspring endpoints. From Durant et al., 2019.

3. Importance of temperature on avian reproduction

3.1. Avian incubation

One of the main challenges of reproduction is ensuring that offspring develop in a suitable environment. Oviparity comes with the challenge of maintaining optimal conditions for embryonic development despite being exposed to the environmental stochasticity (e.g. changes in temperature, humidity; Rahn, 1991). Embryonic development is dependent on the incubation temperature, and the development time decreases with incubation temperature (Gillooly et al., 2002). The physiological zero temperature (PZT; i.e. temperature for which the speed of the embryonic development is null) and the upper lethal temperature (ULT; lethal temperature for the embryo) are believed to be approximately 26°C and 40°C respectively, although they vary considerably between species (Webb, 1987).

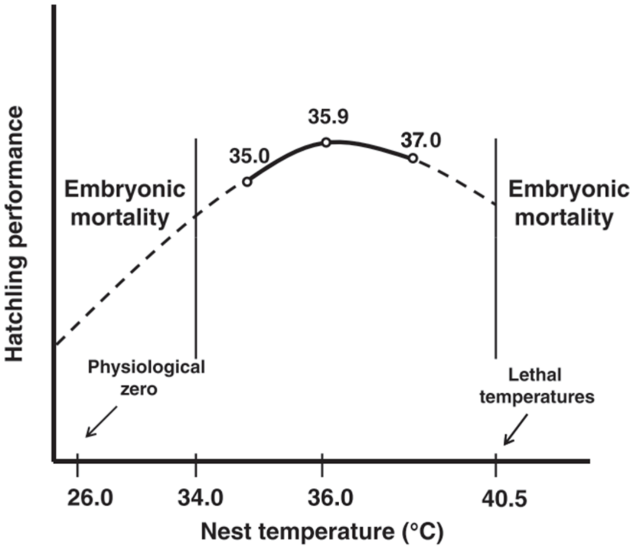

Figure 8. Relationship between average temperature experienced during incubation and hatchling performance in wood ducks (*Aix sponsa*). Individual points on the graph represent physiological performance (e.g., immune responses) of wood duck embryos incubated at either 35.0, 35.9, or 37.0°C. From Durant et al., 2013b.

While avian embryonic development occurs approximately in the 26-40°C range, it is thought to be optimal within much narrower range (e.g; 35-37°C for wood ducks (*Aix sponsa*); Figure 8; Durant et al., 2013a; Hepp et al., 2015). Parents consequently regulate the temperature of the eggs during incubation depending on the ambient temperature (e.g. nest attentiveness, duration and frequency of off-bouts; Deeming, 2004). Since heat production of the embryo is very small, and because optimal incubation temperature usually exceeds ambient temperature, embryonic development is in most cases reliant on parental thermogenesis (Deeming and Reynolds, 2015; Deeming, 2004). Most birds develop a brood patch during the breeding season, i.e. a specialized patch of naked skin facilitating direct heat transfer from the adult to the eggs or hatchlings. On the contrary, parents may avoid eggs to overheat by reducing their time spent incubating, by shading or even wetting the eggs (i.e. through belly-soaking; Grant, 1982). Finally, nest site selection and design (shape, size, composition and orientation) varies substantially between species and play in important role in maintaining a thermal environment that is favorable to offspring development (Figure 9; Carroll et al., 2020; Deeming and Gray, 2016; Mainwaring et al., 2012; Martin et al., 2017; Perez et al., 2020). Quoting Deeming (2004), “the 'incubator' is not the bird alone but a combination of the nest and the bird; it is the bird-nest unit that allows successful incubation”.

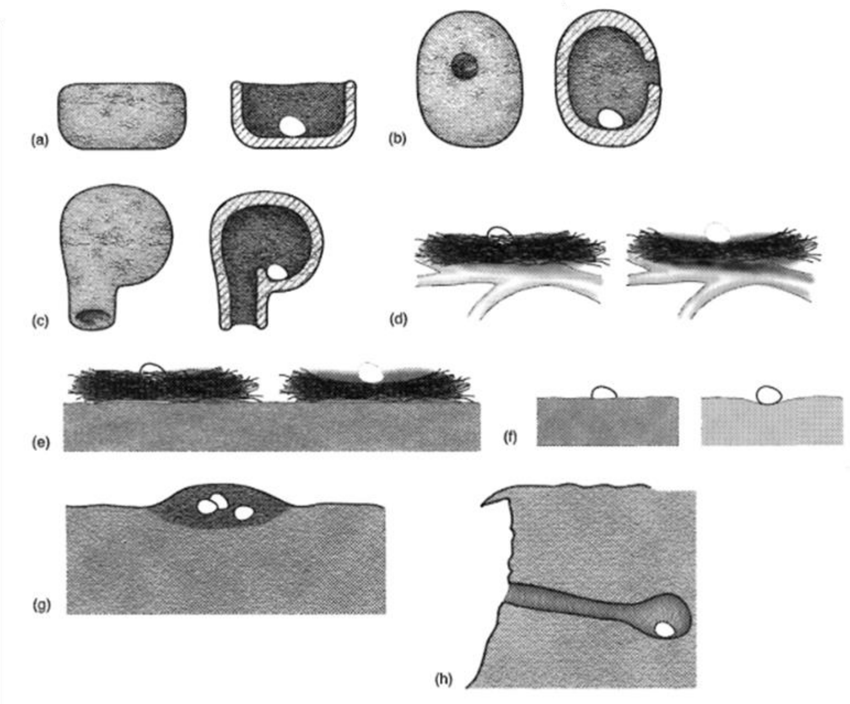

Figure 9. Diversity in bird nest design. Nest shapes can be assigned to one of eight categories: (A): cup; (B) dome; (C) dome and tube; (D) plate; (E) bed; (F) scrape; (G) mound; (H) burrow. From Deeming, 2004.

3.2. Offspring phenotype and performance

Importance of the thermal environment of offspring development is not restricted to incubation, as the offspring continue their development after hatching. It is worth noting that hatchling phenotypes are diverse among bird species, and vary along an altricial to precocial continuum (Ducatez and Field, 2021; Starck and Ricklefs, 1998). Precocial hatchling are born “independent”, with usually a fully covered down, opened eyes and a capacity to forage by themselves. Altricial species typically hatch with closed-eyes, naked or with no functional down, unable of foraging and thermoregulating (Price and Dzialowski, 2017). Thus, nest design and parental care have strong implication on post-hatching development, especially in altricial species (Sauve et al., 2021). Thermal challenges during incubation or post-hatching development can influence offspring phenotype and life-trajectory. On one hand, developmental plasticity in response to a varying thermal environment during development may have long lasting effects on offspring behaviour, phenotype and thermoregulation (Hepp et al., 2015; Nord and Giroud, 2020; Page et al., 2022; Udino and Mariette, 2022). On the other hand, suboptimal environment during early-life can have long lasting effect on offspring fitness (i.e. "silver-spoon hypothesis"; Cooper and Kruuk, 2018; Lindström, 1999). For instance, deviation from the optimal incubation temperature can lead to an increased embryonic mortality, a reduced hatchling growth and early survival, as well as a reduced life-expectancy (Berntsen and Bech, 2016; Berntsen and Bech, 2021; Durant et al., 2013c; Hepp et al., 2015; Nord and Nilsson, 2016).

3.3. Cost of breeding

As aforementioned, parental care and nest design buffers offspring from the environmental stochasticity and allows for development in a suitable thermal environment (DuRant et al., 2019). This has many costs on parents such as increase energy expenditure due to nest thermoregulation (i.e. usually nest warming), increased resources to produce eggs and to fuel hatchling development, limited time dedicated to foraging, and potentially increased predation risk (Magnhagen, 1991; Williams, 1996). Breeding birds usually shows increases in energy expenditure compared to non-breeding individuals, and energy expenditure during incubation is higher for arctic birds, suggesting an increased need for parental nest warming in cooler environments (Nord and Williams, 2015). Consequently, parents may have to trade-off reproductive effort and/or success with self-maintenance during breeding, especially in sub-optimal conditions (Eduardo et al., 2010; Monaghan and Nager, 1997; Schultz, 1991).

3.4. Climate change and temperature extremes: implications for avian reproduction

Temperature is an important phenological cue for avian species (Verhulst and Nilsson, 2008; Visser et al., 2009). This can have important consequences on avian populations since as breeding timing is one of the main drivers of reproductive success. Indeed, breeding success usually decrease during the breeding season (Dunn, 2004; Verhulst and Nilsson, 2008). Match or mismatch between energy needs and food availability seems to be one of the main driver of this seasonal decline (Dunn and Møller, 2014; Thomas et al., 2001; Visser et al., 2006; Visser et al., 2012). Changes in the thermal environment may also have consequences for breeding success, parental investment and associated costs. For instance, experimental heating of nests may alleviate the costs of nest warming by parents, representing a "thermal relief" (i.e. decrease energy expenditure dedicated to thermogenesis; Bryan and Bryant, 1999; Pérez et al., 2008). Conversely, extreme examples of the trade-off between reproductive investment and self-maintenance have been reported during heat events, with some occurrence of nest desertion or parental mortality at the nest (Oswald et al., 2008; Sharpe et al., 2021). Despite nest design and parental care buffering the environmental variation in temperature, egg temperature can reach extreme temperature during extreme heat events resulting in catastrophic embryonic or post-embryonic mortality or offspring survival (Figure 10; e.g. McCowan and Griffith, 2021). Sublethal conditions during embryonic or post-embryonic development may also have long-lasting effects on offspring life-trajectory (Conradie et al., 2019).

Temperature is thus a crucial driver of avian reproduction. Birds balance the demands of self-maintenance and reproductive investment in the face of fluctuating thermal conditions. Understanding how birds respond to thermal challenges is of main importance when assessing individual fitness and predicting population fate. In the following section, we discuss avian thermoregulation, and consideration for avian populations in a context of climate warming.

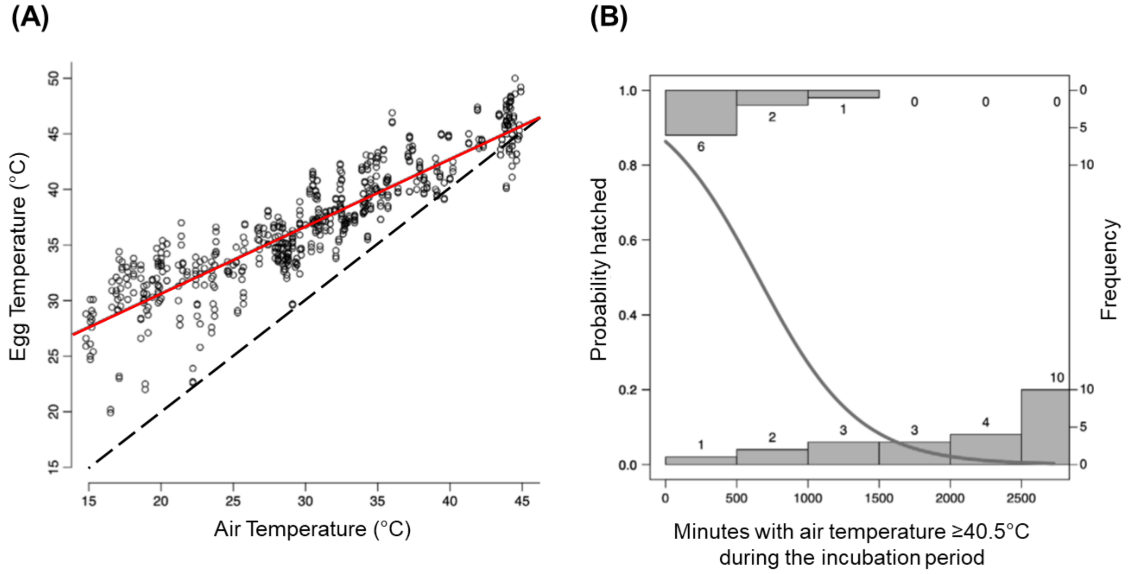

Figure 10. Egg temperature and hatching success during an extreme heat event in in wild zebra finches (*Taeniopygia guttata*). (A) Egg temperature in function of air temperature; relationship between egg temperature and air temperature is represented in red; isothermia is represented in dashed and black; (B) Probability of an egg to hatch depending on the amount of exposure to air temperature equal or higher at 40.5°C during incubation; The number of clutches is represented by each bar is illustrated on the graph. Adapted from McCowan and Griffith, 2021.

4. Avian thermoregulation

4.1. Concept of thermoregulation

Thermoregulation is the process of regulating body temperature (Tb) by balancing heat exchanges with the environment. In realistic scenarios, air temperature does not equate to the “temperature of the environment”, since sources of heat exchanges can be radiative, conductive or convective (Mitchell et al., 2018). In this thesis, we define the notion of environmental temperature (Te) as ambient or operative temperature depending on the context. We define operative temperature as the temperature of an imaginary isothermal ‘black’ enclosure around an animal that would exchange infrared radiant heat with the occupant at the same rate that the occupant exchanges heat with the actual environment by radiation, convection and conduction combined (Bakken et al., 1985; Mitchell et al., 2024). Ambient temperature corresponds to controlled air temperature within experimental settings, thus more closely analogous to operative temperature than to air temperature in the field (Cunningham et al., 2021).

Birds are usually considered to be homeothermic and endotherms, i.e. they maintain a stable Tb, and have high metabolic rates that result in sufficient heat production to maintain a high normothermic Tb (i.e. ‘warm-blooded’ animals; Angilletta et al., 2010; Seebacher, 2020). Normothermia approximates ~40°C in birds but vary depending on the taxa (Prinzinger et al., 1991; Scanes, 2015). It is worth noting that birds are able to display some levels of heterothermy (e.g. lower Tb at night, and higher Tb during high activity phases; McKechnie and Mzilikazi, 2011; Prinzinger et al., 1991). Maximum Tb are believed to be ~45-47°C for birds approximately (Freeman et al., 2022; McKechnie and Wolf, 2019). Avian species have to adjust their heat production and loss across a gradient of Te to maintain their Tb at normothermia (McKechnie and Wolf, 2019). The range of Te at which metabolic heat production (MHP; i.e. metabolic rate) is minimal represent the thermoneutrality zone (TNZ; Figure 11; Dunn and Møller, 2019). Upper and lower limits of the TNZ are usually referred to as UCT and LCT (upper critical temperature; lower critical temperature). Below the LCT, birds gradually increase their MHP in order to maintain normothermia (i.e. via shivering and/or non-shivering thermogenesis; Scanes, 2015). On the contrary, over a threshold of Te, evaporative heat loss (EHL; i.e. heat dissipated by cutaneous and/or respiratory evaporative water loss) start to increase, allowing maintenance of Tb despite increasing Te. Zone of least thermoregulatory effort is usually defined as the range of Te were MHP and EHL are minimal (ZLTE).

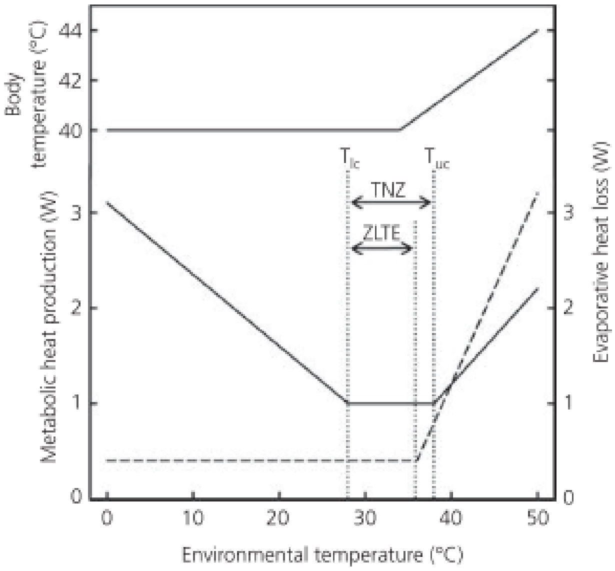

Figure 11. Approximate relationships between avian body temperature (upper panel), metabolic heat production (MHP, solid line, lower panel), and evaporative heat loss (EHL, dashed line, lower panel) at moderate to hot environmental temperatures. At high environmental temperatures, EHL/MHP>1, providing the basis for defense of body temperature below environmental temperature. The thermoneutral zone (TNZ) is the range of environmental temperatures between the lower and upper critical limits of thermoneutrality (LCT, UCT, respectively). Also shown is the zone of least thermoregulatory effort (ZLTE). The patterns of increasing body temperature and metabolic heat production shown are those expected for taxa such as passerines in which panting is the major avenue of evaporative heat dissipation; taxa in which gular flutter or cutaneous water loss predominate generally show much more modest increases in resting metabolic rate above the thermoneutral zone, and in some cases none at all (McKechnie et al., 2021a). Adapted from Dunn and Møller (2019).

4.2. Thermoregulation in the heat

Thermoregulation is achieved via physiological and behavioral adjustments to changes in environmental temperature (Te). Firstly, as long as Tb<Te, postural adjustments and increase in the blood perfusion of extremities with the environment allows for passive heat dissipation, i.e. via "thermoregulatory windows" (e.g. beak, legs, skin; Figure 12; Greenberg et al., 2012; Szafrańska et al., 2020; Tattersall et al., 2018). Alternatively, birds can dissipate heat via evaporative water loss (EWL), and they are completely reliant on it when Tb>Te. In most cases, evaporative heat dissipation is the result of cutaneous and respiratory water loss process. Since birds do not dispose of sweat gland, cutaneous water loss usually represents a minor part of total evaporative water loss during heat exposure for most bird species. Although less common, some species use excretion as cooling mechanism (i.e. urohydrosis, Cabello-Vergel et al., 2021; Cabello-Vergel et al., 2023). In addition, most birds show increases in Tb even when Tb<Te, which some authors refer to as "facultative hyperthermia" (Gerson et al., 2019; Tieleman and Williams, 1999). This may be explained as a "heat storage" strategy, meaning individuals tolerate some level of hyperthermia to reduce water requirements needed to maintain normothermia, suggesting a trade-off between hyperthermia and dehydration during heat exposure. It is also worth noting that birds possess a specialized vascular structure, i.e. the rete ophtalamicum, that allows to cool down brain temperature relative to core Tb, preserving from deleterious effect of hyperthermia (Porter and Witmer, 2016). Secondly, in the same way as bird population seems to track climate change by shifts in their phenology and range of distribution, individuals avoid heat exposure via changes in their pattern of activity and by exploiting thermal refugia (Carroll et al., 2017; Ramos et al., 2023; Ruth et al., 2020). Birds reduce their foraging activity, and increase shading or bathing behaviors during heat events (Austin, 1978; Kemp et al., 2020; Oswald et al., 2008; Playà-Montmany et al., 2023; Smit et al., 2016; Thompson et al., 2018).

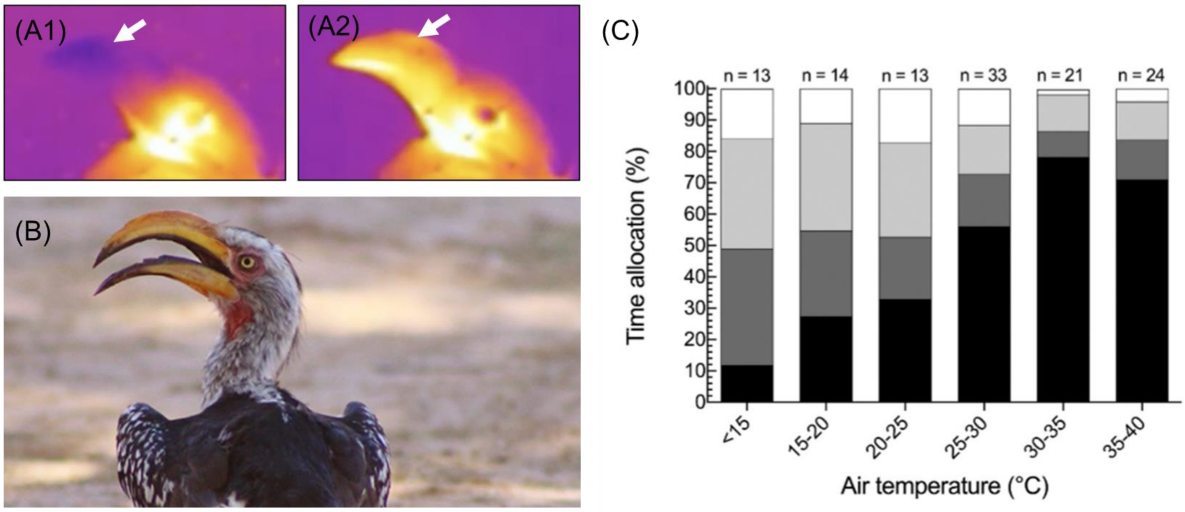

Figure 12. Example of heat dissipation and adjustment of daily activity pattern during exposure to high temperatures. (A) Non-evaporative heat dissipation through the beak, which function as a heat radiator when environmental temperature is still below body temperature. Adapted from McKechnie and Wolf, 2019; (B) Evaporative heat dissipation via panting in the Southern yellow-billed hornbills (*Tockus leucomelas*). Adapted from Cunningham et al., 2021; (C) Pattern of time allocation by non-breeding Red larks (*Calendulauda burra*) in relation with increasing air temperatures; inactivity (black), foraging (dark grey), movement (light grey) and territorial (white) behaviour; From Kemp et al., 2020.

UCT across all birds species seem to be positively correlated with local air temperature, most likely testifying of an adaptation of species to their thermal environments (Qu and Wiens, 2020; Song, 2018; Sunday et al., 2019). Yet, Reaction to norms heat exposure varies between populations, species and taxa (Gerson et al., 2019; McKechnie et al., 2021a; Smit et al., 2018). For instance, desert passerines having relatively low UCT compared to other taxa, potentially because of their reliance on panting, which is thought to be relatively energy and water-inefficient compared to other cooling mechanisms. Additionally, there is also intra-individual variability in reaction to heat exposure (i.e. phenotypic plasticity). Multiples studies have reported varying reaction norm to high temperature depending on the time of the year or after repeated exposure to high temperatures (i.e. acclimatization or acclimation; Cooper et al., 2020; González-Medina et al., 2023; Noakes and McKechnie, 2020; Noakes et al., 2016; Pessato et al., 2023).

4.3. Heat stress effects

Heat stress can promote hyperthermia and dehydration in birds, leading to a wide array of deleterious such as altered hormonal levels (e.g. glucocorticoids and thyroid hormones), metabolism (lipid metabolism, protein homeostasis), oxidative damages, immuno-suppression and chronic inflammation, potentially leading to tissue damages (gut, liver and heart function) and eventually impaired locomotor and cognitive performance, reproduction, growth and survival (Figure 13; reviewed by Bohler et al., 2021; Brugaletta et al., 2022; Oladokun and Adewole, 2022; Teyssier et al., 2022; Vandana et al., 2021). Dehydration itself affects many aspects of avian performance (reviewed by El Sabry et al., 2023), including fertility, reproduction (Giuliano et al., 1995; Giuliano et al., 1998; Koerth and Guthery, 1991; Niranjan and Srivastava, 2019) and growth (e.g. Goldstein and Ellis, 1991; Herr Viola et al., 2009; Mhmoud et al., 2023). Dehydration also upregulates physiological markers of stress in birds (e.g. corticosterone or heterophil to lymphocyte ratio; Cain and Lien, 1985; Iheukwumere and Herbert, 2003; Toghyani et al., 2011).

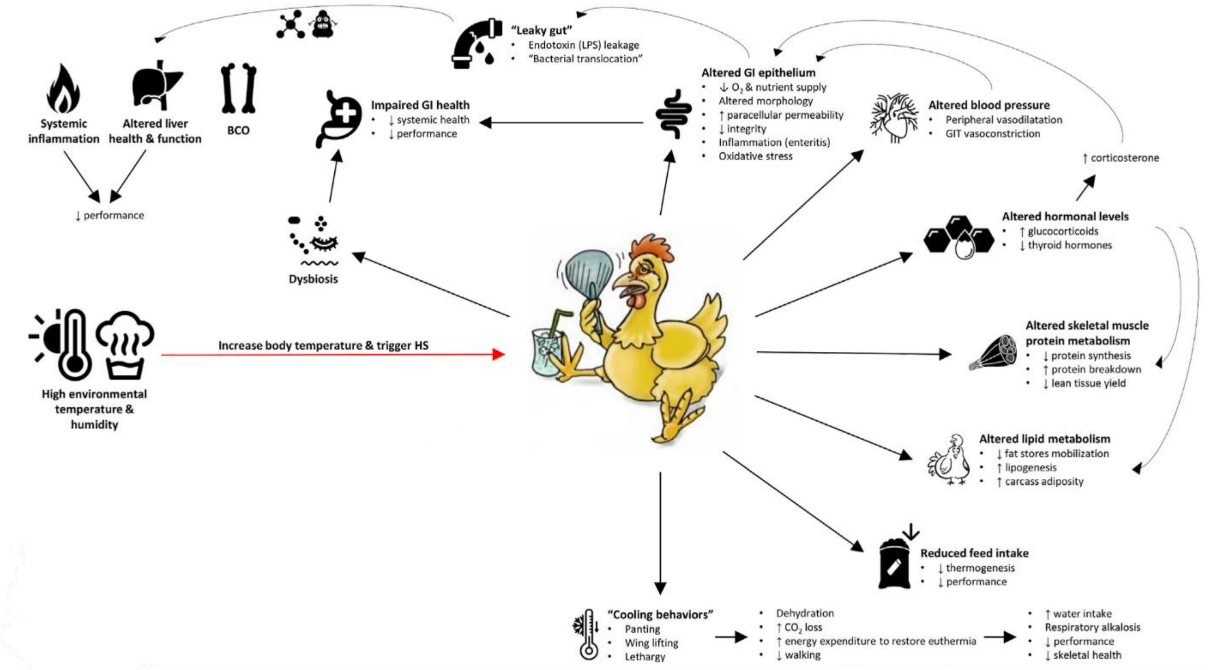

Figure 13. Summary chart of the main effect of heat stress on modern chicken lines (*Gallus domesticus*). Adapted from Brugaletta et al., 2022.

4.4. Consequences for bird populations

Hyperthermia risk and cooling requirements of avian species are expected to increase with climate change, and may consequently threaten several populations (Figure 14; Albright et al., 2017; Cabello-Vergel et al., 2022; Conradie et al., 2020; McKechnie and Wolf, 2010). There have been multiple reports of mass-mortality events during heatwaves (Jones et al., 2023; McKechnie et al., 2021b; Piatt et al., 2020a; Quintana et al., 2022; Saunders et al., 2011). A potential increase in the frequency and intensity of heat events is predicted to have deleterious effects for some avian populations, especially in arid habitats where water supply can be limited during heat events (Iknayan and Beissinger, 2018; Marcelino et al., 2020; Pattinson et al., 2022; Riddell et al., 2019; Riddell et al., 2021). Moreover, variation in activity budgets, increasing competition for thermal refugia and potentially impaired performance during heat exposure may also have deleterious effects on populations (e.g. Danner et al., 2021; van de Ven et al., 2019). Increased time spent thermoregulating during heat events may limit the time budget for other activities such as foraging or nest attendance (Bourne et al., 2020a; Bourne et al., 2023; Funghi et al., 2019; Sharpe et al., 2021; Smit et al., 2016). Quoting Cunningham et al (2021): "For endotherms facing hot conditions, maximizing fitness therefore involves balancing the metabolic, water, and performance costs of physiological thermoregulation against the opportunity costs associated with behavioral thermoregulation”.

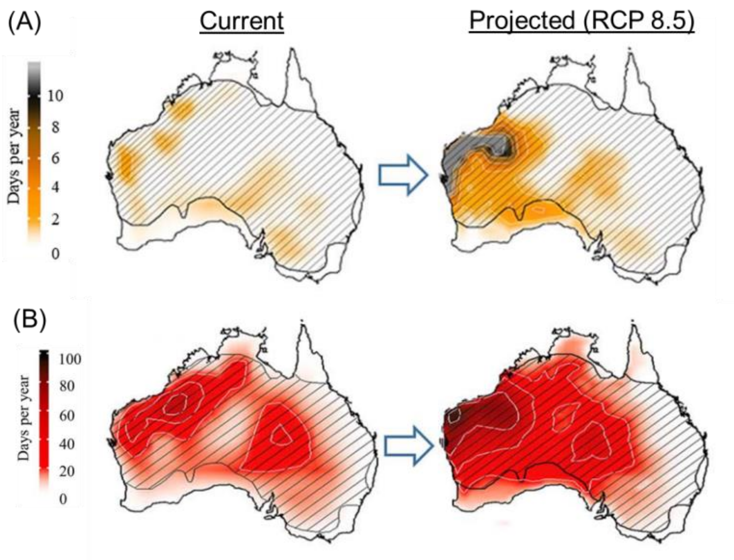

Figure 14. Current and projected lethal hyperthermia and dehydration risk for wild Zebra finches (*Taeniopygia guttata*) across Australia; (A) Average number of days per year with condition associated with lethal hyperthermia risk (i.e. air temperature >46°C); (B) Average number of days per year with conditions associated with a moderate lethal dehydration risk (i.e. survival time <5hr). Current scenario: 2000-2010 CE; Projected scenario: RCP 8.5, 2080-2090 CE. Current range of distribution of zebra finches are illustrated by cross-hatching. Adapted from Conradie et al., 2020.

5. Scope of the thesis

Climate change is emerging as one of the key drivers of the current biodiversity erosion. In this thesis, we aimed to investigate whether an increasing exposure to high temperatures could have an effect of avian species, from the physiological response to the ecological consequences. We consequently structured this thesis in two parts. In the first axis, we investigated the influence of high temperatures on avian reproduction, and its implication at the population level (Theme 1: “Influence of high temperatures on birds reproduction”). In the second axis, we dived deeper in the physiological mechanisms, and focused on the influence of high temperatures on thermoregulation (Theme 2: “Physiological response to heat exposure in birds”).

Among studies on ecological and demographic traits of birds in regard to climate warming (e.g. survival, phenology, distribution), reproduction appears to be one of the most studied traits (Figure 15). As discussed in the introduction, the thermal environment represents an important driver of avian reproduction. Climate change effects on avian populations are consequently likely to be mediated by changes in reproduction. We consequently decided to review the influence of high temperatures on avian breeding success at a global scale (Chapter 1: “The complex relationship between high temperatures and avian breeding success: insights from a global review”). In this review, we aim to provide an overview of the topic, including perspectives and guidelines for future research. We discuss whether the observed association between high temperatures and breeding success are explained by a direct effect on thermoregulation (i.e. heat stress or thermal relief), to an indirect effect mediated through changes in phenology, abiotic factors and trophic relationships (i.e. food availability, predation, parasitism and competition). We expect that high temperatures may have different effects on breeding success depending on the local climate, especially in regards to species thermoregulation.

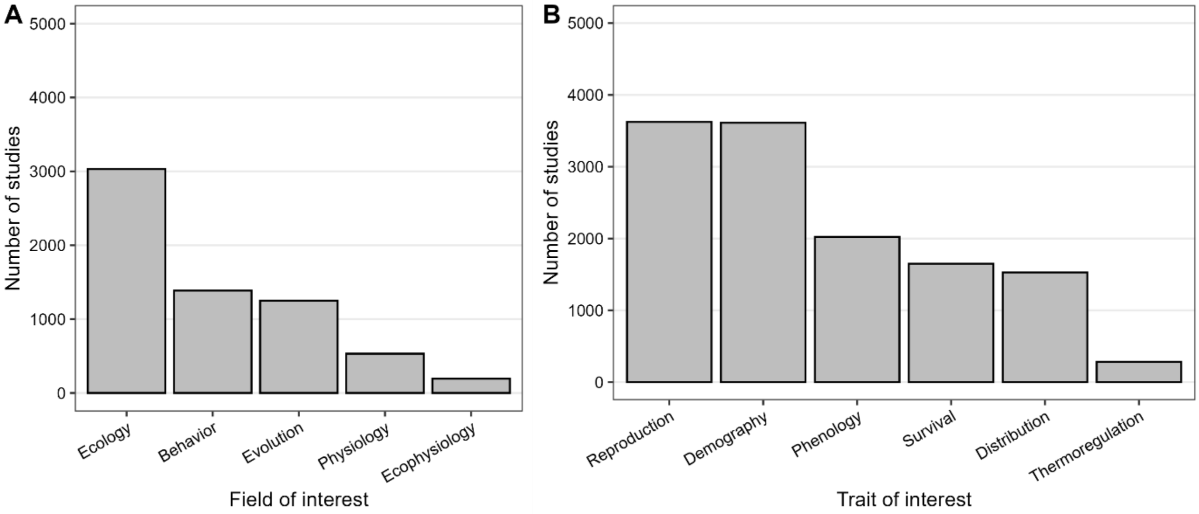

Figure 15. Research effort on different biological fields or traits in regard to climate change in avian species, illustrated as number of studies. Request on the 2024/11/13 in Web of Science library as following: “(TS=climate AND (TS=warming OR TS=change)) AND (TS=avian OR TS=bird$) AND “keywords”. Keywords for reproduction were “(TS=reproduct* OR TS=breeding); Keyword for thermoregulation was “thermoreg*”.

Potential impact of climate change are likely to interact with urbanization (Sumasgutner et al., 2023). In the second chapter, we investigated the influence of weather on great tits phenology and breeding success across an urbanization gradient (Chapter 2: "Effects of weather and breeding timing on great tit (*Parus major*) breeding success in a forest and urban environment"). We take advantage of a long-term monitoring program and use a correlative approach. We assessed whether great tits breeding success was related to rain, temperature and breeding timing in an urban and forest system. We expect temperature to be positively correlated with great tits breeding success (e.g. Ahola et al., 2009; Eeva et al., 2020; Marques-Santos and Dingemanse, 2020), but that extreme temperatures may have deleterious effects (Glądalski et al., 2020; Pipoly et al., 2022). We also expect clutch size and reproductive success to decline during the breeding season (Charmantier et al., 2008; Verhulst and Nilsson, 2008; Verhulst et al., 1995). Environmental and individual quality may buffer potential effects of weather, meaning weather effects may be less pronounced in urban sites. Additionally, urban environments may be less seasonal due to the presence of alternative food sources or predators. We consequently expect a potential seasonal decline in breeding success to be more prevalent for urban compared to forest nests.

Research effort on avian physiology, ecophysiology or thermoregulation in regard to climate change seemed to be relatively underwhelming compared to fields such as ecology, and to a lesser extent behavior or evolution (Figure 15). Yet, understanding the influence of these global changes at a physiological level is crucial to refine our understanding of the current pressures on biodiversity, improve our forecast and set up appropriate conservation strategies (Bozinovic and Pörtner, 2015; MacMillan, 2019; Urban et al., 2016). Disentangling direct from indirect effects of high temperatures on avian reproduction necessitates to increase our research efforts and develop ways to assess effects of heat exposure on wild birds. In the second theme of this thesis, we discuss the physiological response to heat exposure in avian species (Theme 2: "Physiological response to heat exposure in birds").

When exposed to heat, birds can either tolerate hyperthermia and/or dissipate heat through evaporative water loss (Gerson et al., 2019; McKechnie and Wolf, 2019). Birds usually use a combination of heat storage and increased heat dissipation to achieve the most favorable thermal and osmotic balance, i.e. limiting hyperthermia while maintaining homeostasis of body fluids, suggesting a trade-off between hyperthermia and dehydration risk. While cooling costs and dehydration risk of wild birds are expected to increase with climate warming, very few studies have assessed hydration status of wild birds. Several experimental studies have measured various physiological markers during dehydration protocols in birds, but these studies have never been reviewed, and seemed to have found little application in field studies. In the third chapter of this thesis, we review the hyperthermia-dehydration trade-off, and the physiological markers of avian dehydration, using a meta-analysis and systematic approach (Chapter 3: “Physiological markers of avian dehydration: assessing the hyperthermia-dehydration trade-off”). We hypothesized that plasma osmolarity and hematocrit would predict dehydration and scale with dehydration severity. We also expect that other less-invasive markers such as urine osmolarity could be suitable to assess hydration status. We discuss dehydration tolerance and perspectives for future studies.

As aforementioned, increased cooling requirements with climate change is likely to threaten avian species (Albright et al., 2017; Cabello-Vergel et al., 2022; McKechnie and Wolf, 2010). For instance, hyperthermia and dehydration risk is predicted to increase with climate change for wild zebra finches (*Taeniopygia guttata*; Conradie et al., 2020). In the fourth chapter of this thesis, we investigate the physiological response to heat exposure and subsequent recovery in captive zebra finches (Chapter 4: “Physiological response to heat exposure in captive zebra finches (*Taeniopygia guttata*) and inter-individual variation”. Heat response is likely to show inter-individual variation depending on several traits (e.g. body condition, biological age, sex), and we therefore investigated whether heat response would show age or sex-dependent patterns. We expected heat challenge to promote hyperthermia and dehydration. In humans, older individuals have a lower heat tolerance and higher risk of mortality during heatwaves (Cramer et al., 2022; Gallo et al., 2024). We therefore expected heat response and recovery to be age-dependent.

GENERAL METHODS

Lesser kestrels (*Falco naumanni*) extreme breeding failure was reported during heatwaves in 2021-2022 (Italy). Breeding success was buffered from heatwaves in experimentally cooled nests (Corregidor-Castro et al., 2023). Photo from Macaulay Library (ML628193030).

1. Study model

1.1. Great tits (*Parus major*)

Great tit (*Parus major*) is a relatively small bird (body mass ~ 18g; Cramp et al., 1993) from the Passeriformes order and Paridae family. The distribution of great tit ranges mainly encompasses north Africa, western Europe and Eurasia (Figure 1A). Most of the great tit distribution ranges is within temperate or continental climates according to the Köppen-Geiger classification (Figure 1B).

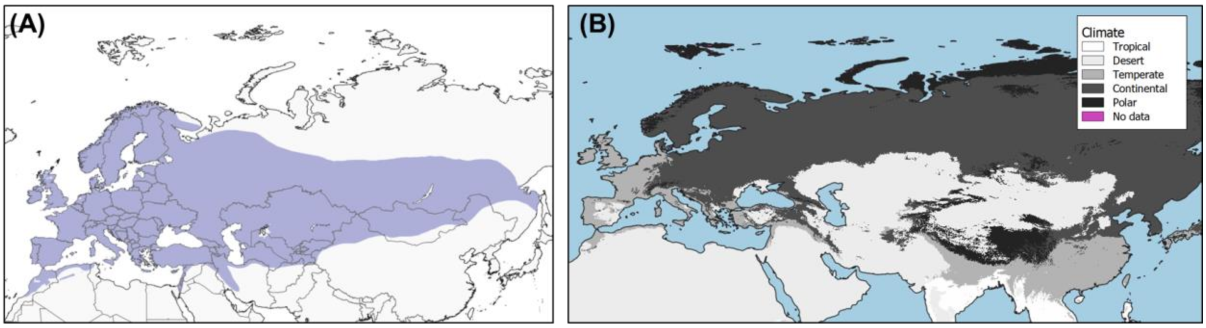

Figure 1. Great tit (*Parus major*) distribution range and climate (A) Great tit distribution range. From Kirwan et al., 2024 (B) Köppen-Geiger climate classification across great tit distribution range (Beck et al., 2018a). Great tits are mainly abundant in temperate and continental climates.

Great tits have a mixed insectivorous and granivorous diet, but mainly feed nestlings with terrestrial arthropods prey (Cowie and Hinsley, 1988). Great tits usually nest in tree-cavities, but also opportunistically breed in artificial structures (Maziarz et al., 2015). Nest is mainly composed of moss, sticks and feathers (Álvarez et al., 2013). Great tits breed during spring (i.e. from March to June; although breeding initiation depends on the latitude; Sanz, 2002). Female lay one egg per day, and clutch size is usually within 6 to 13 eggs. The onset of the incubation most commonly matches clutch completion, and incubation duration last ~13 days (Álvarez and Barba, 2014). While great tits have a bi-parental care, only the female incubates (Bueno-Enciso et al., 2017). The female develops a brood patch during breeding. Hatchling are altricial (i.e. born featherless, unable to move and with non-functional eyes). Offspring fledge at ~18-20 days post-hatching, and have a relatively low natal dispersal range (Greenwood et al., 1979; Naef-Daenzer et al., 2001). Great tit thermoneutrality zone range approximately from 18°C to 35°C (Figure 2; Cabello-Vergel et al., 2022; Playà-Montmany et al., 2021).

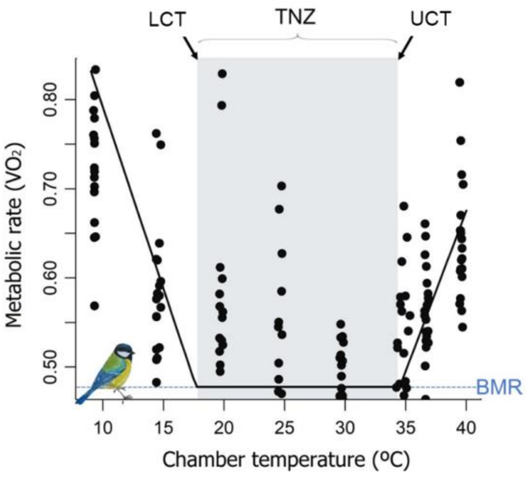

Figure 2. Thermoneutral zone in great tits (*Parus major*). TNZ: thermoneutral zone. BMR: basal metabolic rate. LCT: lower critical temperature (17.7°C). UCT: upper critical temperature (34.5°C). UCT of great tits was reported to be quite similar in Cabello-Vergel et al., 2022 (35.2°C). Adapted from Playà-Montmany et al., 2021.

Great tits are considered as great model species in ecology (Figure 3A). Great tits population are monitored across Europe (e.g. France, Charmantier et al., 2008; Poland, Gladalski et al., 2020; Spain, Greño et al., 2008; Hungary, Pipoly et al., 2013; Sweden, Salmón et al., 2017). Moreover, great tits are considered to be urban exploiters and represent one of the best indicators of environment quality in urban systems (Morelli et al., 2021). Nonetheless, great tits are not common as model species for experimental studies in captivity. In France, great tits are protected since 1981. While rearing great tits in captivity is possible, other study models are usually preferred. In our case, we conducted our laboratory experiment on captive zebra finches.

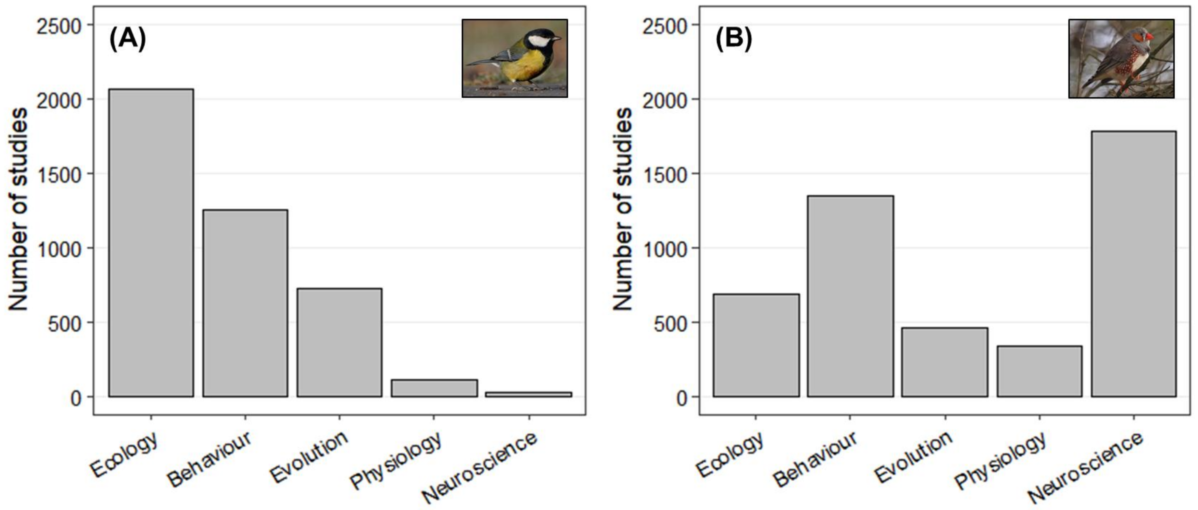

Figure 3. Number of studies in function of the field of research for (A) great tit (*Parus major*) (B) zebra finch (*Taeniopygia guttata*). Web of science survey: (TS="great tit*" OR TS="parus major"), (TS="zebra finch*" OR TS="Taeniopygia guttata"). Survey was conducted on the 2024/12/29. Total number of studies was 5961 and 5949 respectively, ranging from 1975 to 2024 in both cases. Photo from Macaulay Library (ML628180406, ML628119636).

1.2. Zebra finches (*Taeniopygia guttata*)

Zebra finches (*Taeniopygia guttata*) are relatively similar-sized passeriformes as great tits (body mass ~15g) from the estrildidae family. The zebra finch is one of the most studied bird (Griffith et al., 2021). With the exception of poultry models such as the chicken (*Gallus domesticus*) or the japanese quail (*Coturnix japonica*), the zebra finch represents one of the most popular model specie for laboratory experiments. This is because zebra finch breed opportunistically, has a high fertility, a fast growing rate and acclimate relatively well to captive environments (Griffith et al., 2017a; Griffith et al., 2017b; Griffith et al., 2021). Zebra finch was the first passerine to have his genome entirely sequenced and is especially popular as model specie in neurosciences (Figure 3B; Lovell et al., 2020; Warren et al., 2010). Zebra finches are mainly distributed in desert climates across their distribution range (Figure 4). Zebra finches can be exposed to high temperature in their natural habitat, and their thermoregulation has been extensively studied (Figure 5; Cade et al., 1965; Calder, 1964; Cooper et al., 2020a; Cooper et al., 2020b; Pessato et al., 2023; Wojciechowski et al., 2021). In the wild, exposure to heat events may constrain zebra finches time and energy-budget, leading to deleterious effects on their reproduction, from impaired nestling growth to catastrophic breeding failures (Cooper et al., 2019; Funghi et al., 2019; Griffith et al., 2017a; McCowan and Griffith, 2021).

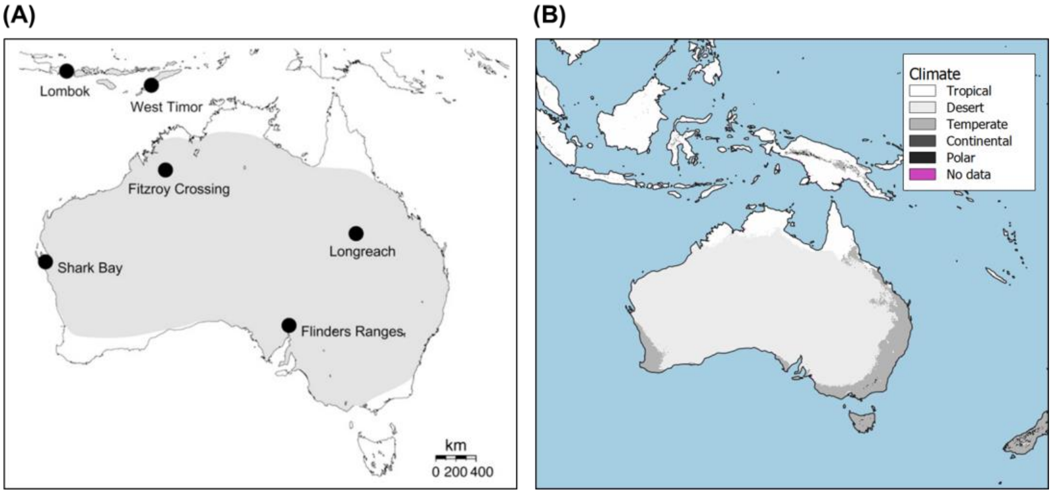

Figure 4. Zebra finch (*Taeniopygia guttata*) distribution range and climate (A) zebra finch distribution range. From Balakrishnan and Edwards, 2009 (B) Köppen-Geiger climate classification across great tit distribution range (Beck et al., 2018a). Zebra finch distribution range encompasses mainly desert climate, but also tropical and temperate climates.

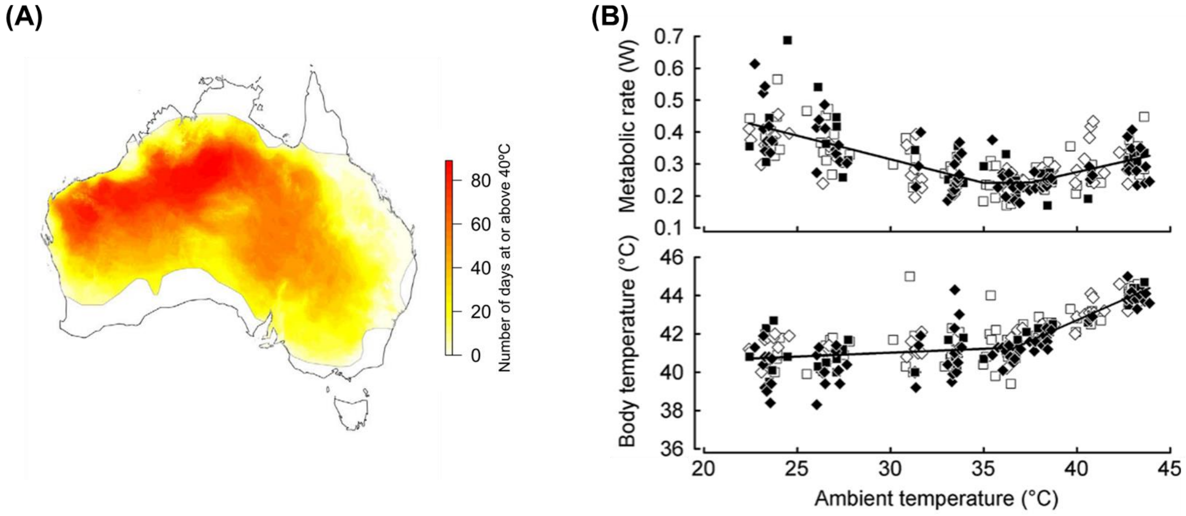

Figure 5. Zebra finch exposure to high temperatures and physiological response to heat exposure (A) number of days exceeding 40°C during the austral summer 2018-2019 across zebra finches (*Taeniopygia guttata castanotis*) range of distribution. Adapted from Danner et al., 2021 (B) Metabolic rate and body temperature in function of the ambient temperature. Zebra finch thermoneutrality zone range from 34.9°C to 37.5°C. Zebra finches body temperature increased linearly above temperature exceeding 35.9°C. Adapted from Wojciechowski et al., 2021.

2. Review of the literature

In this thesis, we conducted two systematic reviews of the literature (chapters 1 and 3). To do so, we used the PRISMA methodology (Figure 6; Nakagawa et al., 2017). We conducted both data searches using the Web of Science (WOS) database. WOS database registers articles title, abstract, keywords, authors, date and journal of publication. Briefly, WOS query system returns a finite number of results. For instance, using the term “color” will not return articles with the term “colour”. We used boolean operator “AND”, “OR” and “NOT” within our query (“AND”: finds records containing all terms separated by the operator; “OR”: finds records containing any of the terms separated by the operator; “NOT”: excludes records containing certain terms from your search). We systematically used “TS” as field tag, meaning we searched for our terms within the title, abstract and keywords of each article. Finally, we used wildcards “$” or “*” when necessary (“bird$” will return terms “bird” and “birds”; “zebra finch*” will return terms “zebra finch” and “zebra finches”). The exact search and date are systematically reported within material and methods section of each chapter. We defined our criteria of eligibility prior to conduct the search. Finally, we used the PlotDigitizer software to extract data from plots when the desired information was not available (Aydin and Yassikaya, 2021).

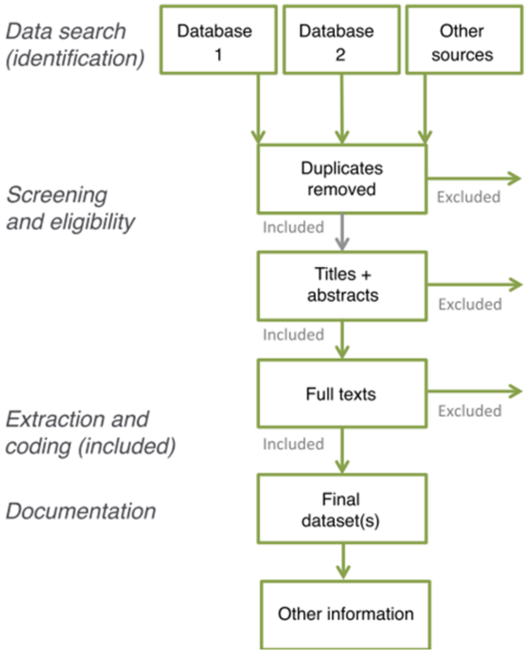

Figure 6. Preferred Reporting Items for Systematic Reviews and Meta-Analysis (PRISMA). From Nakagawa et al., 2017.

3. Correlative approach: great tits population monitoring

3.1. Study site

In chapter 3, we studied the influence of weather and breeding timing on reproductive success in great tits (*Parus major*) in an urban and forest habitat. The great tits population monitoring program started in 2010 in the forest site (La Wantzenau), and in 2014 in Strasbourg. The urban and forest sites are located 20km away from each other (Figure 7). Nests in Strasbourg are spread between 12 sites, ranging from tree-lined routes in the city center to urban parks. Great tits breed in artificial nest boxes in both urban and forest sites. Blue tits also exploit these nest boxes. Great tits represent approximately 75% of the nest box occupancy and blue tits approximately 25%.

Figure 7. Map illustrating the urbanization gradient between Strasbourg city center (left) and La Wantzenau forest (right). Site are 20km away from each other.

The forest site borders the Wantzenau municipality (230 inhabitants/km^2). The vast majority of tree species in the forest are deciduous trees, such as pedunculate oak (*Quercus robur*), field elm (*Ulmus minor*) or silver poplar (*Populus alba*). Nest boxes are placed along trails in the forest. Although there is some level of human disturbance in the forest, the anthropogenic pressure is likely way higher in urban sites. Strasbourg is the 8th most populated city in France, with ~865000 inhabitants, and a density of ~3638 inhabitants/km^2. Most common tree species across urban sites are european hornbeam (*Carpinus betelus*), european beech (*Fagus sylvaticus*) and sycamore (*Acer pseudoplatanus*). Vegetation cover and food availability are considerably lower in urban sites (Figure 8; Saulnier et al., 2022). Clutch size, number of fledging and fledging survival is lower in urban sites (Saulnier et al., 2022). Additionally, urban fledglings have a lower body condition (Saulnier et al., 2023).

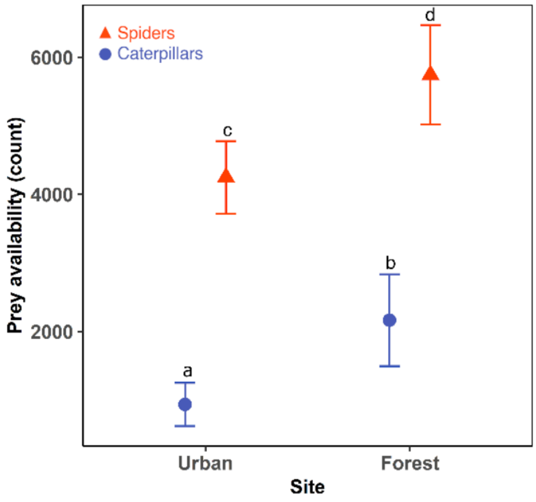

Figure 8. Prey availability in urban (Strasbourg) and forest (La Wantzenau) sites across 2015 and 2016. From Saulnier et al., 2022.

3.2. Monitoring protocol

Monitoring of breeding is monitored every year from the start of March to the end of June. Nest are checked every 2-3 days from egg-laying to the start of the incubation. Once incubation is started, hatching date is estimated, visits are paused until hatching to minimize disturbance during incubation. Nest are visited once or twice times before ringing (i.e. at 13-16 days post-hatch). Fledging are weighed (±0.1g) during ringing. We also measure the tarsus and skull length using a caliper (±0.1mm), and wing length using a small ruler (±1mm). Finally, nests are visited one last time to assess fledging success. Overall, this protocol allows to estimate the laying date (±1 day), hatching date (±1 day), clutch size, hatching success (proportion of eggs hatching) and nestling survival until banding and nest departure. Hourly air temperature and precipitation are monitored by a weather station in the city center of Strasbourg since 1990 (MeteoFrance). Temperature measured by the weather station did not differ from temperature measured by thermologgers (Ibuttons^{TM}; Maxim Integrated®) placed in the shade near nests in urban and forest sites (Saulnier, unpublished).

4. Experimental approach: zebra finches experiment

4.1. Rearing conditions

Zebra finches were provided by the Max Planck Institute of Ornithology. All individuals were born in captive conditions, either at the Max Plank institute or directly at the IPHC (Institut Pluridisciplinaire Hubert Curien). Zebra finches were housed in cages measuring 75*72*93cm (l*L*h) under typical rearing conditions(Griffith et al., 2017a). Temperature was maintained at 22°C with a 14-hour photoperiod (day from 6am to 8pm). Zebra finches had ad libitum access to water, dry seed mix as food source, and to shell grit and cuttlebone. Drinking water was changed twice a week, and birds were provided access to a bath once a week. Males and females were not housed in the same cages. Birds were up to 8 individuals per cages. Birds were never isolated unless showed symptoms of sickness (e.g. diarrhea).

4.2. Experimental design

During the experiment, we exposed zebra finches to ambient temperatures of 30°C and 40°C during 4 hours. During the experiment, we captured 4 birds each day at 8:00. Individuals were placed in individual cages without food but with water available (Figure 9). We deprived individuals from food to ensure individuals were non in a post-absorption state during respirometry, and to limit variation in body mass loss during the respirometry trial (Figure 10; Gavrilov and Gavrilov, 2019). At 11:00, birds were placed in small cylindrical wire mesh cages inside 0.53L airtight polypropylene metabolic chambers (Sistema®). No food or water was available during the respirometry trial. Temperature was initially set at 30°C, and we either maintained 30°C, or progressively increased it so it reached 40°C at 12:00. Respirometry data acquisition started at 12:00 and lasted until 16:00. Birds were kept in small cages with only water available until 17:30 (short-term recovery), and were then reintroduced to their maintenance cages afterward. Overall, birds were food restricted from 08:00 to 17:30, and water-restricted from 11:00 to 16:00. We recaptured these individuals 48h after the end of the respirometry trial to asses mid-term recovery. All birds were exposed to both 30°C and 40°C during the experiment. They were randomly assigned to a temperature treatment during the first respirometry trial (e.g. 30°C), but underwent the other treatment 30 days later (e.g. 40°C).

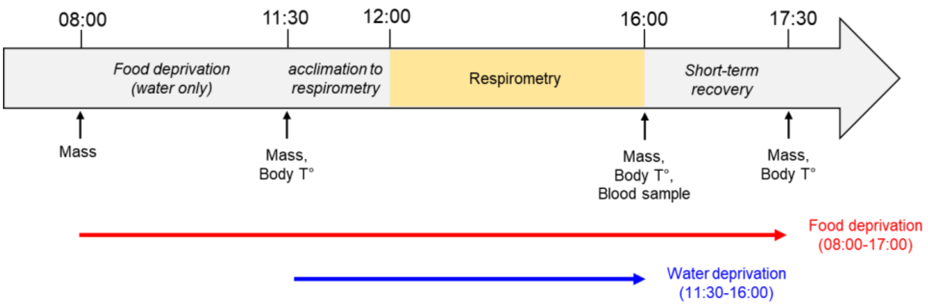

Figure 9. Schematic representation of the experimental design.

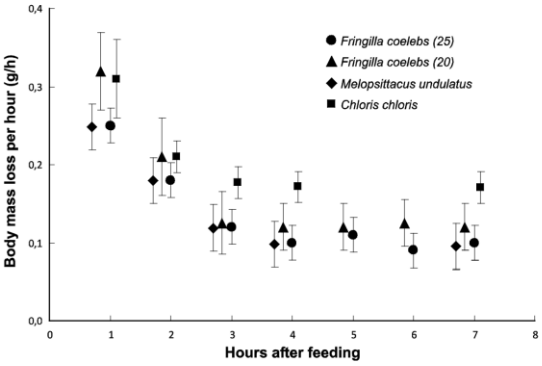

Figure 10. Body mass loss after feeding in three Passeriformes. Body mass loss is stable after ~4 hours post-feeding. From Gavrilov and Gavrilov, 2019.

4.2.1. Respirometry system

We used a respirometry system to assess the physiological response to heat exposure. Briefly, an animal is placed in an airtight chamber with precise control of air flux in the chamber. We used a pull flow system during our experiment (Figure 11; Lighton, 2008). Animal consumption or excretion of gases can be estimated from the difference in concentration between the air pulled from an empty chamber, and the air pulled from the occupied chamber. By measuring partial pressure of O_2, CO_2 and H_2O, we were able to estimate oxygen consumption (VO_2; ml/min), carbon dioxide production (VCO_2; ml/min) and evaporative water loss (PH_2O; mg/min) during exposure at 30°C and 40°C. We sequentially measured five chambers, one being empty (i.e. “baseline”) and the four others being occupied by zebra finches (Figure 12). VO2 and/or VCO2 can be used to estimate metabolic rates (i.e. energy expenditure), and ultimately metabolic heat production (MHP; in W). Additionally, some level of heat is dissipated by evaporation, and we can consequently estimate evaporative heat loss (EHL; in W). The EHL/MHP ratio is referred to as “cooling efficiency”. Considering a non-evaporative heat loss to be null, EHL/MHP<1 would results in a net heat gain, resulting in increasing body temperature. We also estimated the metabolic water production (MWP) and relative water economy (MWP/EWL). Even when considering non-evaporative water loss (i.e. water excretion) to be null, MWP/EWL<1 would results in a net body water loss. Further details on physiological variable calculations can be found in the material and methods section of the chapter 4.

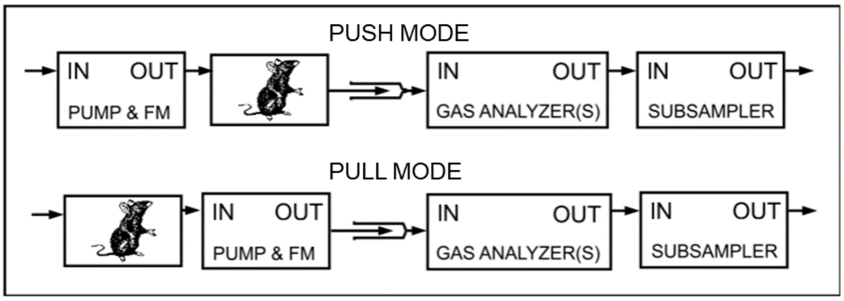

Figure 11. Push and pull flow system in respirometry**.** In this experiment, we used a pull system (i.e. with the pump and flow meter pulling air through the system. From Lighton, 2008.

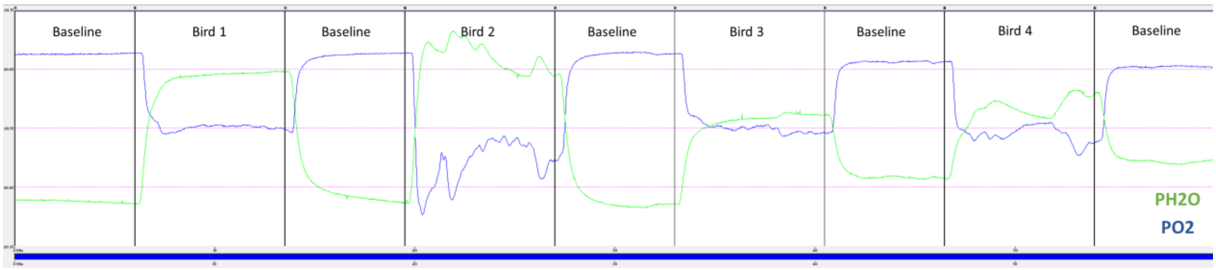

Figure 12. Data acquisition during respirometry. Each metabolic chamber was measured sequentially during a cycle of 60min. Baseline was established before and after each measurement during 6min, and each bird was sampled during 7.5min. This cycle was repeated 4 time in total (from 12:00 to 16:00). Partial pressure of H_2O (PH_2O) and O_2 (PO_2) are represented in blue and green respectively.

4.2.2. Body mass, temperature and blood sampling

Birds were weighed using an electronic scale with 0.01g precision. We measured cloacal temperature as a proxy of core body temperature (Andreasson et al., 2023). Cloacal temperature was measured by insertion of a K-type thermocouple connected to a thermometer (Testo925™; Testo®; precision ~0.1°C). Since cloacal temperature increases rapidly with handling stress, we always measured cloacal temperature directly after bird capture, and we stopped when the reading was stable for 3 seconds. Finally, we sampled blood directly after each respirometry trial, and after mid-term recovery (t_2, t_4). We sampled ~75µL of blood by brachial venipuncture using 26Gx$^1/_2$" needles (Agani™; Terumo®) and heparinized capillary tubes (Hirschmann®). Plasma was placed in ice until centrifugation (10 minutes at 2.10^3G and 4°C) in the hour following the blood sample. All samples were frozen at -80°C until later analyses.

4.2.3. Hematological parameters

Blood volume and plasma osmolarity are likely to decrease during dehydration (chapter 3). We consequently measured blood cell concentration using a flow cytometer (BD Accuri™ C6 Plus; BD Biosciences®). We counted the total number of events in 50µL of $^1/_{500}$ diluted whole blood in PBS. Briefly, flow cytometry allows to focus a sample ideally one cell at a time through a laser. Occlusion of the laser by the cell will be registered by detectors (Figure 13), allowing precise measurements of cell counts. Because we know the volume sampled, we can calculate cell concentration. We measured plasma osmolality of 10µL of $^1/_2$ diluted plasma in ddH_2O using a vapor pressure osmometer (Vapro™; ELITechGroup®). The boiling point of a solution increase with its osmolarity. Vapor pressure osmometer use the relationship between boiling point and vapor pressure to measure solute concentration.

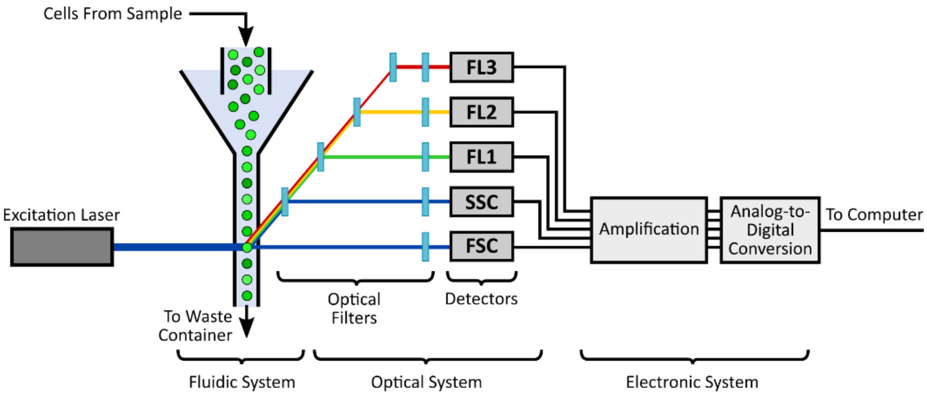

Figure 13. Schematic representation of the detection system of a flux cytometer. Forward scatter (FSC) and side scatter (SSC) measures describes the shape, size and granularity of the cells. FL detectors are used to detect fluorescence.

THEME 1. INFLUENCE OF HIGH TEMPERATURES ON BIRDS REPRODUCTION

Chapter 1. The complex relationship between high temperatures and avian breeding success: insights from a global review

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Picture of Sociable Weavers (*Philetairus socius*) nests (Macaulay Library ML626618255). Sociable weaver breeding success is impacted by high temperatures through direct effects (i.e. heat stress) and indirect effects (increase predation by snakes; D'Amelio et al., 2022).

1. Abstract

Climate change is one of the major threats to biodiversity. Understanding how species cope with increasing temperature is of prime importance when assessing population viability. We present a systematic review of the association between high temperature and wild birds' breeding success. We conducted a survey in the Web of Science library and retained 229 studies based on our eligibility criteria. We qualitatively assessed whether studies investigated high temperatures, and define high temperatures as relative to the average temperature at the study site, or to the species thermoregulation depending on the information available. We focus on avian species, as they are widespread throughout the world and benefit from numerous long-term monitoring programs. We found the relationship between high temperatures and breeding success was most likely multifactorial. We discuss the complex relationship between high temperatures and avian breeding success, and strongly emphasize on the importance of disentangling "direct" effects (mediated through thermoregulation) from "indirect" effects (mediated through phenology, biotic and abiotic factors). Finally, we briefly present some considerations for future studies.

2. Introduction

Climate change is one of the major threats on biodiversity (Maxwell et al., 2016). The main environmental changes associated with climate change are a global warming and an increase in the frequency of extreme stochastic events such as heatwaves, which are predicted to gain in frequency, intensity and duration over time (IPCC, 2014; Meehl and Tebaldi, 2004; Stillman, 2019; Ummenhofer and Meehl, 2017). Climate change may impact diverse populations through varying mechanisms such as variation in species demography (Paniw et al., 2021), phenology (Cohen et al., 2018; Neate-Clegg et al., 2024) and ranges of distribution (Devictor et al., 2008; Kubelka et al., 2022; Pacifici et al., 2020). These observations can find an explanation either through direct variation in the thermal environment (e.g. Albright et al., 2017; Conradie et al., 2020), or indirectly through changes in trophic relationships (e.g. DeGregorio et al., 2015; Pearce-Higgins and Morris, 2023).

From a thermoregulation standpoint and for endotherms, the terms "high temperature" usually refers to temperatures promoting heat stress, which can be defined as a temperature (or something along these lines) that is eliciting behavioral and physiological adjustments to maintain body temperature and/or water homeostasis, and is most commonly represented by the upper critical temperature (UCT, upper limit of the thermoneutrality zone; McKechnie and Wolf, 2019). In ecological studies, different authors refer to "high temperature" as relative to the species sensitivity (e.g. thermoregulatory response, fitness costs) or to the local climate variability. Defining "high temperatures" in an ecophysiological context comes with consequently comes with many challenges, especially focusing on a global scale. Firstly, studies vary widely use their use of temperature variables and statistical procedure (e.g. average of daily mean temperature, number of days exceeding a threshold…), and do not always report temperature data or summary statistics. Moreover, temperature variables are often computed on a large period of time, consequently buffering extreme values. Secondly, field studies most commonly use air temperature, which do not equate to the environmental temperature (i.e. ambient or operative temperature in laboratory and field settings respectively), further limiting the relevance of a direct comparison with species TNZ (Mitchell et al., 2024). Finally, TNZ has limited predictability when considering *in natura* scenarios, and thermal limits for breeding performance may differs from UCT (Clusella-Trullas et al., 2021; MacMillan, 2019; Mitchell et al., 2018). Additionally, species TNZ are not systematically known, especially for polar birds. In this review, we defined "high temperature" as above average temperature for the system studied, or relative to the species thermoregulation depending on the information available (See methods). We qualitatively assessed whether studies investigated "high temperature" as "hot events" or "above average temperature".

Birds represent relevant sentinel species for global changes. They exploit habitats ranging from deserts to polar biomes all around the globe and benefit from a multitude of long-term monitoring programs. Warming temperature have been linked with decreasing abundance (Iknayan and Beissinger, 2018; Milne et al., 2015; Riddell et al., 2019), and heatwaves with mass-mortality events (McKechnie et al., 2021a; Piatt et al., 2020) and complete breeding failures (McCowan and Griffith, 2021; Romano et al., 2020; Sharpe et al., 2021) of various birds species. Overall, reproductive success is a key factor when assessing avian species populations viability and temperature seems to be an important driver of reproduction for multiple populations across the globe (e.g. Jenouvrier et al., 2003; Chase et al., 2005; Kentie et al., 2018; Jansen et al., 2019). Summarizing how birds respond to the thermal environment is a complex task and past reviews have focused on thermoregulation (Boyles et al., 2011; Cunningham et al., 2021), parental care (Du and Shine, 2015; Mainwaring et al., 2016; Durant et al., 2019; Andreasson et al., 2020), growth and development (Hepp and DuRant, 2015; Nord and Giroud, 2020; Sauve et al., 2021) and phenology (Jones and Cresswell, 2010; Møller et al., 2010). More recently, a meta-analysis reported that avian breeding success may decrease in warming areas (Halupka et al., 2023). We present here a systematic review of wild birds' breeding success under high temperatures.

In this review, we aim to highlight potential trends and mechanisms that link avian breeding success and high temperatures (Figure 1). Breeding success can be directly driven by the environmental temperature (i.e. mediated via parents or offspring themoregulation; e.g. McCowan and Griffith, 2021; van de Ven et al., 2020). However, the link between breeding success and temperature can be more elusive and may rely on other mechanisms than thermoregulation alone (e.g. Antoniazzi et al., 2011; D'Amelio et al., 2022; Vatka et al., 2011). In this review, we discuss « direct » effects of high temperature, that is mediated via thermoregulation of parents or offspring. We most specifically provide an overview of how heat stress or a thermal relief (i.e. can drive avian breeding success when exposed to high temperatures (i.e. decreased energy needed to maintain nest or body temperature through thermogenesis). We then provide an overview of potential indirect effects of high temperatures, such as mediated by variation in phenology (e.g. breeding timing, duration of the breeding season), abiotic factors (e.g. snow coverage, water availability) or trophic interactions (e.g. food availability, predation, parasitism and competition). Finally, we briefly present perspectives and consideration for future studies, ranging from experimental design to data analysis, and insist on the importance of disentangling relationships within a system.

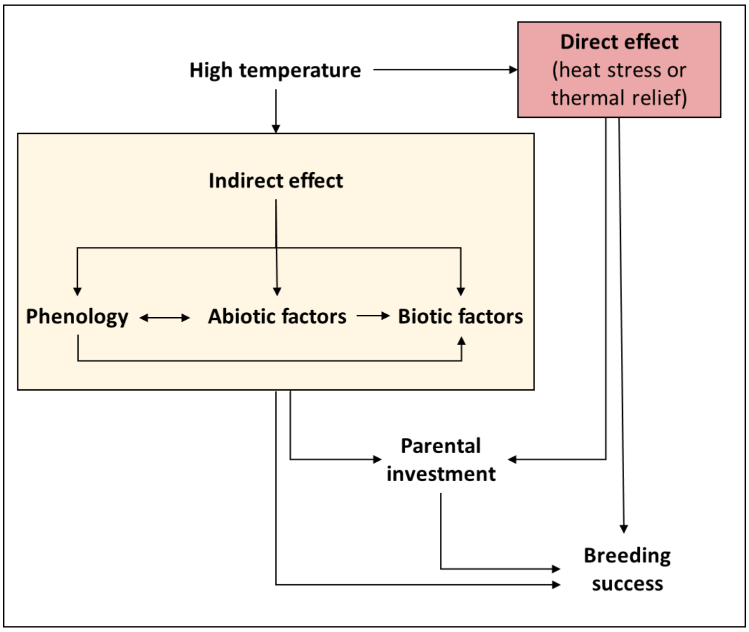

Figure 1. Schematic representation of the mechanisms that potentially mediate the link between high temperature and breeding success. High temperature can influence breeding success through direct (i.e. via thermoregulation of parents and offspring) or indirect ways such as variation in phenology (e.g. breeding timing, breeding season duration), abiotic factors (e.g. snow coverage, water availability) or biotic factors (e.g. food availability, predation, parasitism and competition).

3. Material and methods

3.1. Literature survey

We searched in ISI Web of Science library on 01/13/2022, using the keywords “((ALL="avian$" OR ALL="bird$") AND (TS="high* temperature$" OR TS="warm* temperature$" OR TS="increas* temperature$" OR TS="warm*" OR TS="heat*" OR TS="hot") AND (TS="breeding" OR TS="reproduct*" OR TS="fledg*" OR TS="chick$" OR TS="hatch*" OR TS="nest*") AND (TS="success" OR TS="surviv*" OR TS="mortality" OR TS="productivity" OR TS="recruitment" OR TS="clutch size") NOT (ALL="poultry" OR TS="broiler"))”.

We only retained studies that met our eligibility criteria, i.e. studies that simultaneously: (1) investigated the relationship between high temperature during the breeding season and breeding success *in natura*, meaning we excluded thermal manipulation experiments or captive breeding studies; (2) considered the local air temperature; i.e. studies on nest microclimate or sea surface temperature were not retained to limit the heterogeneity of approaches; (3) described temperature using the keywords “warm(er)”, “hot(ter)”, high(er)”, “increasing”, “heat” or “heatwave”. Monitoring programs spanning more than 10 years were considered to have sufficient temperature variation and were automatically retained; (4) reporting results per species (i.e. either studies focusing on a single species, or report statistical analyses separately for each species when investigating multiple species). In the latter case, data for each species were considered independent and are hereafter referred to as “study”; (5) do not include data duplication. When the same dataset was shared by two articles, they were merged as a single study in our database. The literature search yielded 1214 results ranging from year 1990 to 2022 (Supplementary material). We retained 438 articles upon abstract reading and 118 after full-text inspection for eligibility criteria. We added 37 articles upon reading the selected articles, resulting in a total of 155 articles. After checking all articles for single species analysis, we ended up with a total of 229 studies (Supplementary material).

We defined 5 stages of breeding success: S0 (breeding propensity; probability of breeding, nesting probability, nest occupancy, nest density), S1 (clutch size), S2 (Hatching success; proportion or number of eggs hatching, probability of producing at least one hatchling, daily nest survival), S3 (post-hatching success; proportion or number of hatchling-nestling reaching the nestling-fledgling stage, probability of producing at least one nestling-fledgling, daily nest survival, young to adults ratio) and S4 (post-fledging success; winter-first-year recapture probability, recruitment rate). The daily survival rate computed from the egg stage to the post-hatching stage was considered in the stage S3.

3.2. Definition of high temperature

We defined “high temperature” as relative to the average temperature at the study site, or relative to the species thermoregulation. We qualitatively assessed whether the retained studies investigated either (A) “hot events” : (A1) T_a likely to promote heat stress (T_a>UCT, behavioural signs of heat dissipation, signs of dehydration or hyperthermia), (A2) extreme events according to local climatic variability (e.g. 90th percentile of the hottest days), (A3) according to authors description (e.g. described as “heatwave”); or (B) “above average temperature”: (B1) according to local the local climatic variability (e.g. significant variation in temperature between years), (B2) according to authors description (e.g. “high” or “warm temperature”), (B3) above average temperature assumed to be investigated for long-term studies (≥10 years of monitoring).

3.3. Mapping study location and data acquisition

The locations of the studies were extracted directly from the coordinates or based on the authors' description. No coordinates were extracted for studies investigating multiple sites further than 100km, or with a range exceeding 5000km^2. These thresholds were chosen to remove studies that could potentially span multiple climates from the analysis. We obtained the study location for 135 of a total of 229 studies. We extracted the local climate at each study site from the Köppen-Geiger climate classification map (0.0083° resolution, main climate at 0.5° diameter; Beck et al., 2018). The Köppen-Geiger climate classification distinguishes 31 climates types based on local precipitation and temperature, and regroup them into the 5 main climate groups: “Tropical”, “Arid”, “Temperate”, “Continental” and “Polar”. All spatial data treatment was conducted in QGIS (Version 3.16.16).

4. Overview of the studies

4.1. System and species studied

The distribution of studies retained in our systematic review was uneven across the world, as previously observed in other articles (Figure 2; Cohen et al., 2018; Eyck et al., 2019). Most of the studies were conducted in North America or Europe. Our results are therefore based on a fraction of the globe, and some climates are over-represented while others are under-represented: continental (44.4%; n=60/135), temperate (31.1%; n=42/135), desert (13.3%; n=18/135), polar (10.4%; n=14/135) and tropical (0.7%; n=1/135). Overall, 168 avian species and 17 orders were represented across all studies retained. Passeriformes were the most studied (51.5%; n=118/229), followed by Charadriiformes (13.1%; n=30/229), Anseriformes (10.0%; n=23/229), Accipitriformes (5.2%; n=12/229), Strigiformes (4.4%; n=10/229), Galliformes (4.4%; n=10/229), Falconiformes (3.1%; n=7/229) and others (Piciformes, Bucerotiformes, Suliformes, Procellariiformes, Gruiformes, Columbiformes, Apodiformes, Psittaciformes, Cuculiformes and Ciconiiformes; representing each less than <3%). The high proportion of studies on Passeriformes is expected given that this order contains ~60% of all bird species (Jetz et al., 2012).

The proportion of studies investigating different breeding stages varied substantially, with most-notably post-hatching success being relatively over-represented: breeding propensity (13.1%; n=30/229), clutch size (36.2%; n=83/229), hatching success (36.2%; n=83/229), post-hatching success (72.1%; n=165/229), post-fledging success (10.5%; n=24/229). Relatively few studies investigated breeding propensity and post-fledging success, meaning that the influence of the thermal environment on early breeding investment and fledglings' fate may be under-represented. Monitoring post-fledging success requires an significant research effort, and depending on the species studied it may be difficult to differentiate survival from dispersal when investigating variations in the recruitment rate (Coulson and Coulson, 2008; Steenhof and Heath, 2013; Wiebe, 2020).

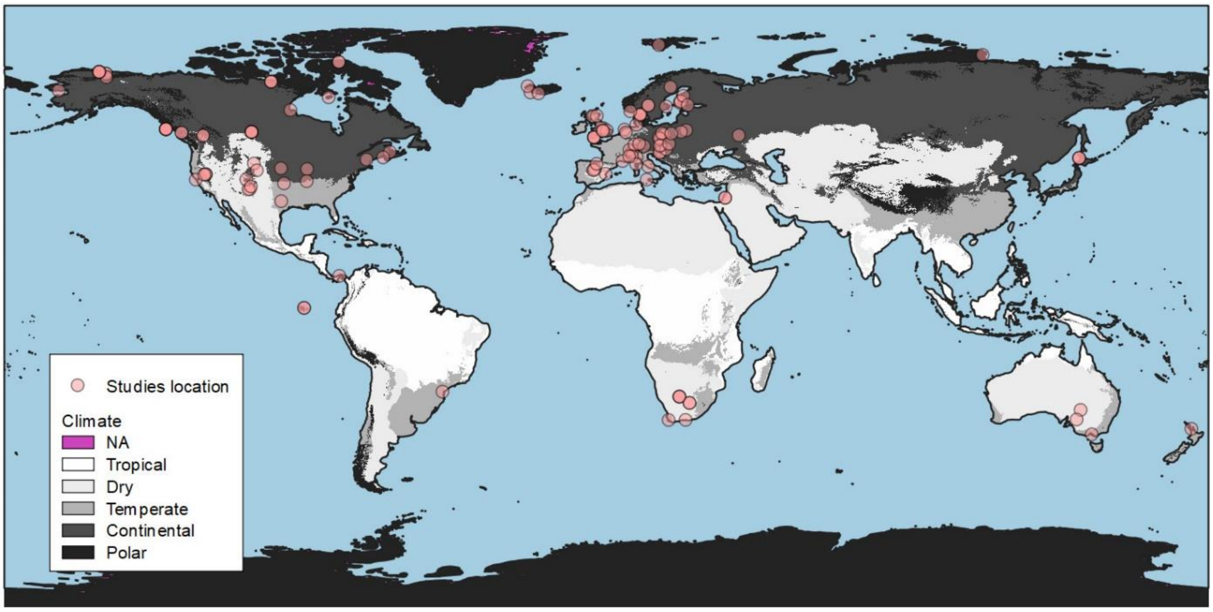

Figure 2. Global map of the study locations (n=135). Symbols and colours represent the associated correlation sign between high air temperature and overall breeding success. The Köppen-Geiger climate classification is represented in shades of grey, and studies location as dots. Location with multiple studies are represent as opaque dots.

4.2. High temperatures or heat stress?

The proportion of studies investigating hot events varied depending on the local climate, and arid climates were largely over-represented (n=12/18 studies; i.e. they represent 66.7% of the studies investigating hot events despite representing only 13.3% of all studies; Table 1). This observation may have two main explanations. Firstly, authors may be more likely to describe extreme events as "heatwaves" or "extremely high temperature" in arid climates compared to cooler climates. This is supported by the fact that fewer studies test the effect of hot days or maximum temperatures in polar, continental or temperate climates compared to arid climates (Table 1), suggesting that most often authors do not consider hot events to be a relevant driver of breeding success. Moreover, the direct effects of heat on breeding success were investigated only in a handful of studies (2.6% of the retained studies), and was mainly considered in arid climates (Table 2). Secondly, birds in cold climates may be less likely to suffer from heat stress during relatively hot events compared with birds in hotter climates. For instance, Dickey et al (2008) described days with T_a>0°C as "extremely high temperatures" in a polar environment, even though these conditions are unlikely to promote heat stress.

Finally, most of the retained studies considered other mechanisms than temperature to be potential drivers of breeding success (i.e. phenology, food availability, predation or intra-specific and inter-specific competition; 75.6% of the studies; Table 2). It is worth noting that authors often only report statistics for the best performing models, and we were thus unable to quantify the proportion of studies testing the interaction between temperature and other drivers. Among indirect drivers, phenology was by far the most studied (70.7%), followed by food availability (15.7%), predation (14.9%) and competition (10.9%). Finally, the relatively few studies investigated trophic factors (i.e. food availability, predation or competition) highlights the need to study relationships between breeding success and weather effects at the ecosystem level.

Table 1. Proportion of the studies investigating the effect of hot event, and of different measures of temperatures on breeding success.

	Local climate				
	Polar (n=14)	Continental (n=60)	Temperate (n=42)	Arid (n=18)	Overall (n=229)
Hot events*	14.3% (2/14)	8.3% (5/60)	9.5% (4/42)	66.7% (12/18)	14.9% (34/229)
Explanatory variable (T°)					
Hot days	7.1 % (1/14)	8.3% (5/60)	1.7% (1/60)	27.8% (5/18)	7.9% (18/229)
Max T_a	14.3% (2/14)	13.3% (8/60)	31.0% (13/42)	55.6% (10/18)	21.4% (49/229)
Mean T_a	42.9% (6/14)	86.7% (52/60)	69.1% (29/42)	33.3% (6/18)	74.7% (171/229)

Min T_a	7.1 % (1/14)	15% (9/60)	23.8 (10/42)	16.7% (3/18)	14.9% (34/229)
T_a deviation	0% (0/14)	0% (0/60)	2.4% (1/42)	22.2% (4/18)	3.1% (7/229)
PCA	28.6% (4/14)	3.3% (2/60)	7.1% (3/42)	5.6% (1/18)	4.8% (11/229)
Cumulative T_a	28.6% (4/14)	6.7% (4/60)	2.4% (1/42)	0% (0/18)	4.4% (10/229)

T_a: air temperature. Hot events: T_a likely to promote heat stress (behavioural signs of heat dissipation, signs of dehydration or hyperthermia, T_a>UCT) or hot days (e.g. 90th percentile of the hottest days). T_a deviation: deviation from the average temperature. Cumulative T_a: sum of the temperature during a period.

Table 2. Proportion of the studies investigating the effect of temperature on breeding success considering heat stress, phenology and trophic relationships.

	Local climate				
	Polar (n=14)	Continental (n=60)	Temperate (n=42)	Arid (n=18)	Overall (n=229)
Heat stress	7.1 % (1/14)	0% (0/60)	2.4% (1/42)	22.2% (4/18)	2.6% (6/229)
Phenology	85.7% (12/14)	81.7% (49/60)	85.7% (36/42)	50.0% (9/18)	70.7% (162/229)
Food	35.7% (5/14)	18.3% (11/60)	9.5% (4/42)	22.2% (4/18)	15.7% (36/229)
Predation	7.1 % (1/14)	6.7% (4/60)	9.5% (4/42)	11% (2/18)	14.9% (34/229)
Competition	14.3% (2/14)	15% (9/60)	21.4% (9/42)	11% (2/18)	10.9% (25/229)

Heat stress: behavioural signs of heat dissipation, signs of dehydration or hyperthermia. Competition: inter-specific and intra-specific competition.

5. Mechanisms underlying the relationship between temperature and breeding success

5.1. Direct effects: thermal environment and parental care

5.1.1. Heat stress as a driver of breeding success

Birds rely primarily on evaporative water loss for cooling and are subject to a trade-off between dehydration and hyperthermia during heat exposure (Gerson et al., 2019; Smit et al., 2016). In warm temperate and arid biomes there are several reports of wild birds showing signs of heat stress such as thermoregulatory behaviours (e.g. panting, urohydrosis, shading; reviewed by McKechnie and Wolf,

2019) and dehydration (Oswald et al., 2021; Salaberria et al., 2014; Sharpe et al., 2019; van de Ven et al., 2019, 2020). Moreover, exposure to high temperatures has been associated with physiological stress markers such as corticosterone levels (Moagi et al., 2021; Newberry and Swanson, 2018) and the heterophils to lymphocyte ratio (H/L ratio; Catry et al., 2015; Skwarska et al., 2021). Finally, the activity pattern of breeding adults can be constrained in the heat and parents may have to trade self-maintenance and reproductive investment (Figure 3; AlRashidi et al., 2010; Amat and Masero, 2004; Oswald et al., 2008).

Decreased breeding frequency and probability of second brooding have been reported during warm periods (e.g. Chambers et al., 2008a; Marques-Santos et al., 2021; Mastrantonis et al., 2019). Clutch sizes were smaller when breeding season have been reported to be warmer in several studies (e.g. Chambers et al., 2008b; Keith Bowers et al., 2016; Londe et al., 2021). One explanation would be that high temperatures may hinder fertility (Hurley et al., 2018; Renthlei et al., 2021; Schou et al., 2021; for a review on poultry models see Vandana et al., 2021).

Hatching success decreased after exposure to high temperature in various studies (e.g. Dreitz et al., 2012; Duchardt et al., 2020; Grisham et al., 2016; Table 1), including some reports of catastrophic egg loss (McCowan and Griffith, 2021a; Sharpe et al., 2021). Egg hatchability was most likely reduced by the direct effect of temperature on egg development and indirect effects mediated through parental care (e.g. Bourne et al., 2021a; Clauser and McRae, 2017; Sharpe et al., 2019). For example, signs of dehydration, reduced incubation consistencies, and decreased hatching success have been associated with high temperature in desert birds (Bourne et al., 2021a; Sharpe et al., 2021). During extreme temperature events, adults have been reported to stop incubating, and to show egg-shading and heat dissipation behaviors, although it is unclear whether the function of such behaviors is to cool the adults or the eggs (Amat and Masero, 2004; Brown and Downs, 2003; Downs and Ward, 1997; Sharpe et al., 2021). Exposure to such temperatures ultimately led to the desertion of the nest by the parents (Bourne et al., 2021a; Sharpe et al., 2021), and nest desertion was related to the distance to a water source in Kentish Plover (*Charadrius alexandrinus*), highlighting a potential dehydration-hyperthermia trade-off (Amat and Masero, 2004).

The same observations apply to post-hatching success: both nestlings and parents can suffer from dehydration in the heat (Bourne et al., 2021b; Oswald et al., 2021; Salaberria et al., 2014; van de Ven et al., 2020). During extreme events, nestlings might even be forced out of nests to avoid lethal temperatures (Catry et al., 2015). Some studies have shown nestling provisioning rate decreased at high temperature (e.g. Barras et al., 2021; Oswald et al., 2021; Wiley and Ridley, 2016), which could be linked with a diminished time spent foraging or foraging efficiency (e.g. Danner et al., 2021; Funghi et al., 2019; Playà-Montmany et al., 2023). Individuals have to dedicate a greater time budget to thermoregulatory behaviours, and hyperthermia may constrain offspring provisioning even for temperate bird (Andreasson et al., 2020; Tapper et al., 2020a, 2020b). This could ultimately lead to a reduction in nestling growth and survival (Bourne et al., 2021b; van de Ven et al., 2020). It is also worth noting that reduced growth when exposed to high temperatures can delay fledging and may increase the depredation probability (Cunningham et al., 2013a).

Thus, exposure to high temperatures can have lethal and sublethal effects on offspring phenotype (Conradie et al., 2019; Durant et al., 2013; Nord and Giroud, 2020; Sauve et al., 2021). Given that growth is a strong predictor of the post-fledging survival (González-Braojos et al., 2017; Maness and Anderson, 2013; Rodríguez et al., 2016), suboptimal incubation, physiological stress, or reduced provisioning could contribute to a reduced offspring condition and post-fledging survival. For instance, high temperatures experienced by offspring was related to decreased growth and reduced fledging and first-year survival for the Southern pied babbler (Bourne et al., 2020c; Bourne et al., 2020d). Importantly, early-life development and thermal environment may influence life trajectories (Berntsen and Bech, 2016; Hepp et al., 2015; Lindström, 1999; Wada et al., 2015). This might have been the case for Gowshawk (*Accipiter gentilis*), which showed lower lifetime reproductive success when born during warmer springs (Herfindal et al., 2015).

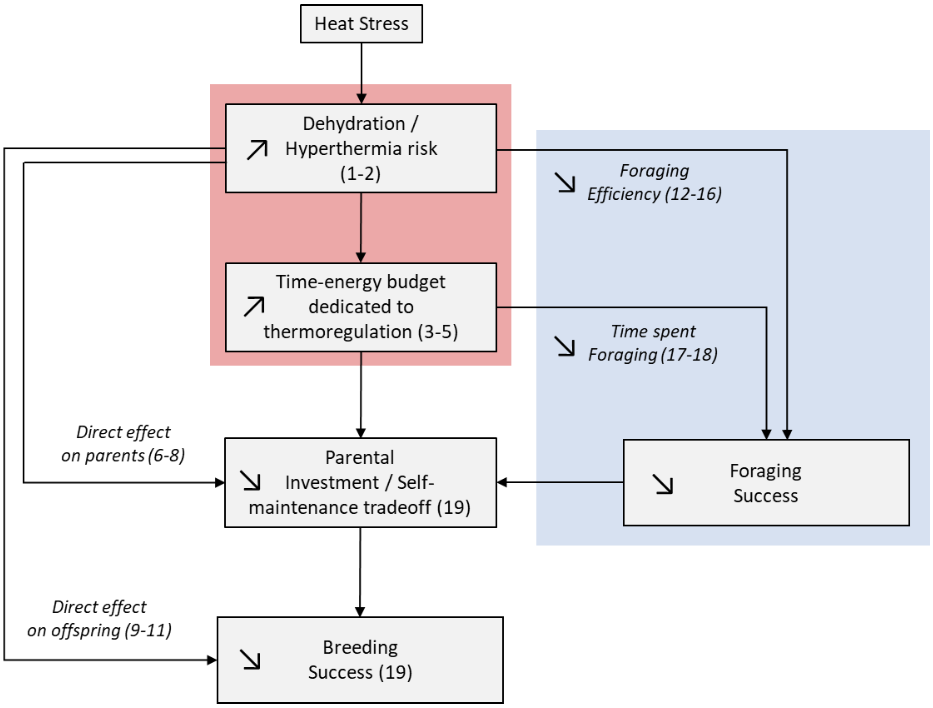

Figure 3. Schematic representation of the direct mechanisms (i.e. through thermoregulation) that mediates the link between heat stress and breeding success. The red and blue boxes correspond respectively to increased expenses and decreased resources. References : (1) Gerson et al., 2019 (2) McKechnie and Wolf, 2019 (3) Smit et al., 2016 (4) Oswald et al., 2008 (5) Sharpe et al., 2021 (6) Moagi et al., 2021 (7) Bourne et al., 2021a (8) van de Ven et al., 2019 (9) Salaberria et al., 2014 (10) van de Ven et al., 2020 (11) Catry et al., 2015 (12) Danner et al., 2021 (13,14) Tapper et al., 2020a, 2020b (15) Oswald et al., 2021 (16) Barras et al., 2021 (17) Funghi et al., 2019 (18) Playà-Montmany et al., 2023 (19) References within text.

5.1.2. Thermal relief as a driver of breeding success

Cold exposure has been reported to impact avian reproduction in various populations from temperate to polar climates (e.g. Glądalski et al., 2020; Martin et al., 2017; Moreno et al., 2015; Tobolka et al., 2015; Winkler et al., 2013). Additionally, there are many reports of positive associations between high temperatures and breeding propensity (e.g. Väli, 2012; Van Oudenhove et al., 2014), clutch size (e.g. Jónsson et al., 2009; Wright et al., 2009), hatching (e.g. Drever and Clark, 2007; Mauck et al., 2017), post-hatching (e.g. Kouba et al., 2020; Meller et al., 2018) and post-fledging success in such systems (e.g. D'Alba et al., 2010; Layton-Matthews et al., 2018). These studies suggest that high temperature may represent improved thermal conditions in some systems.

While avian embryo development occurs approximately in the 26-40°C range, it is thought to be optimal in much narrower ranges (Durant et al., 2013a; Webb, 1987). For instance, optimal range of incubation temperature is ~35-37°C for Wood Ducks (*Aix sponsa*; Hepp et al., 2015). Since avian embryos produce very little heat, and because optimal incubation temperature usually exceeds the environmental temperature, embryonic development is in most cases reliant on parental thermogenesis (Deeming and Reynolds, 2015; Deeming, 2004). Additionally, nestlings reach thermo-independence during post-natal development, although the extent to which they are dependent on parental warming vary alongside the precocial-altricial continuum (Ducatez and Field, 2021; Price and Dzialowski, 2017; Starck and Ricklefs, 1998). Overall, breeding birds usually shows increases in energy expenditure compared to non-breeding individuals, and energetic cost of incubation seem higher for arctic birds, suggesting an increased need for parental nest warming in cooler environments (Nord and Williams, 2015; Williams, 1996). High temperatures may consequently promote a thermal relief in some systems (i.e. decreased energy needed to maintain nest or body temperature through thermogenesis).

Parents energy expenditure during incubation has been reported to be minimal at high temperatures in several studies (De Heij et al., 2007; Haftorn and Reinertsen, 1985; te Marvelde et al., 2012; Tulp et al., 2009). Moreover, there are many reports of decreased nest attentiveness and elongation of off-bout duration with high temperatures in cold climates, suggesting an alleviated time investment of parents (e.g. Arct et al., 2022; Diez-Mendez et al., 2021; Klimczuk et al., 2015; Williams and DeLeon, 2020). This is further supported by studies reporting a decreased parental energy expenditure and nest attentiveness with experimental nest heating (Ardia et al., 2009b; Bryan and Bryant, 1999). For instance, growth of Tree Swallow (*Tachycineta bicolor*) nestlings was positively influenced by experimental nest warming but negatively affected by nest cooling (Ardia et al., 2010; Pérez et al., 2008). Finally, in a subarctic environment, the growth of Dunlin (*Calidris alpina*) nestlings was maintained during a period of below average food availability only when temperature was high, suggesting a thermal relief (McKinnon et al., 2013). In summary, high temperatures may allow for a greater allocation to self-maintenance of breeders, a higher breeding success, and/or better offspring quality (growth and physiological condition) in some systems.

5.2. Indirect effects: phenology and trophic interaction

5.2.1. Phenology: selection for early breeding, false springs and breeding season duration

Bird phenology is plastic and breeding timing has been reported to vary with environmental conditions. In most cases, breeding timing seems to advance with high air temperature (Phillimore et al., 2016; reviewed by Cohen et al., 2018; Radchuk et al., 2019). This phenomenon may be adaptive, as it allows individuals to breed when the conditions are the most suitable (Charmantier and Gienapp, 2014; Charmantier et al., 2008; Lof et al., 2012), explaining the association between breeding dates and reproductive performance (reviewed by Dunn, 2004; Dunn and Winkler, 2010). Interestingly, the strength of the selection for earlier breeding seems to vary with environmental conditions (Kentie et al., 2018; Reed et al., 2009). For instance, the decreasing reproductive success along the breeding season, i.e. for late breeders, was stronger during warmer springs in multiple studies (Bowers et al., 2016; Marrot et al., 2018; Whelan et al., 2017). Several studies reported prolonged or shortened breeding seasons with climate warming (Hällfors et al., 2020; Halupka and Halupka, 2017; Møller et al., 2010). On one hand, high temperatures seem to favour early breeding, leading to an extended breeding season, an increased number of breeding attempts and breeding success (Mingozzi et al., 2021). However, it may also be a misleading signal for the onset of breeding. Several studies reported negative effects of cold snaps on reproductive success after a warm early season, often referred to as the “false spring” phenomenon (e.g. Lehikoinen et al., 2009; Shipley et al., 2020; Skwarska et al., 2015).

On the other hand, high temperatures in the late season may put an end to the breeding season (Jankowiak et al., 2014; Lv et al., 2020; Mares et al., 2017; Sharpe et al., 2021). For example, heatwaves shortened the Superb Fairy-Wren (*Malurus cyaneus*) breeding season, which led to a reduced fledging success (Lv et al., 2020).

The influence of temperature on the timing of reproduction implies that it can also affect trophic interactions such as food availability, competition, predation, and parasitism (i.e. match-mismatch hypothesis). The relationship between breeding success, temperature, these mechanisms and their interaction with phenology are discussed below. We do not extensively review studies on this topic, but intend to provide case studies highlighting the complexity of the relationship between high temperatures and breeding success.

5.2.2.Trophic interactions

Food availability

Temperature may drive breeding success through variation in food availability or quality, but multiple mechanisms may underline this relationship (Barras et al., 2021; Pearce-Higgins and Morris, 2023). First, food availability may be directly dependent on temperature. High temperatures were associated with increased arthropod abundance and greater breeding success in continental and arctic biomes (Winkler et al., 2013; Ruthrauff et al., 2021). Winkler et al. (2013) even reported a similar temperature threshold for nestling mortality and insect availability, highlighting a strong association between them. On the contrary, arthropod abundance and activity decreased at high temperatures in arid climates (Holm and Edney, 1973). This is not limited to insectivores, since avian species with various diet can also experience such effects on food availability (e.g. herbivorous or carnivorous; Doiron et al., 2015; Schmidt et al., 2020). The synchrony between maximum food abundance and breeding timing may differ during warm springs, and may underline influences of high temperatures on breeding success (i.e. "mismatch hypothesis"; Ross et al., 2017, 2018; Vatka et al., 2011, 2014, 2016; for a review see Visser et al., 2012). For instance, synchrony with caterpillar abundance increased during warmer seasons for the Willow Tit (*Poecile montanus*) in a boreal forest and was in turn positively correlated with nestling survival (Vatka et al., 2011). Lastly, temperature and breeding timing can both interact with abiotic factors. As reported by Ruthrauff et al., 2021, high temperatures correlated with early snowmelt, driving the arthropod emergence and thus promoting early breeding and a greater breeding success. For the Greater Snow Goose (*Chen caerulescens atlantica*), the mismatch between hatching date and peak nitrogen concentration in vegetation (an index of food availability and quality; Lepage et al., 1998) increased during warmer springs because of the early snowmelt, predicting in turn a reduced nestling growth (Doiron et al., 2015).

Predation

Nest predation risk can be driven, either directly or indirectly, by the temperature through effects on activity patterns of birds, alternative prey or predators. Birds can show reduced flight initiation distance when exposed to predators during heat events, suggesting a trade-off between thermoregulation and predation risk (Gutiérrez et al., 2023). Predator activity can vary with temperature (Degregorio et al., 2014; 2015; Morris and Conner, 2016), explaining an increased nest predation rate by snakes with high temperatures (e.g. D'Amelio et al., 2022; Oswald et al., 2020). Alternatively, high temperatures may also influence vegetation growth, and depredation rate via changes in nest concealment (inhibit auditory, olfactory and visual cues for predators; Borgmann et al., 2013). Finally, the number of prey available for the predators might vary in warm springs and therefore influence the predation risk (i.e. the alternative prey hypothesis; McKinnon et al., 2014). For example, predation on Eider Duck (*Somateria mollissima*) nests by polar bears increased when ice season was shortened (Iverson et al., 2014). Authors hypothesize that reduced ice coverage could hinder polar bears in their hunt for seals, leading to an increase in the rate of duck nest predation as alternative preys.

Parasitism

The performance of parasites is thought to vary with temperature in a curvilinear fashion (Aleuy and Kutz, 2020; Ogden and Lindsay, 2016). High temperature may increase the abundance of potential parasites in the nest (e.g. Branco et al., 2013; Prudhomme et al., 2015). Moreover, experimental heating of nests led to variation in the abundance of parasites (Dawson et al., 2005; Castaño-Vázquez et al., 2018, 2021, 2022). For instance, the density of blowfly larvae in Tree Swallow (Ta*chycineta bicolor*) nests peaked at 25°C and decreased at both higher and lower temperatures (Dawson et al., 2005). Density of blowfly larvae were also more abundant around 23-25°C in Blue Tits (*Cyanistes caeruleus*) nests, with a strong with a strong decline below 20°C (Mennerat et al., 2021). As a result, increased nest parasitism associated with high temperatures can lead to reduced breeding success (Antoniazzi et al., 2011; Douglas and Pearce-Higgins, 2019; Møller, 2010). Sublethal effects on nestling immunity (Dawson et al., 2005), adult and nestling body condition (Castaño-Vázquez et al., 2021; Espinaze et al., 2020) may also hinder offspring survival later on.

Competition

The intensity of the intra-specific and inter-specific competition may interact with the temperature, but to our knowledge, only few studies seem to investigate it (Table 3). However, there are reports of interactions between temperature, laying date and competition on nest occupancy, clutch size, fledging success and on the probability of producing a recruit (Ahola et al., 2007; Ahola et al., 2009; Ahola et al., 2012; Bodey et al., 2021; Møller et al., 2020). Most notably, birds phenology may shift differently with temperature, which could lead to varying levels of competition during warm seasons (Ahola et al., 2007).

6. Considerations for future studies

Our knowledge seems spatially confined to specific areas of the globe, mainly North America and Europe (Figure 2). It is crucial to increase research effort in overlooked areas and biomes, especially in tropical environments. Moreover, potential effects of high temperature and underlying mechanisms may vary depending on the local climate. High temperatures seems to be consistently linked with negative effects on desert birds reproductions (e.g. McCowan and Griffith, 2021; Pattinson et al., 2022; Ridley et al., 2021), while results seem more contrasted in cooler climates (e.g. Pipoly et al., 2013, 2022). This is highlighted by the intra-specific variation in response to high temperature between different climates. For instance, the breeding success of the Barn Owl (*Tyto alba*) or the Mountain Plover (*Charadrius montanus*) was positively related to temperature in a temperate or continental climate, but negatively in a hotter semi-arid climate (Barn Owl: Charter et al., 2017; Chausson et al., 2014, Mountain Plover: Dreitz et al., 2012; Pierce et al., 2019; Skagen and Adams, 2012). Breeding success also tends to decrease at higher elevation associated with colder temperature in continental climates, while the opposite has been reported in hot deserts (e.g. Hargrove et al., 2011; Nilsson et al., 2020).

Birds in hot environments may be more vulnerable to high temperature because their thermal environment is already close to their physiological limits, while birds in cool environments may benefit from it due to reduced energetic costs of keeping warm in otherwise cold conditions. For instance, energetic costs of thermoregulation are expected to decrease for Dovekies (*Alle alle*) in the arctic (Beaman et al., 2024), while desert species are expected to see their cooling costs increase with global warming (e.g. Albright et al., 2017; Conradie et al., 2020; McKechnie and Wolf, 2010). This may be supported by the variation in thermal limits of birds such as the upper critical temperature (UCT; upper limit of the thermoneutrality zone). Even though avian UCT scales with the temperature in their habitat (Song, 2018; Sunday et al., 2019), there is relatively little variation in the UCT among birds, and especially within taxa (Araújo et al., 2013; McKechnie et al., 2021a). For instance, the thermal tolerance passerines seems highly conserved (desert: average UCT ~37.6°C across 30 species, McKechnie et al., 2021; temperate: 37.7°C across 26 species, Cabello-Vergel et al., 2022; Pollock et al., 2021; Supplementary material), suggesting that hot events may be more likely to promote heat stress in deserts. Quoting Iknayan and Beissinger (2018), desert birds may "persist near the edge of their physiological limit". Overall, deleterious effects on desert birds survival, breeding success or demography are expected to increase with climate warming (Conradie et al., 2019; Riddell et al., 2019; Ridley et al., 2021b).

Understanding the mechanisms underlying the association between high temperatures and breeding success requires a disentanglement of direct and indirect effects. Researchers should first consider the main drivers of breeding success within their system and investigate whether they interact with temperature. Since temperature usually increases during the breeding season, the association between temperature and reproductive output may be artefacts due to the breeding timing. Therefore, the correlation between breeding timing, reproductive success, and temperature should always be assessed. We strongly emphasize the need to measure markers of heat stress, either through behaviour (e.g. panting, gular fluttering; McKechnie and Wolf, 2019) or physiological markers (e.g. body temperature; Linek et al., 2021; plasma osmolarity or hematocrit for dehydration; Brischoux et al., 2020; Salaberria et al., 2014; Scope and Schwendenwein, 2020), to pinpoint thermal constraints of breeding birds in their habitat. Experimental manipulation such as nest warming or cooling, food supplementation, or reducing predation represent important avenues for understanding relationships within a system (e.g. Corregidor-Castro et al., 2023; D'Amelio et al., 2022). Multiple statistical procedures allow researchers to integrate hierarchical structures among predictors and we encourage their use (e.g. Bourne et al., 2020a; Czeszczewik et al., 2020; van de Ven et al., 2020).

Considerations should be given to define relevant temperature measures before performing the data analysis to optimize the quality of the results. For instance, the frequency with which the temperature exceeds a certain threshold has been reported to better predict the growth and survival of nestlings than maximum temperature in some studies (e.g. Conrey et al., 2016; Cunningham et al., 2013a). These thresholds can be defined based on the knowledge of the local climate (e.g. Mastrantonis et al., 2019; Pipoly et al., 2022; Smart et al., 2021), theoretical biological thresholds (e.g. McCowan and Griffith, 2021) or empirical knowledge on species biology (e.g. Cunningham et al., 2013a; 2013b). In addition, water availability most likely interact with temperature, especially in arid systems where adequate water is necessary for survival and reproduction (Coe and Rotenberry, 2003; Tieleman et al., 2004). In these systems, drought intensity is likely to interact and drive breeding success (Bolger et al., 2005; Grisham et al., 2014; Lautenbach et al., 2018; Cox et al., 2020; Londe et al., 2021). Using an index of drought severity rather than temperature and precipitation on their own may be more relevant in these areas (e.g. Palmer Drought Severity Index; Cox et al., 2020). Overall, extreme temperature based on the environmental stochasticity do not necessarily promote heat stress nor deleterious effects on reproduction. There is consequently a need to put local climate variability into perspective with meaningful biological thresholds (Cunningham et al., 2013b). We strongly recommend to systematically discuss report temperature variable and summary statistics (e.g. mean temperature, average of maximum or minimum), and to put these measures in perspective with the local climate variability and the species thermoregulation.

Finally, species traits may influence the sensitivity of their reproductive output to high temperatures and represent relevant avenues for comparative studies. Numerous traits, such as thermal tolerance or breeding strategy should be considered. For instance, drivers of breeding success and vulnerability to high temperatures may differ between migratory and sedentary species (Jones and Cresswell, 2010; Jørgensen et al., 2016; Meller et al., 2018; Telenský et al., 2020), between single and multi-brooded species (Møller et al., 2010; Halupka and Halupka, 2017; Both et al., 2019; Halupka et al., 2023), between single and bi-parental or cooperative breeding species (Covas et al., 2008; Kosztolanyi et al., 2009; Jetz and Rubenstein, 2011; Cornwallis et al., 2017; Bourne et al., 2021; D'Amelio et al., 2022). Passerines may represent relevant sentinel species since they are widespread and have limited heat tolerance compared to other avian taxa, explaining their over-representation during heatwave-induced mortality events (McKechnie et al., 2021a).

Data availability

Data is available as supplementary information.

Competing interest

The authors declare no conflict of interest.

Authors contribution

A.L., S.R., and S.M conceived the review and designed methodology; A.L conducted the investigation and wrote the original draft under the supervision of S.R and S.M; All authors contributed critically to the drafts and gave final approval for publication.

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Chapter 2. Effects of weather and breeding timing on great tit (*Parus major*) breeding success in a forest and urban environment

Levillain, A., Bleu, J., Reichert, S., Massemin, S. Contrasted effects of weather and timing on great tit (*Parus major*) breeding success in a forest and urban environment. **In prep**.

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Keywords: Avian, Breeding success, Phenology, Climate warming, Passerine, Urbanization

Picture of a great tit (*Parus major*; from Macaulay Library ML628196313).

1. Introduction

Climate change is believed to be one of the main drivers of biodiversity erosion (Jaureguiberry et al., 2022; Maxwell et al., 2019; Urban, 2015). Increases in global temperature and extreme weather events are likely to threaten birds populations (Chen and Khanna, 2024; Cunningham et al., 2021; Dunn and Møller, 2019; Halupka et al., 2023; Ma et al., 2023). Climate warming is associated with changes in avian phenology, most commonly leading to phenological advancement in migration and breeding initiation (Cohen et al., 2018; Hällfors et al., 2020; Neate-Clegg et al., 2024). Asymmetric changes across trophic levels are likely to induce potential mismatches, such as increasing asynchrony between food abundance an energy requirement, potentially shaping breeding success and in turn population dynamics (Charmantier and Gienapp, 2014; Kharouba and Wolkovich, 2020; Thackeray et al., 2016). Additionally, direct weather effects can strongly impact avian reproduction, from egg-laying to nest success (D'Amelio et al., 2022; McCowan and Griffith, 2021; Sharpe et al., 2021).

Potential impacts of climate change are likely to interact with urbanization, further shaping avian breeding success (Sumasgutner et al., 2023). Urban systems represent lower-quality environments due to increased human disturbance, pollution levels, reduced availability and/or quality of resources and altered trophic relationships (e.g. Lepczyk et al., 2023; Planillo et al., 2021). Consequently, urban birds usually exhibit lower physiological condition, smaller body size, and reduced clutch size and breeding success (Banbura et al., 2013; Capilla-Lasheras et al., 2022; Chamberlain et al., 2009; Salmón et al., 2023; Vaugoyeau et al., 2016). Moreover, extreme heat events may have further deleterious effects on biodiversity in urban systems due to the urban heat island effect (e.g. higher temperatures in urban areas during hot events; Deilami et al., 2018; Ho et al., 2023).

In this study, we investigate how weather and breeding timing influence reproductive success in an urban and forest environment in great tits (*Parus major*). We expect great tits breeding success to be positively correlated with temperature and negatively correlated with rainfall (Ahola et al., 2009; Eeva et al., 2020; Marques-Santos and Dingemanse, 2020; Schöll and Hille, 2020; Wawrzyniak et al., 2020). Since urban environments are associated with lower environmental and individual quality, breeders may be less capable of buffering environmental variability (Banbura et al., 2013; Gillings et al., 2024; Seress et al., 2020). We hypothesize that weather effects may be more strongly associated with breeding success in urban systems. Additionally, we expect great tits to show a seasonal decline in clutch size and breeding success (Charmantier et al., 2008; Dunn, 2004; Verhulst and Nilsson, 2008; Verhulst et al., 1995). The strength of the selection for early breeding may be reduced lower quality environments (Reed et al., 2009) and urban systems are likely less seasonal (e.g. presence of alternative food resources and predators; e.g. Cowie and Hinsley, 1988; Lepczyk et al., 2023). We consequently predict seasonal decline to be less pronounced in the urban environment.

2. Material and methods

2.1. Study site and population monitoring

We monitored two great tit (*Parus major*) population in an urban and forest environment. Urban sites are dispersed within the town of Strasbourg (France), ranging from tree-lined routes in the city center to urban parks. The forest site is an alluvial forest of deciduous trees, located 20km north of Strasbourg city center (48.647962°, 7.833667°). Great tits breed in artificial nest boxes in both study sites. Further descriptions of study sites can be found in Saulnier et al (2022). Local climate is temperate, classified as oceanic climate based on the Köppen-Geiger classification (Cfb; Beck et al., 2018). Weather data was obtained from a weather station located in Strasbourg city center (MeteoFrance). Forest population was monitored from 2010 to 2023 (13 years), and urban population from 2014 to 2023 (9 years), with the exception of 2020 for both sites. Second broods have been monitored only since 2021, and we therefore excluded them from our analysis. For each occupied nestbox, we monitored the laying and hatching date (±1 day). We measured nestlings body mass (±0.1g) and tarsus length (±0.1mm) at banding (13-16 days post-hatch). In total, we monitored 342 urban and 398 forest nests, representing 990 and 1359 nestlings surviving up to banding respectively. We calculated hatching success (proportion of eggs hatching) and nest success (proportion of nestlings surviving until banding).

2.2. Data processing

Firstly, we analyzed whether weather varied with time between years and during the breeding season. We used weather data from 1990 to 2023 at our study site. Breeding season was assumed to be the period between the first egg-laying event and the last nestling banding (julian day 79-152; i.e. from the 21th of March to the 6th of June in non-leap years). Weather parameters investigated were the daily cumulative rainfall runoff, daily mean temperature, probability of a day to be "hot" and probability of a day to be "cold". We estimated hot and cold days based on the local climatic variability during the breeding season using historic data (i.e. data from 1990 to 2023; Pipoly et al., 2022). Hot days corresponded to days where maximum temperature exceeded 25.4°C (i.e. 90th percentile of daily maximum temperature), and cold days as days where minimum temperature did not exceed 2.6°C (10th percentile of daily minimum temperature). We used generalized linear models using negative binomial distribution to account for zero-inflation when analyzing rainfall, gaussian distribution when analyzing mean temperature, and binomial distribution when analyzing probabilities of a day to be hot or cold.

Secondly, we analyzed the potential effect of weather on laying date by calculating the weather during the early-breeding season. Sliding-window analysis in other studies highlighted that laying date was positively correlated with temperature during the period from the median laying date to 35-69 days prior (Ahola et al., 2007; Ahola et al., 2009; Charmantier et al., 2008; Husby et al., 2010). We consequently calculated the mean temperature (average of daily mean) and rainfall (average of daily cumulative rainfall-runoff) for each year using 30-, 45- and 60-days periods prior to the median laying date (i.e. T30, T45, T60 for temperature).

Thirdly, we calculated for each nest the weather before laying (e.g. during the 3 weeks period before laying), during incubation (i.e. from 14 days before hatching to the hatching date) and during nestling rearing (from the hatching date to nestling ringing; i.e. 14 days on average; Figure 1). We tested the effect of weather on their respective breeding stage (i.e. laying weather on clutch size, incubation weather on hatching success, rearing weather on nestling survival and growth). Rainfall was estimated as the average of daily cumulative rainfall-runoff (Rain). We calculated the number of hot days (Nhot), the number of cold days (Ncold), the average of daily minimum temperatures (Tmin) and daily mean temperatures (Tmean). Following previous analyses on climate variability, hot days were considered to be days with maximum T°≥25.4°C, and cold days as days with minimum T°≤2.6°C. We estimated breeding timing for each nest as the laying date (LD) and hatching date (HD) centered around the corresponding year median.

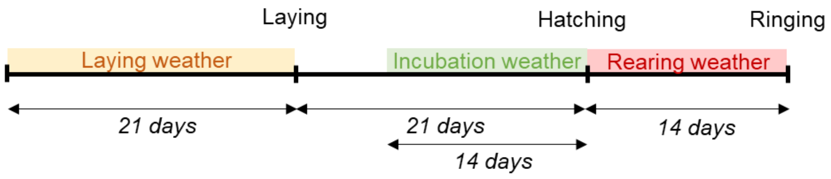

Figure 1. Schematic representation of the weather period calculated for each nest. In latter analysis, we relate clutch size with laying weather, hatching success with incubation weather, and nestling survival and growth with rearing weather.

2.3. Statistical analysis

All statistical analyses were conducted using R (Version 4.3.2). We used generalized linear mixed models, using "Year" and "Nestbox identity" as random factors [formula: measure ~

parameters+(1|Year)+(1|Nestbox identity); Bates et al., 2015]. We only used models that tested our hypotheses (Table 1). Temperature and breeding timing were correlated and we therefore did not include them as parameters within the same models. Environment ("Env", i.e. urban or forest) was included in all models due to the differences in reproductive traits between urban and forest nests (Table 2). When assessing weather and breeding timing correlations with hatching and breeding success, we used clutch size and brood size as a covariate respectively. We used brood size as a covariate, nestling age and brood identity as random factors when analyzing nestling body mass and tarsus length at ringing.

Table 1. Predicted influence of weather and breeding timing on reproductive success with in great tits (*Parus major*) in an urban a forest environment.

Hypothesis	Rational	Full model(s)
Phenology		
H1: reproductive success decreases during the breeding season	Early breeders are of higher quality and/or benefit from a higher quality environment (Verhulst and Nilsson, 2008)	R ~ Env + Date
H2: seasonal decline in reproductive success is less pronounced in urban systems	Strength of selection for early breeding is decreased in lower quality environment, and urban environment is likely less seasonal due to presence of alternative resources and predators (Cowie and Hinsley, 1988; Lepczyk et al., 2023; Reed et al., 2009).	R ~ Env * Date
Weather		
H3: reproductive success increases with temperature and decrease rain or with extreme temperature events	Great tits breeding success is positively correlated with temperature and negatively correlated with rainfall across several studies (e.g. Eeva et al., 2020; Marques-Santos and Dingemanse, 2020; Schöll and Hille, 2020) . Exposure to extreme temperature has negative effects on great tits reproduction (Gladalski et al., 2020; Pipoly et al., 2022).	R ~ Env + Temp + Rain
H4: weather effects are more strongly pronounced urban systems	Breeders may be less capable of buffering environmental variability due to lower quality individuals and environments (Seress et al., 2020; Wawrzyniak et al., 2020).	R ~ Env * Temp + Rain R ~ Env * Rain + Temp
H5: effects of temperature and rain act additively or synergistically	The negative effect of cold temperature is likely to have further impact on reproduction during rainy spells (Eeva et al., 2020).	R ~ Env + Temp * Rain R ~ Env * Temp * Rain

Env: forest or urban. R: clutch size, hatching success, nest success and nestling growth. Date: laying date, hatching date. Temperature: Tmin (average of daily minimum temperature), Tmean (average of daily mean temperature), Nhot (number of hot days), Ncold (number of cold days). Rain: average of daily cumulative rainfall-runoff (RR). "+": main effect of both parameters. "*": main effect of both parameters and two-way interaction between them.

We ranked models based on their AICc. We report all models with ΔAICc<4 and highlight the most parsimonious models (i.e. models with ΔAICc<2 and least number of parameters). All model parameters were standardized, and we report standardized coefficients for each parameter (β). We report marginal means and standard error calculated respectively using the “emmeans” R-package (Lenth, 2024). We used the package “DHARMa” to assess model assumptions (Hartig, 2016).

3. Results

3.1. Comparison of forest and urban reproductive success

Table 2. Comparison of reproductive output and success between forest and urban great tits (*Parus major*) nests.

		Reproductive output			Breeding success		Nestling at ringing	
	Laying date	Clutch size	Brood size	Nestlings ringed	Hatching success (%)	Nestling success (%)	Body mass (g)	Tarsus length (mm)
Forest	97.5±1.63a	9.2±0.16a	7.6±0.22a	5.6±0.44a	87.5±1.69a	77.3±4.20a	16.7±0.29a	19.7±0.14a
Urban	96.0±1.64b	7.7±0.17b	5.8±0.25b	4.1±0.46b	78.9±2.24b	70.5±5.35a	14.7±0.30b	18.9±0.14b
β	-0.20	-0.74	-0.57	-0.42	-0.63	-0.35	-0.91	-0.65
[CI]	[-0.35, -0.05]	[-0.89, -0.59]	[-0.72, -0.43]	[-0.57, -0.27]	[-1.03, -0.23]	[-0.72, 0.02]	[-1.10, -0.72]	[-0.85, -0.46]

We report marginal mean±SE computed using the "emmeans" R-package. Year and nestbox identity were included as random effect in every model. Nest identity and nestling age was included as random effect for body mass and tarsus length models. Hatching success: percentage of laid eggs that hatched. Nestling success: percentage of nestling that survived until ringing. Nestling survival were calculated excluding nests that had no eggs hatching. Values of each parameter in a column with different superscript differ significantly (p-value<0.05). β [CI]: standardize coefficient and 95th confidence interval.

3.2. Local weather

Daily mean temperature during the breeding season at our study site was positively correlated with the julian day and year (Day, β=0.64 [0.61, 0.67]; Year, β=0.08 [0.05, 0.11]), meaning the temperature increased during the breeding season and increased with time from 1990 to 2023 (+0.37°C per decade). The probability of a day being hot (P_{hot}, temperature>25.4°C) or cold (P_{cold}, minimum temperature<2.6°C) increased and decreased respectively during the breeding season, but did not vary with time (P_{hot}, Day, β=1.19 [1.02, 1.38]; Year, β=0.05 [-0.08, 0.19]; P_{cold}, Day, β=-1.65 [-1.89, -1.44]; Year, β=-0.11 [-0.26, 0.04]). Daily cumulative rainfall-runoff increased during the breeding season and decreased with time (Day, β=0.11 [0.04, 0.18]; Year, β=-0.08 [-0.15, -0.02]), while the probability of a day being rainy only decreased with time (Day, β=0.15 [-0.03, 0.13]; Year, β=-0.15 [-0.23, -0.07]). Overall, average daily mean temperature during the breeding season from 1990 to 2023 was 12.82±0.07°C (mean±SE; average daily minimum temperature: 8.18±0.07, average daily maximum temperature: 17.97±0.10).

3.3. Laying date

Daily mean temperatures averaged from 45 days before the median laying date up to it predicted great tits laying date (Table 3; Figure 2; Figure 2; Env: β=-0.20 [-0.35, -0.05]; T45: β=-0.54 [-0.66, -0.42]). Temperature (T30, T45, T60) was significantly negatively correlated with laying date and was best predicted by T45. Precipitation (RR30, RR45, RR60) was consistently positively associated with laying date although not significantly (e.g. model: “Env+T45+RR45”, RR45: β=0.12 [-0.01, 0.26]). Laying date was not related with year (model: “Env+Year”, Year: β=0.03 [-0.05, 0.10]).

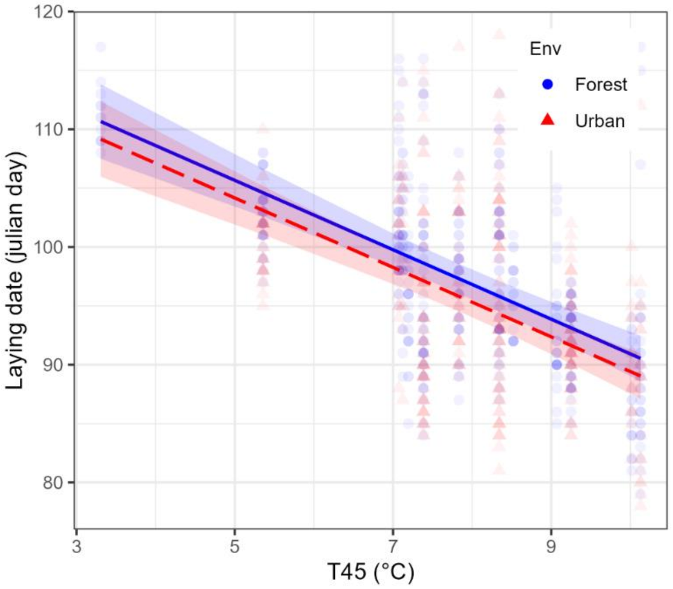

Figure 2. Laying date of great tits (*Parus major*) in an urban and forest environment in function of the temperature during the early-season. Great tits laying date was negatively correlated with T45 and was earlier for urban compared to forest nests (Env: β=-0.20 [-0.35, -0.05]; T45: β=-0.54 [-0.66, -0.42]). T45: daily mean temperature averaged from 45 days before the median laying date up to it (7th of April in non-leap years). Env: forest or urban environment. Red triangles and dashed line represent urban nests. Blue circles and solid line represent forest nests.

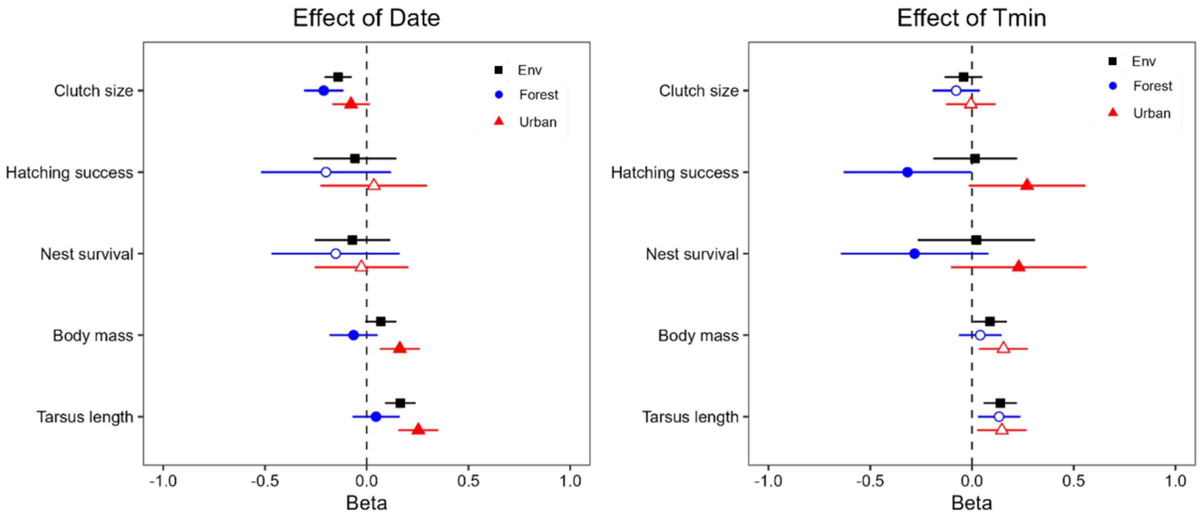

Figure 3. Correlation between date and minimum temperature with clutch size, breeding success and nestling growth. We illustrate standardized coefficient (beta) and their 95th confidence interval. Model represented are "~Env+Var" and "~Env*Var" (Var: date or Tmin). In black: Env, in blue: Forest:Var, in red: Urban:Var. Significant interactions are represented by filled circle and triangle. Significant interactions are represented by filled circle and triangle, while non-significant are represented by open circle and triangle. Interestingly, standardized coefficient for forest nests were consistently lower than for urban nests across all traits investigated.

Table 3. Top models (ΔAICc<4) predicting laying date of great tits (*Parus major*) in an urban and forest habitat.

Formula	AICc	dAICc	df	weight
Env+T45+RR45	4,748.26	0.00	7	0.25
Env*T45+RR45	4,748.60	0.34	8	0.21
Env+T45*RR_45	4,749.08	0.82	8	0.17
Env+T45	**4,749.64**	**1.38**	**6**	**0.13**
T45*Env	4,749.85	1.59	7	0.11
Env*RR45+T45	4,749.98	1.72	8	0.11
Intercept-only	4,780.59	32.33	4	0.00

Random effects: year, nestbox identity. Most parsimonious model is highlighted in bold. RR45, T45: daily cumulative precipitation and daily mean temperature averaged from 45 days before the median laying date up to it.

3.4. Clutch size

Most parsimonious model predicting great tits clutch size was “~Env+LD” (Table 4; Figure 4; LD: β=-0.14 [-0.21, -0.07]). Clutch size was not significantly correlated with rainfall or temperature, but decreased with laying date. The interaction between the site and the laying date was significant in an alternative model (model: Env*LD; Env:LD, β=0.13 [0.00, 0.27]). Post-hoc analysis revealed that clutch size was negatively correlated with laying date for forest nests (Forest:LD, β=-0.21 [-0.31, -0.12]), but not for urban nests (Urban:LD, β=-0.08 [-0.17, 0.02]).

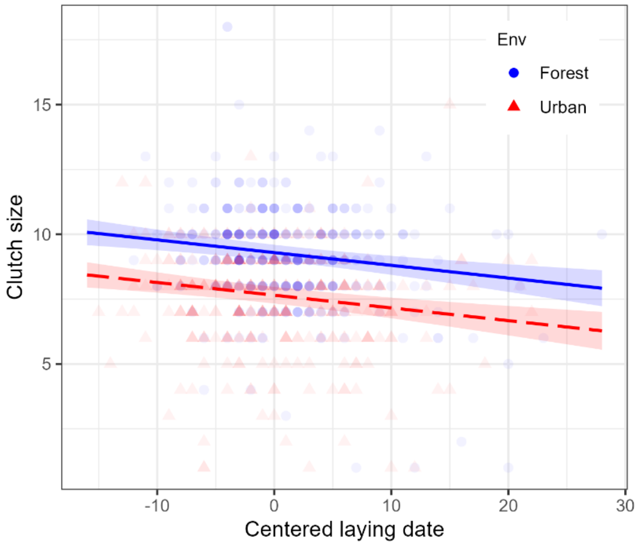

Figure 4. Clutch size of great tits (*Parus major*) in an urban and forest environment in function of the centered laying date. Great tits clutch size was negatively correlated with centered laying date for urban and forest nests (β=-0.14 [-0.21, -0.07]). Laying date is centered around each year median. Env: forest or urban environment. Red triangles and dashed line represent urban nests. Blue circles and solid line represent forest nests.

Table 4. Top models (ΔAICc<4) predicting clutch size of great tits (*Parus major*) in an urban and forest environment.

Formula	AICc	dAICc	df	ω
Env+LD	**2,976.25**	**0.00**	**6**	**0.52**
Env*LD	2,976.43	0.18	7	0.47
Intercept-only	3,058.93	82.67	4	0.00

Random effects: year, nestbox identity. Most parsimonious model is highlighted in bold. Env: forest or urban. LD: centered laying date.

3.5. Hatching success

The most parsimonious model predicting hatching success was "~Env+Nhot", and Nhot was positively correlated with hatching success (Table 5; Figure 5A; Nhot, β=0.29 [0.04, 0.54]). Centered laying date and precipitation were not correlated with hatching success. While main effects of other temperature variables were not significant, the interaction between Tmin and Tmean with the environment was significant (ΔAICc<2; model: "Env*Tmin", Env:Tmin, β=0.59 [0.16, 1.01]; model "Env*Tmean", Env:Tmean, β=0.46 [0.04, 0.89]). Post-hoc analysis revealed that Tmin was negatively correlated with hatching success for forest nests (Forest:Tmin, β=-0.32 [-0.63, 0.00]), but tended to be positively correlated with hatching success for urban nests (Urban:Tmin, β=0.27 [-0.02, 0.57]).

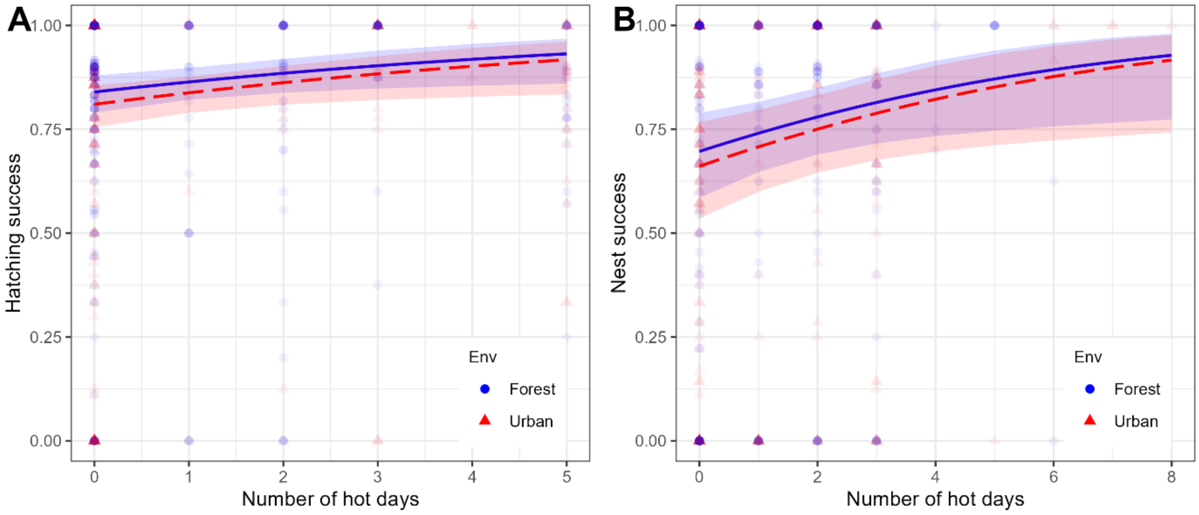

Figure 5. Relationship between the number of hot days (A) during incubation on hatching success (B) during nestling rearing on nest success. Number of hot days positively correlated with hatching success (β=0.29 [0.04, 0.54]) and nest success (β=0.31 [0.05, 0.57]). Proportion of eggs hatching and proportion of nestlings surviving up to ringing represent respectively the hatching and nest success. Hot days were defined as days with maximum temperature exceeding 25.4°C (90th percentile). Env: forest or urban environment. Red triangles and dashed line represent urban nests. Blue circles and solid line represent forest nests.

Table 5. Top models (ΔAICc<4) predicting hatching success of great tits (*Parus major*) in an urban and forest environment.

Formula	AICc	dAICc	df	ω
Env+Nhot	**579.31**	**0.00**	**6**	**0.16**
Env*Tmin	579.81	0.50	7	0.13
Env*Nhot	580.03	0.72	7	0.11
Env*Ncold*RR	580.17	0.86	11	0.11
Env+Nhot+RR	580.65	1.34	7	0.08
Env+Nhot*RR	581.04	1.73	8	0.07
Env*Nhot+RR	581.36	2.05	8	0.06
Env*Tmin+RR	581.72	2.41	8	0.05
Env*Tmean	582.67	3.35	7	0.03
Env+Ncold*RR	582.82	3.51	8	0.03
Env*Ncold	582.91	3.60	7	0.03
Env	583.22	3.90	5	0.02
Intercept-only	605.82	26.51	3	0.00

Clutch size is in covariate in all models. Random effects: year, nestbox identity. Most parsimonious model is highlighted in bold. Env: forest or urban. N_{hot}: number of hot days during incubation.

3.6. Nest success

The most parsimonious models predicting nest success were “Env+Nhot” and “Env+Tmean”, and both temperature variables were positively correlated with nest success (Table 6; Figure 5B; Nhot, β=0.31 [0.05, 0.57]; Tmean, β=0.38 [0.19, 0.57]). However, the interaction between the breeding environment and Tmin or Tmean was a significant in other competitive models (model: “Env*Tmin”, Env:Tmin, β=0.51 [0.13, 0.89]; model: “Env*Tmean”, Env:Tmean, β=0.49 [0.09, 0.90]). Post-hoc analysis revealed that Tmin and Tmean tended to be positively correlated with nest success for urban nests (Urban:Tmin, β=0.23 [-0.10, 0.56]; Urban:Tmean, β=0.43 [0.06, 0.79]), but negatively for forest nests (Forest:Tmin, β=-0.28 [-0.65, 0.08]; Forest:Tmean, β=-0.07 [-0.48, 0.35]). Rainfall was negatively associated with nest success although non-significantly (model: “~Env+Tmean+RR”, RR, β=-0.16 [-0.34, 0.03]).

Table 6. Top models (ΔAICc<4) predicting nestling survival of great tits (*Parus major*) in an urban and forest environment.

Formula	AICc	dAICc	df	ω
Env*Tmean+RR	689.14	0.00	8	0.11
Env*Tmean	689.31	0.17	7	0.10
Env*Tmin+RR	689.49	0.35	8	0.09
Env+Nhot+RR	689.64	0.50	7	0.09
Env+Nhot	**689.79**	**0.64**	**6**	**0.08**
Env*Tmin	690.31	1.17	7	0.06
Env+Tmean+RR	690.36	1.21	7	0.06
Env+Ncold+RR	690.57	1.43	7	0.05
Env*Nhot+RR	690.83	1.69	8	0.05
Env+Tmean	**690.86**	**1.72**	**6**	**0.05**
Env*Nhot	690.88	1.74	7	0.05
Env+Ncold	691.26	2.11	6	0.04
Env+Nhot*RR	691.27	2.13	8	0.04
Env*Ncold+RR	691.97	2.83	8	0.03
Env+Tmean*RR	692.40	3.26	8	0.02
Env+Ncold*RR	692.54	3.40	8	0.02
Env*Ncold	692.74	3.60	7	0.02
Env+RR	692.82	3.68	6	0.02
Intercept-only	707.48	18.34	3	0.00

Brood size is in covariate in all models. Random effects: year, nestbox identity. Most parsimonious model is highlighted in bold. Env: forest or urban. N_{hot}: number of hot days during incubation. N_{rain}: number of rainy days during incubation

3.7. Nestling growth

Most parsimonious model predicting nestling body mass at ringing was “Env*HD”, i.e. main effect of environment, centered hatching date and their interaction (Table 7; Figure 6A; Env:HD, β=0.23 [0.08, 0.38]). Nestling mass was positively correlated with centered-hatching date for urban nests (Urban:HD, β=0.16 [0.06, 0.26]), but not for forests nests (Forest:HD, β=-0.07 [-0.18, 0.05]). Tmin and Tmean were also positively correlated with nestling mass but models were less supported (model: “Env+Tmin”, ΔAICc=3.61, Tmin, β=0.09 [0.00, 0.17]; “Env+Tmean”, ΔAICc=3.86, Tmean, β=0.09 [0.00, 0.18]). Rainfall was not associated with nestling mass (model: “Env+RR”, RR, β=-0.03 [-0.14, 0.08]).

Nestling body mass and tarsus length were correlated (R^2_m=0.46; β=0.67 [0.64, 0.71]). Most parsimonious model predicting nestling tarsus length was “Env*HD” (Table 7; Figure 6B; Env:HD, β=0.21 [0.06, 0.36]). Nestling tarsus length was positively correlated with hatching date for urban nests (Urban:HD, β=0.30 [0.19, 0.42]), but was not related with it for forest nest (Forest:HD, β=0.05 [-0.08, 0.19]). Models including any temperature variables were less supported (ΔAICc>4), but some temperature variables were positively correlated with tarsus length (model: “~Env+Tmin”, Tmin, β=0.18 [0.08, 0.28]; model: “~Env+Tmean”, Tmean, β=0.17 [0.08, 0.27]; model: “~Env+Nhot”, Nhot, β=0.14 [0.06, 0.22]). Rainfall was not associated with tarsus length (model: “~Env+RR”, β=0.00 [-0.10, 0.10])

Table 7. Top models (ΔAICc<4) predicting nestling mass of great tits (*Parus major*) nestlings at ringing in an urban and forest environment.

Formula	AICc	dAICc	df	ω
Body mass				
Env*HD	**8497.75**	**0.00**	**10**	**0.51**
Env	8500.59	2.84	8	0.14
Env+Tmin	8501.35	3.61	9	0.08
Env+Tmean	8501.61	3.86	9	0.07
Intercept-only	8568.41	70.66	6	0.00
Tarsus length				
Env*HD	**5,843.28**	**0.00**	**10**	**0.70**
Env+HD	5,845.57	2.29	9	0.22
Intercept-only	5,884.81	41.53	6	0.00

Brood size is a covariate in all models. Random effects: year, brood identity, nestbox identity, nestling age. Most parsimonious model is highlighted in bold.

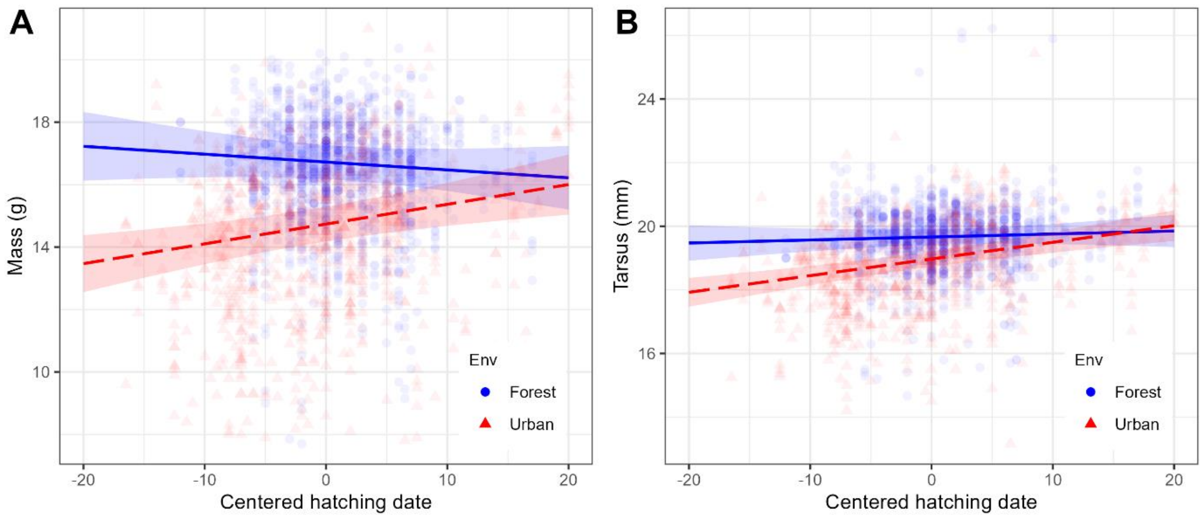

Figure 6. Relationship between the centered hatching date with (A) nestling body mass at ringing (B) nestling tarsus length at ringing. Centered hatching date positively correlated with nestling body mass and tarsus length for urban nests (Mass: β=0.16 [0.06, 0.26]; Tarsus: β=0.30 [0.19, 0.42]), but was not related with it for forests nests (Mass: β=-0.07 [-0.18, 0.05]; Tarsus: β=0.05 [-0.08, 0.19]). Hatching date is centered around median for each year. Env: forest or urban environment. Red triangles and dashed line represent urban nests. Blue circles and solid line represent forest nests.

4. Discussion

Temperature during the breeding season increased since 1990 at our study site, and great tits seemed to breed earlier with higher early-season temperature similar to other studies (Ahola et al., 2007; Ahola et al., 2009; Charmantier et al., 2008; Husby et al., 2010). Great tits breeding initiation did not advance with time. However, considering the between-year weather variability and duration of our monitoring program (13 and 9 years in forest and urban environments respectively), it is not surprising that we did not identify a phenological advancement of great tits breeding initiation. We however expect great tits to show earlier breeding with time and climate warming (e.g. Bailey et al., 2022; Charmantier et al., 2008; Husby et al., 2010).

Contrary to our expectations, rainfall was not related to any of the reproductive traits investigated (Bordjan and Tome, 2014; Marques-Santos and Dingemanse, 2020; Schöll and Hille, 2020). Clutch size showed a seasonal decline similar to other studies (Ahola et al., 2009; Orell and Ojanen, 1983; Perrins and Mccleery, 1989; Vaugoyeau et al., 2016). Causes of this decline are likely due to differences in breeders' quality (e.g. earlier breeders have a higher phenotypic quality) and/or direct effect of breeding timing (e.g. synchrony with food availability; Both et al., 2009; Verhulst and Nilsson, 2008; Visser et al., 2006)**.** As expected, main effect of temperature was consistently positively related with breeding success (i.e. hatching success, nest success) and nestling growth (e.g. Eeva et al., 2020; Marques-Santos and Dingemanse, 2020; Wawrzyniak et al., 2020). Great tits may benefit from milder temperature, promoting hatching success, nestling survival, and nestling growth (te Marvelde et al., 2012; Tulp et al., 2009). For instance, experimental heating of great tits nests led to a decreased in female daily energy expenditure during cold periods (i.e. temperature <5°C), suggesting that nest heating alleviated thermoregulatory costs (Bryan and Bryant, 1999). Sublethal costs on nestling growth and condition may impair later post-fledging survival (Naef-Daenzer et al., 2001; Rodríguez et al., 2016; Ronget et al., 2018)

Exposure to hot days (i.e. days with maximum temperature ≥25.4°C) was positively correlated with hatching success and nestling survival. This contrasts with Pipoly et al (2022) results, which reported a negative correlation between exposure to hot days (i.e. days with maximum temperature ≥28.7°C) and nestling growth and survival. We discuss hereafter potential explanations to such differences. High temperatures thresholds relative to the local climatic variability were higher in Pipoly et al (2022), and thus potentially more likely to promote heat stress. Moreover, authors investigated first and second broods concomitantly, while we restricted our study to the first broods. Since temperature increases during the breeding season, second broods are likely exposed to higher temperatures than first broods. On one hand, such exposure may promote heat stress, potentially explaining why the effect of high temperature may hinder reproductive output only in second broods in some instances (Bowers et al., 2016; Møller, 2011; Salaberria et al., 2014). On the other hand, clutch size and breeding success are likely to show a seasonal decline, and to be lower in second broods. Consequently, negative effects of exposure to high temperature may be due to the correlation with the breeding timing.

In line with previous studies, clutch size, brood size, number of nestling ringed and hatching success were significantly lower in urban environments (Biard et al., 2017; Chamberlain et al., 2009; Vaugoyeau et al., 2016; Wawrzyniak et al., 2020). Although nestling survival was not significantly different between urban and forest nests, nestling body mass and size was lower in the urban environment similar to other studies (Biard et al., 2017; Caizergues et al., 2021; Pipoly et al., 2022). Such differences are likely the results of the quality of the environment and parents. Lower food availability, higher pollution levels likely drive a diminished individual quality and reproductive output at our study site (Saulnier et al., 2022; Saulnier et al., 2023).

Nestling growth has been reported to be limited by food availability in urban systems, and temperature to be more strongly associated with breeding success only in urban systems (Seress et al., 2020; Wawrzyniak et al., 2020). Here, positive effects of temperature on breeding success seemed more pronounced in the urban environment, similar to Wawrzyniak et al (2020). Conversely, negative effects of the breeding timing were only found for forest nests. Interestingly, seasonal decline in clutch size tended to be stronger in the forest environment, although this model was not the most parsimonious. Overall, temperature and breeding timing tended to be positively and negatively associated with breeding success, consequently representing confounding effects. Contrasted effects between urban and forest nests are likely the results of varying relative influence of weather and breeding timing depending on the environments.

Food is likely a limiting factor of reproduction in urban environments and synchrony with food availability is likely to drive breeding success (Seress et al., 2020; Visser et al., 2006). Food availability seems to be lower for urban nests in our system, and our research protocol would therefore benefit from monitoring food availability during the breeding season (Saulnier et al., 2022). Moreover, thermal environment may vary between urban and forest sites, and monitoring temperature at the nest-level would likely help to better identify thermoregulatory costs during breeding (e.g. outside and inside nest boxes, and clutch or brood temperature). Nestling growth and survival seemed impaired when nest temperature exceeds 30-35°C for great tits (Rodríguez and Barba, 2016; Van Balen and Cavé, 1969). Ultimately, there are limitations to correlative approaches and experimental manipulation, such as delaying breeding initiation or warming nests are required to disentangle potential confounding effects.

Theme 1. Discussion

Barn owl (*Tyto alba*) breeding success was positively correlated with high air temperatures in a temperate climate but negatively correlated desertic climate (Charter et al., 2017; Chausson et al., 2014). Picture from Macaulay Library (ML628245008).

1. Overview of high temperatures and breeding success

When reviewing breeding success association with high temperatures, only a minor proportion of studies assessed the effect of hot events (i.e. 14.9%), among which studies in desert climates were over-represented (66.7%). Researchers seem more likely to use the terms “extreme temperatures” or “heatwaves” and test their potential effects on species breeding in desert environments. We were consequently not able to restrict the analysis to studies assessing the effect of hot events (i.e. relative to local weather stochasticity; e.g. hot days, heatwaves), representing a strong limitation of our review. Most importantly, exposure to hot days does not necessarily promote heat stress depending on the specie of interest and study site. For instance, air temperature exceeding 0°C was described as “extremely hot days” in Dickey et al 2008, which was unlikely to promote heat stress. Moreover, very few studies reported direct effect of exposure to high temperature to be likely to promote heat stress, and among which desert climates were also over-represented (2.6%). Consequently, we emphasize that our results should be regarded as a first step when looking at the effect of high temperatures on avian reproduction at a global scale.

Overall, there was a high variation in the response to high temperature between studies. Part of this variation may be explained by the breeding stage investigated. For instance, clutch size was most often not related with high temperatures, and was not related with increasing temperature in a recent meta-analysis (Halupka et al., 2023). When assessing weather effects on great tits reproduction at our study site, clutch size was also non-related with temperature and rain before laying. Clutch size may be mainly driven by the environment experienced before the breeding season rather than during the early-season, such as winter or pre-migratory conditions (i.e. "carry-over effect"; Harrison et al., 2011; Tobolka et al., 2018). Alternatively, there is a high diversity of traits and reproductive strategies among avian species, which could explain part of this observed variation.

Firstly, thermoregulatory responses to heat exposure and thermoregulatory mechanisms differ between avian taxa (McKechnie and Wolf, 2019; McKechnie et al., 2021a). Secondly, there is considerable diversity in breeding strategy between avian species. Nests shows a wide variety of characteristics (e.g. shapes, location, composition) and parental care is a highly diverse trait (e.g. species with uni-, bi- or cooperative parental care; Deeming, 2004). Thermal requirements may also differ depending on the offspring phenotype, and most specifically according to the altricial-precocial continuum (Ducatez and Field, 2021). Finally, drivers of breeding success and sensitivity to high temperature exposure may differ depending on varying traits such has migratory strategy (Jones and

Cresswell, 2010; Meller et al., 2018), capital or income breeders (Ruthrauff et al., 2021), single or multi-brooded species (Halupka and Halupka, 2017; Møller et al., 2010).

2. Importance of the local climate

High temperature was strongly associated with negative effects on birds breeding success in hot and arid climates, while this relationship seemed to be more contrasted in other climates (temperate, continental and polar). This is consistent with results presented in Sauve et al (2021), which suggested that increased temperature was positively tied with nestling growth in cold climates, but negatively in hot climates. This trend seems to also apply at intra-specific level (e.g. Dubos et al., 2019; Redpath et al., 2002). For instance, nestling survival was positively correlated with high temperature for great tits (*Parus major*) in continental climates in most cases (Ahola et al., 2009; Eeva et al., 2020; Marques-Santos and Dingemanse, 2020; Schöll and Hille, 2020; Wawrzyniak et al., 2020). We investigated the relationship between great tits breeding success and weather in a temperate study site chapter 2. We also found that Great tits breeding success in a temperate climate were positively correlated with high temperatures (i.e. number of hot days). Nevertheless, the only study on great tit breeding success in a desert climate reported a decreased post-fledging survival with high temperature (Greño et al., 2008b).

Our review suggests that hot events are likely to promote heat stress and thus constrain bird reproduction in hot and arid areas. Even though birds' upper critical temperature (UCT; upper limit of the thermoneutrality zone) scales with temperature in their habitat, adaptation to high temperature may be constrained , potentially explaining why the range of UCT is relatively narrow among birds (i.e. "Brett rule"; Araújo et al., 2013; Gaston et al., 2009). For instance, average UCT seems quite similar between desert and temperate passerines (~37-38°C; Cabello-Vergel et al., 2022; McKechnie et al., 2021; Pollock et al., 2021). Moreover, there may be little variation in optimal egg incubation temperature between species. Optimal incubation temperature is believed to be approximately 35-37°C and 36-38°C for wood ducks (*Aix sponsa*) and zebra finches (*Taeniopygia guttata*) respectively, despite exploiting drastically different habitats (Berntsen and Bech, 2016; Durant et al., 2013b; Wada et al., 2015a; Zann and Rossetto, 1991). For instance, air temperature (Tair) can frequently exceed 40°C during zebra finches reproduction, consequently exceeding UCT and optimal incubation temperature (UCT ~ 37.5°C; Danner et al., 2021; Griffith et al., 2016; Pessato et al., 2023; Wojciechowski et al., 2021), leading to changing patterns of activity, decreased nest attentiveness, incubation duration, hatching success and impaired nestling growth (Andrew et al., 2017; Funghi et al., 2019; McCowan and Griffith, 2021; Wheeler et al., 2023).

Conversely, high temperature could be more likely to represent a thermal relief (i.e. decreased heating costs) and promote breeding success for birds in colder areas (McKinnon et al., 2013). In our case, the number of hot days during incubation and chick rearing was positively correlated with hatching success and nestling survival. Moreover, across relatively similar air temperature (i.e. minimum temperature within 2-12°C), experimental heating of great tits nests reduced parental energy expenditure during colder days, suggesting a thermal relief (Bryan and Bryant, 1999). Overall, our results suggest that high temperature in our system do not promote heat stress, which was corroborated by the absence of observation of heat dissipation behaviors (e.g. panting). While, great tits did not seem to show any heat dissipation behavior during hot days at our study site, temperature may influence their activity pattern. Future studies should therefore focus on assessing the relationship between temperature, behavior and time-energy budget on great tits in our system. It is worth noting that Pipoly et al (2022) reported a negative correlation between exposure to high temperature (i.e. days with temperature ≥28.7°C) and great tits breeding success in temperature study site. However, as far as we are aware, authors did not assess a potential effect of breeding timing. Breeding success usually show a seasonal decline and this effect may be due to the increase probability to observe a hot day later in the breeding season. Ultimately, there are inherent limitations to correlative approaches, as correlation does not equate causation. Conducting field experiments such as nest temperature manipulation or parental feather-clipping is necessary to characterize the influence of the thermal environment and predict climate warming effects on populations (Andreasson et al., 2020c; Nord and Nilsson, 2019).

3. Importance of phenology and trophic interactions

In this thesis, we highlight that high temperature can also drive breeding success through direct (i.e. mediated via thermoregulation of parents or offspring) and indirect effects (i.e. not mediated by thermoregulation; e.g. phenology and trophic interactions). On one hand, high temperatures during the early-breeding season can promote advancement of the breeding phenology, which may lead to an environmental mismatch (i.e. with biotic or abiotic factors). While most birds show earlier breeding with time and warming temperatures, it is most often unclear whether populations are able to track optimal conditions (Figure 1A). In some cases, despite warming temperatures at a study site, the advancement of the breeding initiation may result in an average cooling of the breeding season and further exposure to cold events (i.e. “false spring” phenomenon; e.g. Lehikoinen et al., 2009; Shipley et al., 2020; Socolar et al., 2017). On the other hand, asymmetric phenological shifts between birds and their predator or food resources may also impact breeding success (Figure 1B; Ross et al., 2018; Vatka et al., 2014; Vatka et al., 2016; Visser et al., 2012).

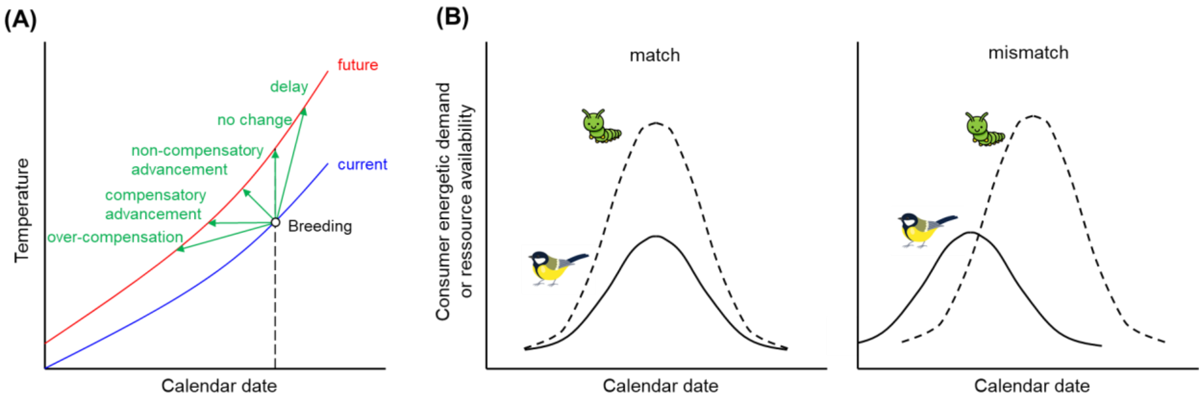

Figure 1. Phenological shift and environmental mismatch. (A) Potential effect of climate change and phenological shift on the temperature experienced during breeding. In case of warming temperature, species that show no advancement in their phenology will face higher temperatures (i.e. “thermally delayed”; Saino et al., 2011). Alternatively, advancement is not systematically compensatory and can even results in birds facing cooler temperatures (e.g. Socolar et al., 2017). (B) Potential effect of climate change and phenological shift on synchrony of energy demand and food availability during breeding. A decrease in consumer fitness is expected if consumer shift their phenology relative to resource availability (i.e. mismatch; adapted from Kharouba and Wolkovich, 2020). Curves represent energetic demands of the consumer (solid lines) and seasonal changes in the availability of the resource (dotted lines).

Great tits advanced their breeding initiation during warmer years at our study site. Since breeding timing and its interaction with food availability seem to be an important driver of breeding success, long-term effect of climate warming may be mediated by changes in phenology at our study site. Moreover, the relationship between weather, breeding timing and reproductive success in great tits seemed to vary between urban and rural sites. This is likely explained by artificialization differences due to the geographical proximity between forest and urban sites rather than weather itself (~20km away). The forest environment is characterized by a higher individual and environmental quality, potentially allowing parental care to buffer environmental stochasticity (Figure 3; Seress et al., 2020; Sumasgutner et al., 2023). Additionally, seasonal variation in food availability is likely lower in the urban environment due to the presence of alternative prey items. Consequently, we hypothesize that breeding timing is likely a stronger driver of breeding success for forest nests relatively to urban nests.

Disentangling direct and indirect effects of high temperature would necessitate monitoring of environmental and nest temperature, parental care and thermoregulatory costs (i.e. heating and cooling costs of parents and offspring). Identifying whether hot days promotes heat stress would need to directly monitor behavior, body temperature and water-balance homeostasis of parents and offspring. In the following theme of this thesis, we focus on the response to heat exposure in birds, discussing and providing ways to monitor direct effect of heat exposure.

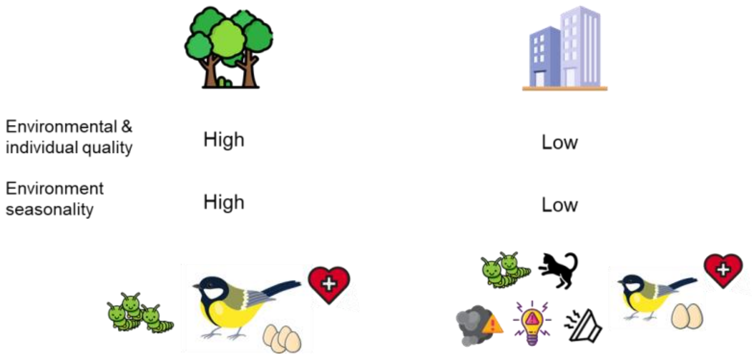

Figure 3. Expected differences in environmental and individual quality for great tits (*Parus major*) in urban and forest environments. Urban environment is likely of lesser quality (e.g. pollution, alternative predators, lower food availability and/or quality; Lepczyk et al., 2023; Planillo et al., 2021). Great tits individuals in urban environment are likely of lesser quality (e.g. lighter and smaller, lower body condition index, paler color Banbura et al., 2013; Biard et al., 2017; Caizergues et al., 2021; Salmón et al., 2023). Great tit clutch size and breeding success are lower in urban environments (e.g. Biard et al., 2017; Chamberlain et al., 2009; Pipoly et al., 2022; Vaugoyeau et al., 2016; Wawrzyniak et al., 2020).

THEME 2. PHYSIOLOGICAL RESPONSE TO HEAT EXPOSURE IN BIRDS

Chapter 3. Physiological markers of avian dehydration: assessing the hyperthermia-dehydration trade-off

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Southern Yellow-billed Hornbill (*Tockus leucomelas*) in the Kalahari Desert (South Africa) showed behavioral and physiological sign of heat stress during exposure (i.e. panting and potential dehydration), leading to reduced breeding success and population decline (Pattinson et al., 2022; van de Ven et al., 2019; van de Ven et al., 2020). Photo from the Macaulay Library (ML628079051).

1. Glossary

Ambient temperature: controlled air temperature within experimental settings, more closely analogous to operative temperature than to air temperature in the field. Operative temperature corresponds to the concept of the 'temperature of the environment'. It is formally defined as the temperature of an imaginary isothermal 'black' enclosure around an occupant (human or other animal) that would exchange infrared radiant heat with the occupant at the same rate that the occupant exchanges heat with the actual environment by radiation, convection and conduction combined.

Capillary refill time: time taken for color to return to an external capillary bed after pressure is applied to cause blanching.

Environmental temperature: refers to ambient temperature or operative temperature, depending on the context.

Demography: study of the characteristics of populations (e.g. population dynamic, size, density or structure).

Diuresis: increased urine production, as opposed to 'anti-diuresis' (decreased urine production).

Faecal sac: a mucous membrane surrounding excreted faeces.

Filtration: filtration of the blood from the vascular compartment to the tubule lumen at the renal corpuscle.

Phenology: study of the timing of life cycle events at the population level (e.g. timing of reproduction, migration).

Post-renal modification: modification of the ureteral urine (i.e. urine excreted by the kidney) within the cloaca (coprodeum), colon and ceca. The term 'cloacal urine' usually refers to the urine produced after these post-renal modifications.

Reabsorption: movement of solutes and water from the tubule lumen to the blood compartment in the nephron.

Resting metabolic rate: energy expenditure observed under strict resting conditions (i.e. when the animals is undergoing very limited locomotor activity and is in a fasting state).

Salt gland: a nasal organ specialized for the excretion of salt in birds.

Secretion: movement of solute from the blood compartment to the tubule lumen in the nephron.

Sentinel species: species that respond to ecosystem variability and/or change in a timely and measurable way, and can indicate an otherwise unobserved change in ecosystem function.

List of symbols and abbreviations:

$P_{[compound]}$: concentration of a specific compound in the plasma or serum.

P_{osm}: Plasma or serum osmolarity

T_a: ambient temperature

T_{air}: air temperature

T_b: body temperature

T_e: environmental temperature

UA: uric acid

U_{osm}: Urine osmolarity

W_d: water obtained by drinking

W_{ev}: evaporative water loss

W_{ex}: water loss via excretion (urine and faeces)

W_m: metabolic water production

W_p: water preformed in food

2. Abstract

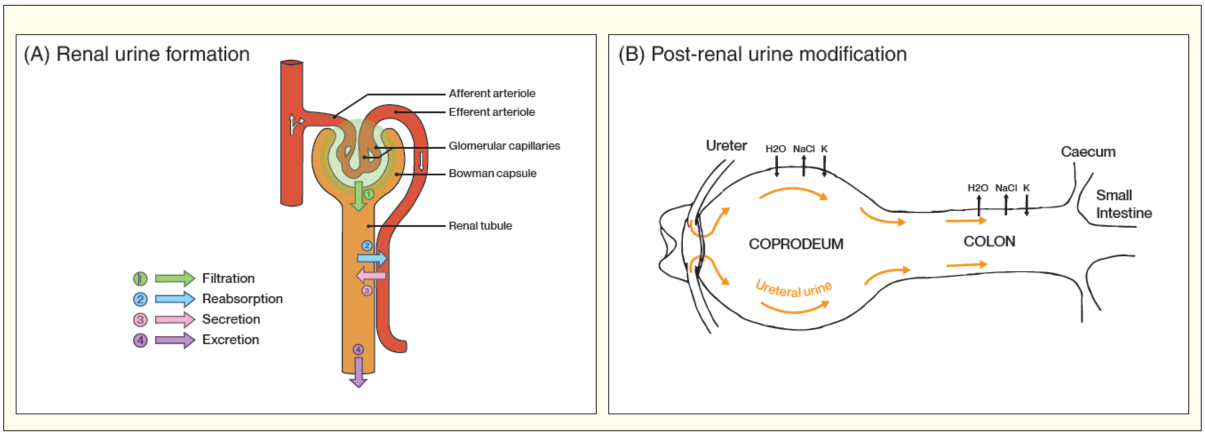
During heat exposure, birds may face a trade-off between hyperthermia and dehydration. Numerous studies have attempted to predict cooling costs for birds, which are expected to increase with global warming. Although modelling dehydration risk is important, it does have its limitations, and models do not replace direct measurement of hydration status. In fact, studies assessing the effects of temperature on the hydration status of wild birds are surprisingly rare. In this Review, we discuss the experimental evidence for the hyperthermia–dehydration trade-off, and the limitations of modelling avian dehydration risk through set thermal limits. In addition, we present a systematic review of physiological markers of dehydration for avian species. When exposed to heat, water-restricted individuals reduce their evaporative water loss at the expense of increases in body temperature compared to hydrated individuals, suggesting a trade-off between hyperthermia and dehydration risk. We find that plasma osmolarity and plasma concentrations of sodium and chloride are the most reliable markers of dehydration, and seem to scale with dehydration severity. Hematocrit appears to predict dehydration but multiple concerns impede its suitability as a marker. Plasma concentrations of uric acid, urea and creatinine may represent adequate markers of dehydration. Alternatively, characteristics of the excreta – such as urine osmolarity – may represent less-invasive means to assess hydration state.

3. Introduction

Climate change is marked by an increase in global mean temperature, but also an increase in the frequency, duration and intensity of heatwaves (Diffenbaugh and Field, 2013; IPCC, 2014; Simolo and Corti, 2022), which represents a threat for biodiversity (Maxwell et al., 2019; Moreno and Pape Møller, 2011). Improving our ability to forecast the effects of climate change on wild species will require us to develop mechanistic models using key parameters that drive a population's sensitivity to environmental change (e.g. evolution, demography, physiology; Urban et al., 2016). In this Review, we focus on the response of birds to high temperatures, particularly focusing on the interaction between heat exposure and dehydration risk. Birds are important sentinel species (Clark-Wolf et al., 2024). They exploit a wide range of habitats, are easily observable, are sensitive to environmental changes and respond to these changes in a detectable manner (e.g. with changes in thermoregulatory behaviors, parental care, breeding success, population dynamics; Hazen et al., 2019; Oswald and Arnold, 2012). Moreover, high environmental temperatures (see Glossary) have already had drastic effects on some avian populations, leading to decreased abundance (Iknayan and Beissinger, 2018; Riddell et al., 2019), mass mortality events (McKechnie et al., 2021b; Piatt et al., 2020b) and complete breeding failures (McCowan and Griffith, 2021; Romano et al., 2020; Sharpe et al., 2021). When exposed to high ambient temperatures (see Glossary), birds can either tolerate hyperthermia and/or dissipate heat (Gerson et al., 2019; McKechnie and Wolf, 2019). Birds dissipate heat mainly through evaporative water loss (W_{ev}), via the respiratory and cutaneous pathways (McKechnie et al., 2016; McKechnie et al., 2021a; Ro and Williams, 2010; Smit et al., 2018). However, birds usually use a combination of heat storage and increased heat dissipation to achieve the most favorable thermal and osmotic balance, i.e. limiting hyperthermia while maintaining homeostasis of body fluids (Gerson et al., 2019; Tieleman and Williams, 1999). This suggests that there may be a trade-off between hyperthermia and dehydration risk, especially during extreme heat and/or water restriction. In this Review, we discuss the evidence for the hyperthermia–dehydration trade-off in birds, and review the physiological makers of avian dehydration, providing relevant ways of assessing heat stress in field studies.

Several studies have used measurement of metabolic rate, W_{ev} or behavioral markers of thermoregulation to predict cooling cost and dehydration risk of birds, which are expected to increase with climate warming (e.g. Albright et al., 2017; Conradie et al., 2019, 2020; Cook et al., 2020; McKechnie and Wolf, 2010; Riddell et al., 2019, 2021). Unfortunately, this approach has its limitations, including the fact that it does not involve assessment of body temperature and hydration state of wild birds in their natural environment. Yet, surprisingly few studies assessing the direct effect of high air temperature on body temperature or hydration state of wild birds (e.g. Goldstein and Zahedi, 1990; Linek et al., 2021; Salaberria et al., 2014; Smit et al., 2013). Measuring these physiological variables in the wild is challenging, and recent tools for physio-logging are not yet widely used in birds (Williams et al., 2021). Although body temperature can be measured directly or indirectly in a number of ways (e.g. Andreasson et al., 2023; McCafferty et al., 2015), physiological markers of avian hydration state in particular are not widely used; in this Review, we discuss potential means for direct assessment of hydration state, including measurement of total body water, body mass loss under controlled conditions, or blood and urine characteristics (e.g. osmolarity, ions concentrations; Cheuvront et al., 2010; Cheuvront et al., 2013; Shirreffs, 2003). Osmoregulatory system in birds have been extensively reviewed and we do not cover this topic (Braun, 1982; Goldstein, 2006; Hughes, 2003; Laverty and Skadhauge, 2008; Orosz and Echols, 2020; Skadhauge, 1981; Takei, 2000). Urine production in the kidney and post-renal urine handling are briefly summarized presented in Box 1. Research addressing physiological markers of dehydration for birds appears to have peaked during the 1980s; however, we are unaware of any comprehensive published reviews of this topic (Figure 1). The majority of the published studies focus mainly on poultry models: consequently, this research may not be well known to researchers in the fields of ecophysiology, ecology and conservation biology.

In this Review, we begin by presenting an overview of the experimental evidence for the hyperthermia–dehydration trade-off, and we discuss the dehydration risk faced by wild birds. We then consider the limitations of modelling dehydration risk through respirometry measurements (i.e. metabolic rate or W_{ev}) or behavioral observations (e.g. panting) when assessing dehydration risk, and we present a systematic review of physiological markers of avian dehydration. Based on our systematic review, we identify the most relevant physiological markers of avian dehydration, providing suggestions for researchers and revealing exciting perspectives for future studies.



Box 1. Renal and post-renal modification of the urine in birds. Regulation of urine flow rate and concentration are crucial processes in the regulation of body fluids homeostasis in birds. These processes have been extensively reviewed elsewhere (Braun, 1982; Goldstein, 2006; Orosz and Echols, 2020; Skadhauge, 1981), And we recommend Orosz and Echols (2020) for a recent review of avian nephron morphology and renal physiology. Briefly, urine flow rate (UFR) is determined by the glomerular filtration rate (GFR) and the rate of tubular water reabsorption. Concentration of the excreted ureteral urine is dependent on the sum of the filtration, reabsorption and secretion processes (panel A; see Glossary). Water reabsorption in the renal tubules depends mainly on sodium and chloride reabsorption. Dehydrated individuals have a reduced GFR and increased rate of tubular water reabsorption, reducing the UFR (anti-diuresis) and producing a hyperosmolar ureteral urine, ultimately conserving water. Avian species are also capable of post-renal urine modification (panel B; figure adapted from Skadhauge (1981) with permission; reviewed by Hughes, 2003; Laverty and Skadhauge, 2008). Panel B represents the retrograde transport and post-renal modification of ureteral urine in the domestic fowl (*Gallus gallus*). Retrograde peristalsis (orange arrows) allows the movement of ureteral urine from the urodeum to the upper part of the cloaca (coprodeum) and lower part of the gut (colon,

ceca). Active sodium and chloride reabsorption during this process can induce water reabsorption by osmosis. Note the initial dilution of urine in the coprodeum and subsequent reabsorption of water in the colon and ceca. The fluid produced by renal and post-renal modification is sometimes referred to as ‘cloacal urine’ or ‘cloacal fluid’. Additionally, some avian species possess a salt gland (see Glossary), which is an organ specialized for salt excretion. The salt gland plays an important role in water and salt homeostasis (Goldstein, 2001; Hughes, 2003). Salt-gland fluid contains high concentrations of sodium and chloride, and its composition may vary during dehydration (Stewart, 1972).

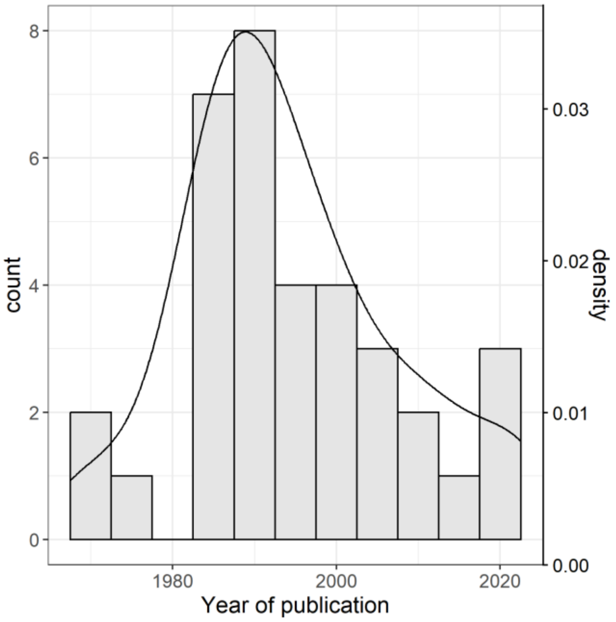


Figure 1. Histogram and density curve of the publication dates of articles investigating the effect of dehydration on various physiological markers in birds (n=35). Median, 1991. Mean, 1995. Dehydration is defined as a significant loss of body mass or total body water during water restriction.

4. Why should we assess dehydration in avian species?

4.1. The hyperthermia–dehydration trade-off

Birds exposed to high environmental temperatures (T_e) potentially face a trade-off between hyperthermia and dehydration (Dawson, 1982; McKechnie et al., 2021a; Pollock et al., 2021). At high T_e, birds actively dissipate heat through evaporation, primarily through respiratory pathways (i.e. panting, gular fluttering), and secondarily through cutaneous evaporation or alternative pathways (e.g.

urohidrosis; Cabello-Vergel et al., 2021; McKechnie and Wolf, 2019). Consequently, a bird attempting to maintain normothermia at high T_e uses a lot of water, potentially risking dehydration. Alternatively, most birds display some increase in body temperature (T_b) when exposed to heat, which is commonly referred to as 'facultative hyperthermia' (Freeman et al., 2022; Tieleman and Williams, 1999). Facultative hyperthermia reduces evaporative heat loss demand, increasing water economy (Gerson et al., 2019). For example, zebra finches (*Taeniopygia guttata*) exposed to an ambient temperature of 40°C for 8 hours drastically increase their T_b (>4°C increase in T_b; Cooper et al., 2020). Tolerating hyperthermia rather than increasing their W_{ev} leads to a saving of ~0.8g of water over the duration of the heat exposure, representing ~7.3% of their body mass.

Several studies on various avian species report a higher T_b in water-restricted individuals compared to non-restricted individuals when exposed to heat (e.g. Arad, 1983; Arad et al., 1987; Greenwald et al., 1967; Maloney and Dawson, 1998; Zhou et al., 1999). This can be explained by a reduced W_{ev} and a delay in the onset of heat dissipation when exposed to heat for water-restricted individuals, which consequently leads to further increase in T_b. For instance, water-deprived emus (*Dromaius novaehollandiae*) exposed to increasing T_a show a greater T_b, a decreased W_{ev} and a time-delay for the onset of panting compared with hydrated emus (Maloney and Dawson, 1998). Water-restricted domestic fowl (*Gallus domesticus*) and budgerigar (*Melopsittacus undulatus*) also show reduced W_{ev} and greater T_b after heat exposure compared with non-restricted individuals (Arad, 1983; Greenwald et al., 1967). Thus, dehydrated individuals tolerate hyperthermia in order to limit their water loss during heat exposure, a finding that provides support for the hyperthermia–dehydration trade-off.

Evidence for the hyperthermia–dehydration trade-off in the wild is sparse, simply because we are not aware of any field studies having monitored body temperature and hydration status simultaneously in wild birds. There are few reports of breeding birds losing weight during heat events, which may be linked with a decreased food intake (time spent foraging and foraging efficiency; Oswald et al., 2021; van de Ven et al., 2019, 2020) and/or an increased water loss (e.g. more time spent dissipating heat through panting; du Plessis et al., 2012; Oswald et al., 2021). Ultimately, these heat events may have led to a decreased adult survival and breeding success (Bourne et al., 2021a; Gardner et al., 2016; Sharpe et al., 2019; van de Ven et al., 2020). Adequate water is necessary for survival and breeding success in arid environments (e.g. Bolger et al., 2005; Coe and Rotenberry, 2003; Tieleman et al., 2004). For instance, supplementing water leads to increased clutch sizes for black-throated sparrows (*Amphispiza bilineata*; Coe and Rotenberry, 2003). Moreover, some studies have reported an interaction between drought and temperature, meaning that negative effects of high temperature are stronger during drought events (e.g. Bourne et al., 2020; Conrey et al., 2016; Londe et al., 2021;

Pattinson et al., 2022). The propensity for nest desertion by Kentish plovers (*Charadrius alexandrinus*) during a heat event is related to the distance to a water source (Amat and Masero, 2004). This could also apply to the lesser prairie-chickens (*Tympanuchus pallidicinctus*), which seem to select sites close to water sources for nesting, and for which breeding success and survival is strongly affected by heat exposure and drought intensity (Grisham et al., 2015; Grisham et al., 2014; Grisham et al., 2016; Lautenbach et al., 2018).

4.2. Limitations of behavioral and respirometry-based predictions

Being able to accurately determine thermal limits is crucial to the modelling of individual fitness and population dynamics under climate change scenarios (Clusella-Trullas et al., 2021; MacMillan, 2019). However, this is not a trivial task, as each of the many measurable aspects of organismal function (e.g. survival, reproductive output, loss of homeostasis, increase in metabolic rate or increase in W_{ev}) may have different thermal limits. Most studies addressing heat exposure of birds consider thermal limits that are based on measurements of metabolic rate and W_{ev} at high temperatures as a way to predict cooling requirements and dehydration risk, which are expected to increase with global warming (Albright et al., 2017; Cabello-Vergel et al., 2022; Conradie et al., 2019; Conradie et al., 2020; McKechnie and Wolf, 2010; Riddell et al., 2019; Riddell et al., 2021). However, the predictive significance of this approach is limited by multiple assumptions.

Firstly, water balance is attained when water influx matches water efflux: $W_d + W_p + W_m = W_{ev} + W_{ex}$, where W_d is drinking water, W_p is preformed water in food, W_m is the metabolic water produced, W_{ev} is the evaporative water loss and W_{ex} is the water loss through excretion (faeces and urine). However, most studies that predict dehydration risk only consider W_{ev}, thus assuming that water influx is negligible during heat exposure (e.g. Albright et al., 2017; McKechnie and Wolf, 2010). This is because activity – such as foraging – is likely to be reduced during heat exposure, consequently limiting water and food intake (i.e. Wd, Wp; Austin, 1978; Playà-Montmany et al., 2023; Thompson et al., 2018). Yet, there are reports of birds maintaining some level of activity on hot days (Smit and McKechnie, 2015; Smit et al., 2016), and zebra finches do not seem to lose body water as long as free water is available (Cooper et al., 2019; Funghi et al., 2019). Moreover, estimating dehydration risk only through W_{ev} implies that W_m and W_{ex} are negligible, which is unlikely to be the case. For hydrated zebra finches under laboratory conditions (Ta=23°C), W_m represents ~30% of water influx and W_{ex} represents ~38% of water efflux (Skadhauge and Bradshaw, 1974). Field W_m is 24-30% of water influx for wild zebra finches (Cooper et al., 2019). It is worth noting that both W_{ex} and W_m may vary depending on the hydration state and fasting state. For instance, W_{ex} and W_m decrease by ~66% and ~22%, respectively, in water-deprived zebra finches compared to hydrated individuals (Skadhauge and Bradshaw, 1974). Alternatively, an increase in lipid and protein catabolism during sustained dehydration or fasting may increase W_m (Gerson and Guglielmo, 2011; Rutkowska et al., 2016).

Secondly, most of the studies modelling the dehydration risk of wild birds usually use air temperature (T_{air}) as a predictor of cooling costs: they consider T_{air} to be a good proxy for T_e (e.g. Cabello-Vergel et al., 2022; Conradie et al., 2019). This is because T_e tends to match T_{air} in shaded microsites due to reduced direct solar radiation, and thus relies on the assumption that birds cease activity during heat exposure and have access to completely shaded microsites (Cunningham et al., 2021; Mitchell et al., 2018). Yet, temperatures in shaded microsites are still subject to some radiative, conductive or convective heat exchange (reviewed by Mitchell et al., 2018). In the case of breeding birds, nest temperature is also likely to be different from T_{air} (e.g. Carroll et al., 2018; Combrink et al., 2017; O'connor et al., 2018).

Thirdly, predicting dehydration risk using set values from the literature (e.g. mean W_{ev} for a specific T_a) does not account for the variability in responses, both at the population and individual levels. Even under laboratory conditions, there is still considerable variation between individuals in their response to heat or dehydration. If we take an extreme example, mourning doves (*Zenaida macroura*) deprived from water die after a mean duration of ~7 days and a mean body mass loss of ~37% (Bartholomew and Macmillen, 1960). However, survival time ranges from 3 to 11 days, and body mass loss at death ranges from ~25% to ~45%. Moreover, several studies have described physiological flexibility in the response to heat in avian species (i.e. acclimation and acclimatization; González-Medina et al., 2023; Noakes and McKechnie, 2020; Noakes et al., 2016; Pessato et al., 2023). For instance, resting metabolic rate and T_b vary between season for white-browed sparrow-weaver (*Plocepasser mahali*; Noakes et al., 2016). Wild and captive zebra finches show reduced resting metabolic rate and W_{ev} after repeated heat exposure; thus, using acclimated versus non-acclimated individuals as a base for modelling may result in different predictions (Cooper et al., 2020a, 2020b).

Finally, data used in modelling – such has T_b, metabolic rate and W_{ev} – are usually obtained using respirometry protocols, meaning they are measured at rest (i.e. individuals have limited locomotor activity and are often fasted), which limits their applicability to real-life scenarios (Clusella-Trullas et al., 2021; Mitchell et al., 2018). This approach may overestimate upper critical limits, potentially leading to the underestimation of the actual costs (e.g. hyperthermia or cooling requirements). For instance, although resting Cape rockjumpers (*Chaetops frenatus*) initiate heat dissipation through W_{ev} at T_a ~35°C, breeding individuals show behavioral signs of heat dissipation and nestlings show signs of dehydration when T_{air} exceeds 23°C in field studies (Oswald et al., 2018, 2020, 2021). It is worth noting that some studies have used behavioral markers of thermoregulation (e.g. panting) to assess thermal limits in natural environments (Conradie et al., 2019; Cook et al., 2020). Although this approach may provide a more realistic temperature threshold at which individuals start dissipating heat when compared to controlled-respirometry experiments, it ultimately falls short as a direct predictor of body temperature and hydration state.

Modelling cooling costs and dehydration risks is an extremely valuable approach to predict current and future impacts of climate change on birds. However, the reliability of such models has led to some debate within the scientific community. For instance, Pacheco-Fuentes et al (2022) argue that dehydration risk was likely overestimated in Conradie et al (2020), which led authors to reply in Conradie et al (2022). Field studies on body temperature and hydration state are ultimately necessary to validate models and refine our prediction. To date, only a few studies have attempted to assess the hydration state of wild birds, either through repetitive weighing (i.e. using daily body mass loss; Bourne et al., 2021; du Plessis et al., 2012; Kemp et al., 2020; Oswald et al., 2021; Sharpe et al., 2019; van de Ven et al., 2019; van de Ven et al., 2020), by using isotopic markers (Bourne et al., 2021a; Cooper et al., 2019), hematocrit (Ardia, 2013; Goldstein and Zahedi, 1990), or by using plasma and urine osmolarity (Goldstein and Zahedi, 1990; Sabat et al., 2009; Salaberria et al., 2014). It is worth noting that daily body mass changes are not a very reliable means of determining changes in hydration state. Foraging activity and efficiency are also likely to decrease during hot days; thus any loss of body mass could result from decreased food intake (Oswald et al., 2021; van de Ven et al., 2019; van de Ven et al., 2020).

Overall, showing heat dissipation behaviors or an increase W_{ev} does not guarantee dehydration and/or the maintenance of normothermia. On one hand, individuals may be able to maintain their water balance even if W_{ev} increases, as long as they have access to water (W_d, W_p). On the other hand, having access to water does not guarantee that the drinking and absorption rate will exceed the evaporation rate, nor does it guarantee a sufficient rate of heat dissipation to maintain T_b below harmful levels. The rates of W_{ev} for birds in shaded microsites may exceed 5% of their body mass per hour, especially for small species (McKechnie and Wolf, 2010; Wolf and Walsberg, 1996a). Despite W_{ev} increasing with T_e above a threshold, T_b usually increases concomitantly until reaching a heat tolerance limit, at which point individuals experience uncontrolled hyperthermia or loss of coordination (Czenze et al., 2020; Freeman et al., 2024; McKechnie and Wolf, 2019; Pollock et al., 2021). Moreover, dehydrated individuals can delay heat dissipation, meaning the absence of heat-dissipating behaviors does not guarantee euhydration (e.g. Greenwald et al., 1967; Maloney and Dawson, 1998). There is thus a need to assess hydration state at a physiological level if we are to investigate the possibility of a dehydration–hyperthermia tradeoff in birds. Results derived from both modelling of dehydration risk and studies of wild birds should ideally be considered in conjunction. But what is the best way to assess the hydration state of wild birds? Below, we address this challenge by presenting a systematic review of the physiological markers of avian dehydration. While we review physiological markers of avian dehydration, we do not cover basis of avian osmoregulation (reviewed by Braun, 1982; Goldstein, 2006; Hughes, 2003; Laverty and Skadhauge, 2008; Orosz and Echols, 2020; Skadhauge, 1981; Takei, 2000).

5. How can we assess avian dehydration?

5.1. Methods

To review potential physiological markers of avian dehydration, we searched in ISI Web of Science on 4th December 2023, using the terms “(TS="bird$" OR TS="avian") AND (TS="dehydration" OR (TS="Water" AND (TS="restriction" OR TS="deprivation")))”, which yielded 610 articles (Dataset 1). Adding the terms (OR (TS="heat" AND (TS="stress" OR TS="exposure"))) greatly increased the number of articles (>3000 articles), and we consequently assumed that studies inducing a dehydration through heat exposure were likely to use “dehydration”, “water restriction” or “water deprivation” in their abstract, title or keywords.

Only studies that met our four eligibility criteria were retained for further analysis. Firstly, we only considered studies that induced dehydration through water restriction or deprivation, including thermal dehydration (i.e. the combination of water restriction and heat exposure). Studies that induced dehydration through salt exposure or by using restriction of both water and food were rejected. Secondly, we specified that the study should report a significant decrease in either body mass or total body water mass during the experiment. We rejected studies on growing individuals because we could not assess body mass loss. Because the studies did not always report whether the decrease in body mass was significant, we retained articles reporting a mean body mass loss of at least 11% during water restriction (this mass loss is representative of severe dehydration according to McKechnie and Wolf, 2010; Wolf, 2000). Thirdly, in order for a study to be included in our analysis, we also specified that it should measure some potential markers of dehydration within plasma or excreted body fluids (urine/faeces, salt gland excreta, tears, saliva) and report statistics. Note that we do not distinguish plasma from serum because it is likely that their content of potential dehydration markers (e.g. electrolytes, nitrogenous compounds; Kiseleva et al., 2022) is similar; both are referred to as plasma hereafter. Finally, we only retained papers that were written in English. When an article investigated multiple species, we considered the analyses for each species to be independent, and we counted them as separate ‘studies’.

The initial literature search on Web of Science yielded 610 results (Dataset 1). We retained 140 articles after reading the abstracts, and 22 after reading the full text to assess whether the eligibility criteria were met. We added 13 articles from parallel reading; these were mainly articles published before 1990 and thus not indexed in Web of Science. This resulted in a total of 35 articles or 37 studies (Dataset 2). Summary findings of these studies are presented in Table 1.

Data on body mass loss, hematocrit, plasma osmolarity and plasma ionic concentration (sodium, chloride and potassium) were extracted from articles using a longitudinal design (i.e. repeated measure before and during water restriction; Dataset 3). We did no rejected studies that did not reported significant body mass loss, or a body mass loss ≤11%, as we investigated whether hematocrit and plasma osmolarity scale with body mass loss during water restriction across multiple studies. Results from these analyses are presented in Table 2. When data was not available, we extracted the data from plots using the PlotDigitizer software (Aydin and Yassikaya, 2021). We used linear mixed models to take into account pseudo replication, as well as bird species and order [model formula: measure ~ predictor + (1|Study)+(1|Species/Order); Bates et al., 2015] (we had to account for pseudo-replication because some studies measured markers of dehydration multiple times during the protocol; e.g. after 8, 12 and 16 hours of water deprivation). The model intercept was fixed at 0 because of the longitudinal nature of these studies. We also conducted the analysis using phylogenetic generalized least-squares regression to account for phylogenetic distance between species (Supplementary material, Figure SI-1, Table SI-1, Table SI-2). Results were highly similar and interpretations identical. We report only our linear mixed models in this review to homogenize our statistics, and because the phylogenetic signal estimated was most-often null. We report statistics as follows: n=number of observations, N=number of studies, sp=number of species, ord=number of avian orders. We report marginal (R^2_m) and conditional (R^2_m) R^2 respectively as measures of the variance explained by fixed effects, and total variance explained by fixed and random effects (Nakagawa et al., 2017b).

5.2. Physiological markers of avian dehydration

5.2.1.Overview of the studies

Overall, the median year of publication for the selected articles was 1991 (ranging from 1970 to 2021; Figure 1). Among the seven bird orders studied, Galliformes was the most highly represented (n=19/37; 51.4%), followed by Passeriformes (n=8/37; 21.6%), Casuariiformes (which was represented only by the emu, *Dromaius novaehollandiae*; n=4/37; 10.8%), Anseriformes (represented only by the Pekin duck, *Anas platyrhynchos domesticus*; n=3/37; 8.1%) and others (Columbiformes, Psittaciformes and Struthioniformes; n=1 per order). The relative over-representation of Galliformes is mainly owing to the high proportion of studies on the domestic fowl (*Gallus domesticus*; n=9/37; 24.3%) and Japanese quail (*Coturnix japonica*; n=5/37; 13.5%).

5.2.2.Total body water

Dehydration is defined as a deficiency in total body water (TBW; Lacey et al., 2019). Consequently, assessing dehydration should be best achieved by a direct measurement of TBW. There are several available methods for measuring TBW; here, we discuss isotopic methods and quantitative magnetic resonance (QMR), as these are the most applicable to field studies (reviewed by Guglielmo et al., 2011; McWilliams and Whitman, 2013). Isotopic methods have been the “gold standard” for TBW estimation for decades (reviewed by Speakman, 1997; Speakman and Hambly, 2016; Westerterp, 2017). These methods rely on the injection or oral administration of labeled water, and later sampling of blood, excreta or even breath (Bourne et al., 2019; Mitchell et al., 2015; Whiteman et al., 2019)). This method is labor intensive, requiring calibration for the particular system studied, is quite expensive and requires some specialized equipment. However, it can also provide estimation of water influx and efflux, as well as energy expenditure, contrary to other methods (for field application see Bourne et al., 2019; Bourne et al., 2021; Cooper et al., 2019; Sabat et al., 2021; Smit and McKechnie, 2015). Triple-labelled water has recently been used to dissociate metabolic water production from exogeneous water acquisition (i.e. water from drinking or in food), which opens interesting perspectives for field studies (Whiteman et al., 2019; Sabat et al., 2021).

When compared to isotopic methods, QMR yields similar estimates of body composition for avian species (Guglielmo et al., 2011; Mitchell et al., 2015), and has been applied in field studies (e.g. Guglielmo et al., 2022; Kelsey and Bairlein, 2019). Coefficient of variation in QMR for TBW has been reported to be <3% (Guglielmo et al., 2011). QMR necessitates the contention of birds but measurements are rapid (~2min) and no sedation is required. The main drawbacks of QMR are the price and weight of the equipment. In contrast to isotopic methods, QMR measurements do not require any prior administration of a marker and subsequent biological sampling. QMR has been used to estimate body condition in water-restricted rufous-collared sparrows (*Zonotrichia capensis*; Navarrete et al., 2021), in which body mass and TBW loss under water restriction are significant and tightly correlated, suggesting that water-restricted individuals are indeed dehydrated (12% body mass loss and 11% TBW loss). Interestingly, QMR allows researchers to dissociate 'free' water (i.e. tissue-free body fluids) from total body water. On this basis, Navarrete et al (2021) suggested a "hydration index", calculated as follows: TBW-free water/lean mass. In their study, hydration index was 2% lower in water-restricted individuals (although this was non-significant).

5.2.3.Hematocrit

Dehydrated individuals are likely to suffer from a decrease in blood volume (e.g. Dawson et al., 1983; Stewart, 1972; Takei et al., 1988), potentially explaining the observed increase in the concentration of blood cells (Chikumba et al., 2013) and hemoglobin during water restriction (Arad, 1983; Carmi et al., 1993). Although 72.2% of the retained studies report a positive effect of water restriction on hematocrit (Table 1), our analyses also highlighted multiple concerns limiting the suitability of hematocrit as a marker of dehydration. When compiling data from multiple studies, the relationship between body mass loss during water restriction and hematocrit was significant, but the low R^2_m value suggests that hematocrit is a poor predictor of body mass loss, both for all species (Figure 2A; Table 2, p-value<0.001, R^2_m=0.10, n=36, N=12, sp=9, ord=6) and for analyses restricted to the domestic fowl (*Gallus domesticus*; est=0.73, SE=0.30, t=2.44, p-value=0.029, R^2_m=0.06, n=16, N=4). Hematocrit therefore does not seem to be the most reliable marker of dehydration severity. This is probably because plasma volume loss during water restriction is compensated for by the movement of fluid from the intracellular or interstitial compartment to the blood compartment, meaning that birds are 'plasma conservers' (Arad et al., 1989; Carmi et al., 1993, 1994; Dawson et al., 1983). For instance, Carmi et al (1994) reported an increase in hematocrit for rock pigeons (*Columbia livia*) only during extreme dehydration (≥19% body mass loss). Hematocrit can also be influenced by other events such as salt loading, variation in body condition or flight activity in addition to dehydration (Bradley et al., 2020; Fair et al., 2007; Jenni et al., 2006; Roberts, 1992), and its measurement may have limited precision relative to the effect size (Cheuvront and Kenefick, 2014; Goldstein and Zahedi, 1990).

Table 1: Number and proportion of studies reporting significant effects of water-restriction on blood and excreta characteristics in avian species.

Physiological markers	Number of studies (n/N)	Percentage of studies (n/N)	Effect sign
Blood characteristics			
Blood volume	4/4	100%	(-)
Hematocrit	13/18	72.2%	(+)
P_{osm}	31/33	93.9%	(+)
$P_{[Na]}$	14/17	82.4%	(+)
$P_{[Cl]}$	8/9	88.9%	(+)
$P_{[K]}$	3/14	21.4%	Unclear
$P_{[UA]}$	2/2	–	(+)
$P_{[Urea]}$	1/1	–	(+)
$P_{[Creatinine]}$	1/2	–	(+)
$P_{[AVT]}$	7/7	100%	(+)
$P_{[AII]}$	3/3	100%	(+)
Excreta characteristics			
U_{osm}	8/8	100%	(+)
Excreta water content	3/3	100%	(-)
Defecation rate	1/1	–	(-)

The proportion of studies was calculated when the sample size was equal to at least three studies. The list of studies is available as a supplementary file (Dataset 1). AVT, vasotocin; AII, angiotensin II; Cl, chloride; K, potassium; n=number of studies with significant effect; N=total number of studies; Na, sodium; $P_{[compound]}$, concentration of a specific compound in the plasma; P_{osm}, plasma osmolarity; UA, uric acid; U_{osm}, urine osmolarity.

5.2.4. Plasma osmolarity and ions

Plasma osmolarity (P_{osm}) was consistently increased with water restriction in most of the studies retained (93.9%; Table 1). The change in P_{osm} was also positively correlated with body mass loss during water restriction across multiple studies, meaning that it seems to increase linearly with dehydration severity (Figure 2B; Table 2; p-value<0.001, R^2_m=0.39; the removal of outliers did not change the results). The relationship between body mass loss and the increase in P_{osm} was also significant when analyses were restricted to the domestic fowl (est=0.64, SE: 0.06, t=11.28, p-value<0.001, R^2_m=0.61, n=17, N=5). This is consistent with the literature, because plasma osmolarity seems to be the most suitable marker of hydration state for humans (Cheuvront and Kenefick, 2014) and has been reported to increase with dehydration in other taxa (e.g. mouse, Bekkevold et al., 2013; snake, Brusch and DeNardo, 2017; lizard, Chabaud et al., 2023; tortoise, Peterson, 2002). Measurements of plasma osmolarity may therefore represent an important mean to assess avian dehydration in the field. These measurements require little plasma volume, are relatively inexpensive and have previously been shown to be highly repeatable for birds under both laboratory and field conditions (Goldstein and Zahedi, 1990). However, P_{osm} increases with salt intake, and therefore may be less reliable to predict dehydration in seabirds (Hughes, 2003; Peña-Villalobos et al., 2013; Roberts, 1992).

There are a couple of physiological mechanisms that might explain the increase in P_{osm} with dehydration. Firstly, this relationship might be partly explained by hemoconcentration resulting from reduced plasma volume during water restriction. However, as discussed above, plasma volume does not decrease linearly during dehydration. Moreover, the P_{osm} increase was not significantly correlated with changes in hematocrit across multiple studies (Table 2; t=1.57, p-value=0.139). Another mechanism contributing to the relationship between P_{osm} and dehydration is the retention of electrolytes during water loss. In birds, electrolytes represent ~95% of P_{osm}, mainly owing to relatively high concentrations of sodium ($P_{[Na]}$) and chloride ($P_{[Cl]}$; Scanes, 2015). During periods of water restriction, increased sodium and chloride reabsorption in the nephron and in the cloaca-coprodeum allow for water reabsorption through osmosis, thus limiting water loss through excretion (Box 1; Laverty and Skadhauge, 2008; Skadhauge, 1981). Moreover, an increase in P_{osm} may allow plasma volume to be conserved through the creation of an osmotic gradient between the intracellular or interstitial compartments and the blood (e.g. Roberts, 1992).

Both $P_{[Na]}$ and $P_{[Cl]}$ consistently increased with water restriction (Table 1), and variation in their levels during water restriction seems to correlate with changes in P_{osm} (Figure S2; Table 2; $P_{[Na]}$: p-value<0.001, R^2_m=0.26; $P_{[Cl]}$: p-value<0.001, R^2_m=0.75). Conversely, the plasma concentration of potassium ($P_{[K]}$) do not seems to vary in a predictable way with water restriction (Table 1), and its variation during water restriction does not correlate with variation in P_{osm} (Table 2; t=0.11, p-value=0.914). This is likely to be because $P_{[K]}$ is relatively low, and because potassium is secreted in the nephron and cloaca-coprodeum, whereas sodium and chloride are reabsorbed (Laverty and Skadhauge, 2008; Skadhauge, 1981).

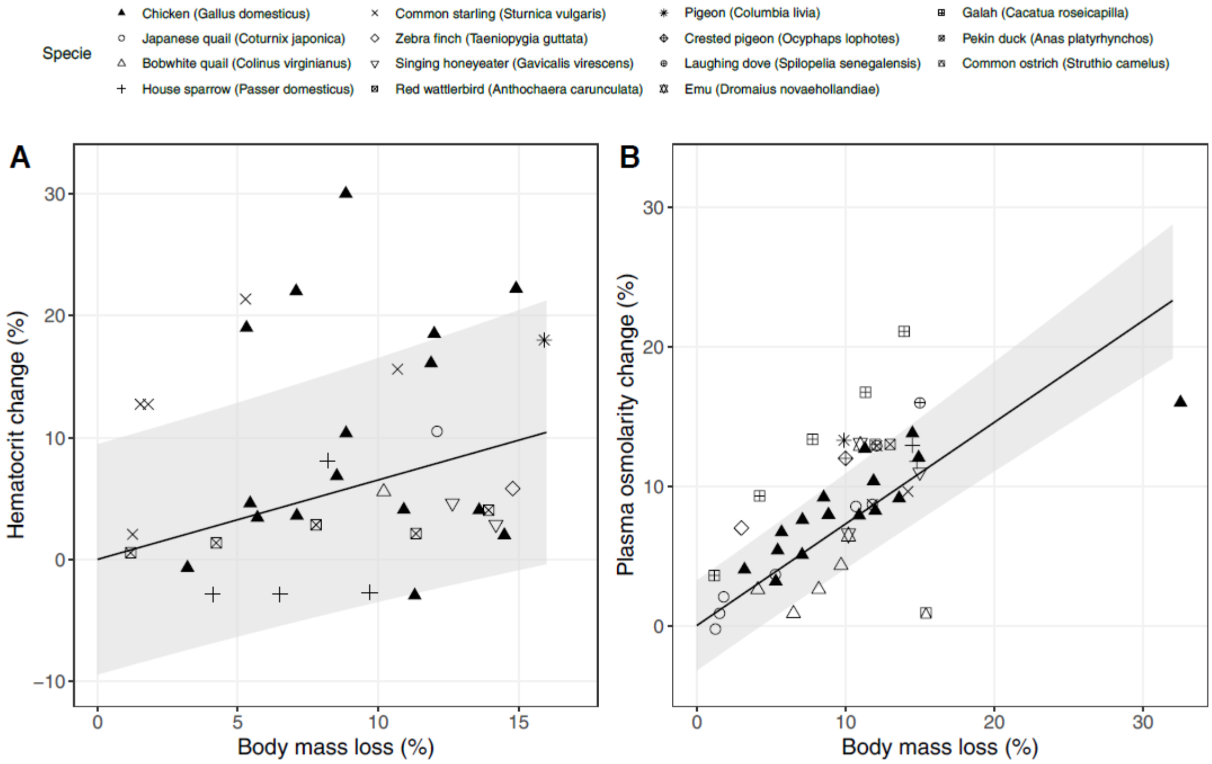


Figure 2. Relationship between body mass loss during water restriction and hematocrit or plasma osmolarity. (A) Hematocrit change is expressed as a percentage of the initial value; n=36, N=12, sp=9, ord=6. (B) Plasma osmolarity change is expressed as a percentage of the initial value; n=47, N=24, sp=16, ord=8. The relationship is still significant when outliers are removed. Regression lines and prediction intervals of the models are plotted. n: number of observations, N: number of studies, sp: number of species, ord: number of avian orders.

Table 2. Summary statistic of models assessing the link between changes in plasma osmolytes, hematocrit and body mass during water restriction across multiple studies.

Model	estimate±SE	p-value	t-value	R^2_m	R^2_c	n/N	sp/ord
ΔHct ~ BML	0.65±0.16	<0.001	4.04	0.10	0.72	36/12	9/6
ΔP_{osm} ~ BML	0.73±0.06	<0.001	12.02	0.39	0.93	47/24	16/8
ΔP_{osm} ~ ΔHct	0.17±0.11	0.139	1.57	0.02	0.87	34/11	8/5
ΔP_{osm} ~ $\Delta P_{[Na]}$	0.65±0.05	<0.001	12.86	0.26	0.97	28/15	13/8
ΔP_{osm} ~ $\Delta P_{[Cl]}$	0.77±0.04	<0.001	18.18	0.75	0.86	17/11	10/6
ΔP_{osm} ~ $\Delta P_{[K]}$	0.03±0.25	0.914	0.11	0.00	0.99	24/15	13/8

Model formula: [y~x + (1|Study) + (1|Specie/Order)]. Δ, changes during water restriction; BML, body mass loss; CI, 95th percentile confidence interval; Cl, chloride; Hct: hematocrit; K, potassium; Na, sodium; n, number of observations; N, number of studies; ord, number of avian orders; $P_{[compound]}$, concentration of a specific compound in the plasma; P_{osm}, plasma osmolarity; R^2_c, conditional R^2; R^2_m, marginal R^2; SE, standard error; sp, number of species.

5.2.5. Nitrogen excretion

Byproducts of metabolism, such as uric acid (UA), urea and creatinine (Table 1) in the plasma also represent potential markers of dehydration. Plasma concentrations of UA ($P_{[UA]}$; Arad and Marder, 1983; Chikumba et al., 2013; Gerson and Guglielmo, 2011; Lumeij, 1987; Radin et al., 1996), urea ($P_{[Urea]}$; Arad et al., 1987, 1989; Arad and Marder, 1983; Lumeij, 1987) and creatinine ($P_{[Creat];}$ Lumeij, 1987; Vanderhasselt et al., 2013) increase with water restriction in multiple avian species. Unfortunately, many of the studies cited above used a protocol involving food restriction in combination with water restriction and were therefore excluded from our systematic review, explaining the fact that a smaller number of studies investigating concentrations of nitrogenous byproducts are reported in Table 1 than for other blood characteristics. It is worth noting that few studies report unchanged plasma concentration of creatinine during water restriction, suggesting that creatinine has less support than other markers to assess dehydration (Chikumba et al., 2013; Radin et al., 1996).

Uric acid, urea and creatinine may become concentrated in the plasma during dehydration as a result of a reduced rate of excretion. Although these compounds are all partially excreted through glomerular filtration, the mechanisms regulating their excretion (Box 1, figure A) are different. Approximately 90% of the UA is excreted through tubular secretion, meaning that it is largely uncoupled from glomerular filtration (Dantzler, 1978; Dudas et al., 2005; Skadhauge, 1981). By contrast, urea is subject to tubular reabsorption, and its rate of excretion depends on the urine flow rate (see Glossary). Urine flow rate is reduced during dehydration, causing a greater fraction of urea to be reabsorbed: when a bird is well hydrated, close to 100% of urea is excreted, whereas ~99% is reabsorbed during dehydration (Baum et al., 1975; Skadhauge, 1981). Finally, creatinine is mainly excreted through glomerular filtration; however, tubular secretion and reabsorption may play a secondary role (Gasthuys et al., 2019; Wani and Pasha, 2021).

Owing to the tubular reabsorption of urea during water restriction, the magnitude of increase in $P_{[Urea]}$ may greatly exceed the increase in P_{osm}, $P_{[Na]}$, $P_{[Cl]}$, $P_{[UA]}$ or $P_{[Creatinine]}$; thus, urea could represent an important marker of the hydration state (Arad et al., 1987; Arad et al., 1989; Lumeij, 1987; Scope and

Schwendenwein, 2020). For instance, in rock pigeons, $P_{[Urea]}$ increases by 603% with water restriction, whereas P_{osm} increases by 13.3% (Lumeij, 1987). Using urea:UA and urea:creatinine ratios may also be a relevant way to assess dehydration (Baum et al., 1975). Some authors have hypothesized that higher $P_{[UA]}$ or $P_{[Urea]}$ during water restriction may be linked to increased protein catabolism, which might act as source of metabolic water. This hypothesis is supported by a decrease in lean mass during water restriction in multiple studies (Gerson and Guglielmo, 2011; Navarrete et al., 2021; Rutkowska et al., 2016).

Although uric acid, urea and creatinine could all be considered as potential markers of dehydration, there are potential drawbacks to their use that should be noted. For example, factors other than hydration state – such as protein intake, fasting state or chronic stress – can affect $P_{[UA]}$ or $P_{[Urea]}$, meaning that they are not strictly specific markers of hydration state (Beattie et al., 2022, 2023; Goldstein et al., 2001; Lumeij and Remple, 1991). Even though creatinine tends to be more stable during changes in feeding compared to urea or UA, its low concentration in the plasma of birds presents challenges for its detection (Gasthuys et al., 2019; Lumeij and Remple, 1991; Scope et al., 2013).

5.2.6.Alternative markers

A number of physiological parameters, such as the glomerular filtration rate (Roberts, 1991a, 1991b; Roberts and Dantzler, 1989), urine flow rate (Dawson et al., 1991; Williams et al., 1991) and hormone levels (i.e. vasotocin: Goldstein and Braun, 1988; Koike et al., 1977; Seth et al., 2004; angiotensin II: Goldstein, 1995; Gray and Simon, 1987; Takei et al., 1988; aldosterone: Arad, 1985; Arnason et al., 1986) have been linked with avian hydration state in several studies. However, these variables are involved in the regulation of homeostasis, and may thus be interpreted as markers of anti-diuresis rather than of dehydration *per se*. Moreover, measuring the glomerular filtration rate or urine flow rate necessitate the injection of an exogenous marker and later sampling of either blood or urine to assess the clearance rate, which is invasive and labor intensive, and therefore not suited to work in field environments (Levey et al., 2020).

Alternatively, excreta characteristics – such as urine osmolarity (U_{osm}; Goldstein and Braun, 1988; Navarrete et al., 2021; Roberts and Dantzler, 1989; Skadhauge et al., 1991), water content (Dawson et al., 1985; Goldstein and Braun, 1988; Moldenhauer and Wiens, 1970; Withers, 1983) or defecation rate (Brischoux et al., 2020) – may represent less-invasive potential markers of avian hydration state. The concentration of UA in the excreta may also increase during water restriction, but evidence for this is lacking (Gerson and Guglielmo, 2011). U_{osm} is expected to increase while excreta water content decreases during dehydration as a result of a decrease in renal plasma flow, glomerular filtration rate, urine flow rate and increasing renal and post-renal water reabsorption (Box 1; Skadhauge, 1981). However, as mentioned for the various physiological variables discussed above, the increase in U_{osm} is part of the early response to water restriction and thus most likely precedes significant body mass loss and the increase in P_{osm} (for example, U_{osm} varies with overnight fasting whereas P_{osm} does not; Alberts et al., 1988; Goldstein and Bradshaw, 1998). It is important to note that the term 'urine' can be used to refer to different fluids in the literature, and it can be sampled using various methods with different degrees of invasiveness, from the insertion of a cannula into the cloaca, centrifugation of whole fresh excreta or using a capillary to collect the liquid fraction of the fresh excreta (e.g. Alberts et al., 1988; Lee and Schmidt-Nielsen, 1971; Navarrete et al., 2021; Skadhauge and Dawson, 1980). These methods may lead to varying results, especially when directly sampling urine in the cloaca, where the fluid obtained may be a mix of ureteral urine and cloacal urine (i.e. that formed by post-renal modification; Box 1, Alberts et al., 1988; Laverty and Skadhauge, 2008). We recommend that urine is sampled from the fresh excreta, as this will favorize the sampling of cloacal urine. Of course, one of the benefits of using excreta to assess hydration state is that they can easily be sampled (especially for some nestlings, which produce faecal sacs; see Glossary). This potentially allows the assessment of the hydration state without blood sampling.

It is possible that other body fluids (such as salt-gland fluid or saliva) could also be used to assess hydration state in birds; however, literature on using alternative fluids in this way is lacking. This represents an important avenue for future studies. It is believed that the salt gland mediates most of the sodium and chloride excretion in species that possess one (Goldstein, 2001; Hughes, 2003), and some researchers have hypothesized that the osmolarity of this fluid may vary depending on the hydration state (Stewart, 1972). Regarding the use of tears or saliva, we found no studies assessing the osmolarity of these fluids in birds during water restriction, but these markers have shown some potential to predict dehydration in humans and may be useful as less-invasive sampling methods in birds (Villiger et al., 2018). Finally, non-invasive methods, such as assessing skin turgor or capillary refill time (See glossary), may provide insight into hydration state, but we currently have very limited insight into their reliability (Baker-Cook et al., 2021; Vanderhasselt et al., 2013).

5.3. Dehydration diagnostic and tolerance

Because few of the studies included in our review actually assessed TBW, here, we have used body mass loss under water restriction as a proxy for TBW loss. Water restriction leads to a hypertonic dehydration, and markers of osmolarity (e.g. P_{osm}, $P_{[Na]}$, $P_{[Cl]}$) are consequently relevant for determining whether an individual is dehydrated. Although we have identified some markers of dehydration, dehydration diagnostic is not trivial. Homeostasis is a dynamic process and the levels of the markers discussed above are likely to vary (Billman, 2020). For instance, does a 5% increase in P_{osm} represent dehydration, or a physiological adjustment to maintain water balance? We could define 'dehydration' as the threshold at which TBW loss exceeds baseline variation, or as the threshold at which TBW loss induces negative effects. In human physiology, a TBW loss of 2% exceeds the day-to-day variation in TBW, and body mass loss under water restriction exceeding 2% promotes thirst, induces variation in levels of physiological markers and impairs performance (Cheuvront and Kenefick, 2014; Cheuvront et al., 2010; Cheuvront et al., 2013; Villiger et al., 2018). Current consensus is that P_{osm} exceeding 300 $mOsm.kg^{-1}$ (i.e. a ~3.5% increase in baseline P_{osm}) in humans predicts a TBW loss exceeding 2%, and thus dehydration (Lacey et al., 2019).

In the case of birds, several studies have used varying thresholds of body mass loss to predict 'moderate', 'severe' or 'lethal' dehydration (e.g. loss of 11%, 15% or 22% of body mass; Albright et al., 2017; Conradie et al., 2019, 2020; McKechnie and Wolf, 2010) However, there is little discussion of the reliability of such estimates. As far as we are aware, the 11% threshold was initially suggested by Wolf (2000), and is based on the observation that verdins (*Auriparus flaviceps*) can lose ~11% of their body mass before losing the ability to move effectively (Wolf and Walsberg., 1996). To put that into perspective, captive water-deprived domestic fowls and mourning doves lose ~45% and ~37% of their body mass by the time of death (Bartholomew and Macmillen, 1960; Mulkey and Huston, 1967), and there are multiple reports of birds losing >15% of their body mass without direct effects on survival (e.g. Arad et al., 1987; Bartholomew and Macmillen, 1960; Mulkey and Huston, 1967; Skadhauge, 1974; Withers, 1983).

Experimental studies are needed to identify water-deficit thresholds eliciting a physiological response (i.e. thirst, variation in levels of physiological markers), and thresholds for impaired performance (cognitive, locomotor) or survival. We expect tolerance to be lower in more suboptimal environments (such as in the wild), and we expect performance to be hindered at much lower thresholds than survival. Estimation of such thresholds would allow us to better identify dehydration and to refine models that predict the effects of climate change on wild populations.

6. **Conclusions and future directions**

If we are to accurately predict avian population demography and viability in the future, we must refine our understanding of the pressures associated with climate change (Urban et al., 2016). Avian species usually exhibit a combination of heat storage (i.e. hyperthermia) and heat dissipation through evaporative pathways when exposed to heat. When dehydrated individuals are exposed to heat, they reduce their evaporative heat loss relatively to hydrated individuals at the expense of further increase in body temperature, highlighting a trade-off between hyperthermia and dehydration (e.g. Arad, 1983; Greenwald et al., 1967). Several field studies highlight the importance of water availability on survival or breeding success, especially during heat events (e.g. Bourne et al., 2020; Conrey et al., 2016; Londe et al., 2021; Pattinson et al., 2022), and there is a growing evidence that repeated heat exposure may promote dehydration for various desert birds (Bourne et al., 2021a; Goldstein and Zahedi, 1990; Salaberria et al., 2014). Under laboratory conditions, water restriction affects many aspects of avian performance (reviewed by El Sabry et al., 2023), including fertility, reproduction (Giuliano et al., 1995; Giuliano et al., 1998; Koerth and Guthery, 1991; Niranjan and Srivastava, 2019) and growth (e.g. Goldstein and Ellis, 1991; Herr Viola et al., 2009; Mhmoud et al., 2023). Dehydration also upregulates physiological markers of stress in birds (e.g. corticosterone or heterophil to lymphocyte ratio; Cain and Lien, 1985; Iheukwumere and Herbert, 2003; Toghyani et al., 2011). These effects may threaten birds exposed to dehydration in their natural environment.

When looking at the direct effects of heat, researchers have to consider both behavioral markers of thermal stress (e.g. activity pattern, heat dissipation behaviors) and physiological effects (i.e. body temperature and water homeostasis). There is a need to model the costs and risks for avian species associated with climate warming (i.e. cooling costs, water requirements, dehydration and hyperthermia risks), but we must also develop ways to directly measure physiological state in the wild. Previous studies have reviewed ways to measure body temperature in free-living animals; here we hope to have provided ways to assess the hydration state of birds (Andreasson et al., 2023; McCafferty et al., 2015; Williams et al., 2021). Plasma osmolarity is the most studied marker of avian hydration state, and seems to be the most reliable marker of dehydration, but we recommend measuring several behavioral and physiological markers if possible. Further research, especially on wild birds, is needed to validate the use of some of these markers and represents exciting perspectives for future studies.

Research on the topic of avian hydration state would also benefit from a better understanding of osmoregulation and water requirements, especially as they relate to the life stage, the diet and/or drinking habits. For instance, birds exploiting marine habitats have been reported to be susceptible to heat exposure, but – as far as we are aware – studies on their water balance and hydration state are scarce (Cook et al., 2020; Hughes, 2003; Oswald and Arnold, 2012; Stewart, 1972). Even if we make the assumption that they have unlimited access to water, there is still an energetic cost associated with drinking saline water (Peña-Villalobos et al., 2013; Sabat et al., 2021). Increased research efforts are necessary to shed light on this topic, especially with respect to water balance and salt gland excretion. We also have very limited into heat tolerance and osmoregulation in nestlings, which develop endothermy and osmoregulatory ability during growth (Grabowski, 1967; Price and Dzialowski, 2017), and may have limited heat tolerance compared to adults (Diehl et al., 2023). Consequently, even though parents buffer temperature variation within the nest (Du and Shine, 2015), nestlings may be threatened by hyperthermia and dehydration during extreme events (Bourne et al., 2021a; Oswald et al., 2021; Salaberria et al., 2014; van de Ven et al., 2020). We consequently encourage researchers to monitor nest temperature in the field, as well as to conduct laboratory experiments to better define the physiology and water requirements of nestlings.

Acknowledgments

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7. Supplementary material

7.1. Supplementary figures

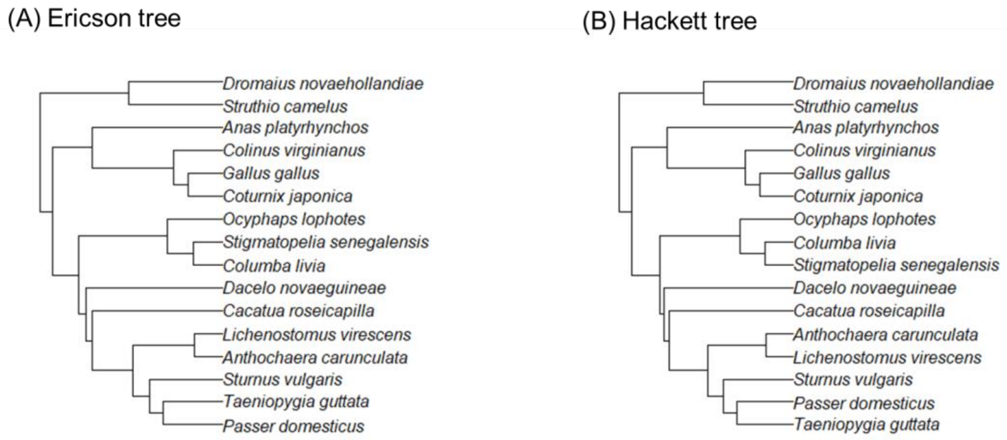

Figure SI-1. Consensus phylogenetic trees computed from 10,000 phylogenetic trees using either (A) Ericson or (B) Hackett backbone. Phylogenetic trees were generated from the Birdtree database.

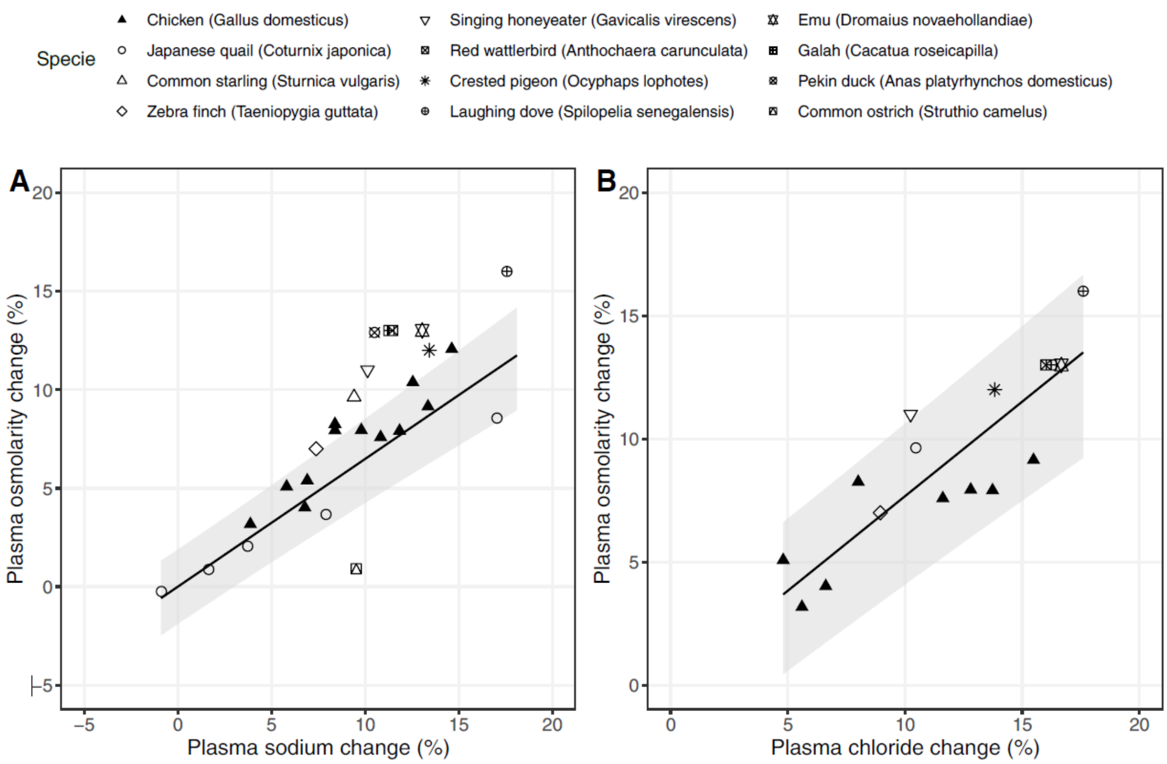

Figure SI-2. Relationship between plasma osmolarity change and (A) plasma sodium concentration change. n=28, N=15, sp=13, ord=8; (B) plasma chloride concentration change. n=17, N=11, sp=10, ord=6. Regression lines and prediction intervals of the models are plotted. n=number of observations, N=number of studies, sp=number of species, ord=number of avian orders.

7.2. Supplementary tables

Table SI-1. Models estimate and *p*-value for MCMCglmm and LMER models.

	MCMCglmm models		LMER models	
Model	Estimate [CI]	p_{MCMC}	Estimate [CI]	*p*-value
ΔP_{osm} ~ BML	0.764 [0.589, 0.909]	<0.001	0.729 [0.574, 0.880]	<0.001
ΔHct ~ BML	0.641 [0.286, 0.967]	<0.001	0.651 [0.297, 0.978]	<0.001
ΔP_{osm} ~ $\Delta P_{[Na]}$	0.649 [0.524, 0.789]	<0.001	0.648 [0.541, 0.783]	<0.001
ΔP_{osm} ~ $\Delta P_{[Cl]}$	0.761 [0.653, 0.877]	<0.001	0.768 [0.652, 0.855]	<0.001
ΔP_{osm} ~ $\Delta P_{[K]}$	0.041 [-0.106, 0.180]	0.570	0.027 [-0.473, 0.555]	0.914
ΔP_{osm} ~ ΔHct	0.135 [-0.098, 0.452]	0.330	0.167 [-0.110, 0.453]	0.139

LMER model formula: [y~x + (1|Study) + (1|Specie/Order)]. MCMCglmm models formula: [y~x + (1|Study) + (1|Specie)]. Δ, changes during water restriction. BML: body mass loss; CI: 95th percentile confidence interval; Cl, chloride; Hct: hematocrit; K, potassium; Na, sodium; $P_{[compound]}$, concentration of a specific compound in the plasma; P_{osm}, plasma osmolarity.

Table SI-2. Summary statistics of MCMCglmm models.

			Posterior mode [CI]			
Model	Estimate [CI]	p_{MCMC}	Specie	Study	Unit	Lambda
P_{osm} ~ BML	0.764 [0.589, 0.909]	<0.001	0.045 [0.000, 21.236]	0.075 [0.000 26.325]	2.287 [1.271, 5.308]	0.003 [0.000, 0.877]
Hct ~BML	0.641 [0.286, 0.967]	<0.001	0.389 [0.000, 29.686]	33.468 [13.494, 124.010]	21.110 [11.592, 38.277]	0.001 [0.000, 0 0.571]
P_{osm} ~ $P_{[Na]}$	0.649 [0.524, 0.789]	<0.001	12.111 [0.001, 33.611]	0.094 [0.000, 5.997]	0.722 [0.338, 2.442]	0.948 [0.683, 0.996]
P_{osm} ~ $P_{[Cl]}$	0.761 [0.653, 0.877]	<0.001	0.043 [0.000, 4.402]	0.031 [0.000, 3.059]	1.881 [0.682, 5.540]	0.002 [0.000, 0.719]
P_{osm} ~ $P_{[K]}$	0.041 [-0.106, 0.180]	0.570	54.154 [17.606, 154.875]	-0.046 [0.000, 8.952]	6.168 [2.343, 15.769]	0.924 [0.725, 0.984]
P_{osm} ~Hct	0.135 [-0.098, 0.452]	0.330	0.127 [0.000, 160.982]	0.271 [0.000, 50.768]	12.405 [7.297, 24.258]	0.001 [0.000, 0.922]

The variance explained by random effects (specie, study), the residual variance (unit) are represented by their posterior mode and confidence interval (CI: 95th percentile confidence interval). Cl, chloride; Hct: hematocrit; K, potassium; Lambda: phylogenetic signal; Na, sodium; $P_{[compound]}$, concentration of a specific compound in the plasma; P_{osm}, plasma osmolarity.

7.3. Supplementary analysis

We used generalized linear mixed model with Markov Chain Monte Carlo estimation methods ($MCMC_{GLMM}$) to take into account phylogenetical distance between species in our analysis, using the MCMCGLMM package (Hadfield, 2010). We generated 10,000 phylogenetic trees from the database Birdtree using for both Hackett and Ericson backbones (Birdtree.org; Jetz *et al.*, 2012). Phylogenetic trees were restricted to our species of interest. We then computed consensus trees. Because both Hackett and Ericson consensus trees were similar, we decided to use the Hackett tree following (Tomasek et al., 2019). The $MCMC_{GLMM}$ models were set to run for 6.10^6 iterations, with a thinning interval of 1.10^3 and a burn-in of 1.10^6. We observed no autocorrelation between sampled iterations. Convergence of models was assessed by visual inspection of trace and density plots of the posteriors. We set weakly informative priors for both random and fixed effect (V=1, nu=0.002). Parameter expansion was not used.

Chapter 4. Physiological response to heat exposure in captive zebra finches (*Taeniopygia guttata*) and inter-individual variation

Levillain, A., Péric, L., Zahariev, A., Stier, A., Mata, A., Massemin, S., Reichert, S. Old but cool: no evidence for an age-related increase in sensitivity to acute heat in captive zebra finches. **In prep**.

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Keywords: Avian, Heat stress, Ageing, Hyperthermia, Dehydration, Bird, Passerine.

Photo of a zebra finch (*Taeniopygia guttata*). Macalau Library (Macaulay Library ML627761746).

1. Abstract

Climate warming is characterized by an increase in global temperature, but also an increase in the frequency, duration and intensity of heatwaves. Cooling requirements, hyperthermia and dehydration risk of wild birds are expected to increase with climate warming, potentially threatening birds populations. In this study, we assess the response and recovery to an acute heat exposure in captive zebra finches (*Taeniopygia guttata*) in function of age and sex. Acute heat exposure promoted a significant increase in cloacal temperature, metabolic rate and evaporative water loss in captive zebra finches. Heat exposure eventually led to a considerable a loss of body water and increased plasma osmolarity, promoting thirst during recovery, and testyfing from a physiological state of dehydration. While cloacal temperature and metabolic rate were lower in older individuals, reaction norm to heat exposure and subsequent recovery did not vary with age contrary to our expectations. Finally, reaction norm to heat exposure varied between sexes, as only females increased their metabolic rate at 40°C compared to 30°C. Overall, acute heat exposure promoted hyperthermia and dehydration in an arid-adapted passerine, and heat response in function of age and sex represents exciting perspectives for future studies.

2. Introduction

Climate change represent one of the drivers of the current biodiversity erosion (Maxwell et al., 2016; Maxwell et al., 2019). Climate change has been associated with population and community stability (Ghosh et al., 2024; Paniw et al., 2021), ranges of distribution (Kubelka et al., 2022; Pacifici et al., 2020) or phenology (Cohen et al., 2018; Loughnan et al., 2024) across a wide variety of species and populations across the globe. While a global warming is observed, frequency, intensity and duration of heatwaves are also predicted to increase (Diffenbaugh and Field, 2013; IPCC, 2014). Heatwaves have been related with mortality events in humans and wildlife (Ballester et al., 2023; Barton et al., 2023; Gallo et al., 2024; Lüthi et al., 2023), and deleterious effects of heatwaves are predicted to increase with global warming (e.g. Maxwell et al., 2019; Moreno and Pape Møller, 2011; Murali et al., 2023; Stillman, 2019).

In this study, we focus on birds as they represent great sentinel species. Indeed, birds are ubiquitous, are sensible to these heat events, and integrate their effect in a detectable manner (Clark-Wolf et al., 2024; Hazen et al., 2019; Oswald and Arnold, 2012). For instance, extreme breeding failure and mass-mortality events during heat events have been recently reported in various bird species (e.g. McCowan and Griffith, 2021; McKechnie et al., 2021b; Piatt et al., 2020; Romano et al., 2020; Sharpe et al., 2021). Evaporative water loss is the main mechanism allowing heat dissipation in birds, and birds usually use a combination of hyperthermia and increased evaporative water loss when exposed to heat, suggesting a trade-off between hyperthermia and dehydration (Gerson et al., 2019; Tieleman and Williams, 1999). Consequently, cooling requirements, hyperthermia and dehydration risk of wild birds are expected to increase with climate warming (Albright et al., 2017; Conradie et al., 2020; Cook et al., 2020; Kemp et al., 2020; McKechnie and Wolf, 2010), and may drive population and community collapses (Albright et al., 2010; Conradie et al., 2019; Ma et al., 2023; Riddell et al., 2019; Riddell et al., 2021). Among birds, passerines seems to have a lower ability to conserve their water resources as effectively as other taxa and larger birds during heat events (McKechnie et al., 2021a; Smit et al., 2016; Smit et al., 2018). This may explain why they seems over-represented during mass-mortality events, and may consequently represent great model species to study heat stress (McKechnie et al., 2021b).

In laboratory studies, water-restricted birds seem to reduce their evaporative water loss at the expense of a further increase in body temperature during heat exposure, representing evidences for the hyperthermia-dehydration trade-off (Arad, 1983; Arad et al., 1987; Greenwald et al., 1967; Maloney and Dawson, 1998; Zhou et al., 1999). Consequently, several studies assessed the effect of heat exposure physiological markers of dehydration such as the hematocrit, plasma osmolarity or hormones levels (e.g. Arad, 1983; Arad, 1985; Carmi et al., 1993; Carmi et al., 1994; Dawson et al., 1983; Itsaki-Glucklich and Arad, 1992; Maloney and Dawson, 1998; Zhou et al., 1999). Yet, most of the studies measuring both body temperature and physiological markers of dehydration during heat exposure focus on poultry models, and we are unaware of such studies on passerines. In this study, we aim to address whether an acute heat exposure promotes hyperthermia and/or dehydration in zebra finches (*Taeniopygia guttata*), an arid-adapted passerine.

Additionally, performance and physiological responses of are known to vary between individuals within a population. In humans, reaction norms to heat exposure and mortality risk varies depending of the sex and age of the individuals (Cramer et al., 2022; Gallo et al., 2024). Interestingly, older individuals have notably a lower heat tolerance and a drastically greater mortality risk during heatwaves. While literature on this topic is far less documented in birds, body temperature or reaction norm to heat exposure have been reported to vary with sex and age (Andreasson et al., 2020b; Pessato et al., 2023; van Jaarsveld et al., 2021; Zagkle et al., 2020). Moreover, patterns of senescence have been reported across multiples traits and birds populations (e.g. survival, reproductive success, locomotor performance, hematocrit, oxidative balance; Bize et al., 2013; Cam et al., 2002; Elliott et al., 2015; Labocha et al., 2015; Nussey et al., 2008). In this study, we address whether the physiological response to heat exposure vary with age and/or sex in zebra finches.

Overall, we assess the effect of simulated hot day on the thermoregulatory response, body temperature and physiological markers of dehydration in captive zebra finches, as well as their subsequent recovery. We also investigate whether the response to heat exposure and recovery varied depending on the age or sex of the individuals. We exposed zebra finches to ambient temperature of 30°C and 40°C during 4 hours and measured body mass loss, thermoregulatory response (rate of evaporative water loss and oxygen consumption), body temperature and various physiological markers of dehydration (Chapter 3). Zebra finches have been reported to experience increased body temperature as well evaporative water loss when exposed to heat (Calder, 1964; Cooper et al., 2020a; Cooper et al., 2020b; Wojciechowski et al., 2021). We thus expected an acute heat challenge to promote both hyperthermia and dehydration. Moreover, median lifespan in zebra finches is 4 years, and occurrence of senescence has been described for similar aged individuals (≥5 year old; e.g. Briga et al., 2019; Coughlan et al., 2022; Labocha et al., 2015; Moe et al., 2009). We consequently expect younger individuals to exhibit a more moderate response to heat exposure, i.e. the maintenance of a lower EWL and/or body temperature during heat exposure, as well as to better recover from it.

3. Material and methods

3.1. Experimental design

65 captive zebra finches (*Taeniopygia guttata*; 37 males, 28 female) were housed in maintenance cages measuring 75*72*93cm (l*L*h), with males separated from females. Birds were from various age, and we defined 2 age classes: young (0.5-2 years old, n=28), and old (5-7 years old, n=37). Sample size was 17 young males, 18 old males, 11 young females and 17 old females. Zebra finches were maintained under typical rearing conditions (Griffith et al., 2017a). Birds were fed with a diet of ad libitum water and dry seed mix (food quotient=0.72; Black et al., 1986). They had ad libitum access to shell grit and cuttlebone. Temperature was maintained at 22°C and with a 14h photoperiod (day: 6:00-20:00).

During the experiment, we captured 4 birds each day at 8:00 (t_0), and we food-restricted them until 11:00 (t_1). At 11:00, birds were placed in small cylindrical wire mesh cages inside 0.53L airtight polypropylene metabolic chambers (Sistema®). No food or water was available during the respirometry trial. Temperature was initially set at 30°C, and we either maintained 30°C, or progressively increased it so it reached 40°C at 12:00. Respirometry data acquisition started at 12:00 and lasted until 16:00 (t_2). Birds were kept in small cages with only water available until 17:30 (t_3; short-term recovery), and were then reintroduced to their maintenance cages afterward. Overall, birds were food restricted from 08:00 to 17:30, and water-restricted from 11:00 to 16:00. We recaptured these individuals 48h after the end of the respirometry trial to asses mid-term recovery (t_4). All birds were exposed to 30°C and 40°C during the experiment. They were randomly assigned to a temperature treatment during the first respirometry trial, but also underwent the other treatment 30 days later.

Birds were weighed at all times (t_0, t_1, t_2, t_3, t_4) using an electronic scale with a 0.01g precision (Ohaus®). We measured cloacal temperature (T_c) as a proxy of body temperature (Andreasson et al., 2023), before (t_1) and after the respirometry trial (t_2), as well as after short-term recovery (t_3). To do so, we inserted a K-type thermocouple connected to a thermometer (Testo925^{TM}; Testo®; precision ~0.1°C) ~0.8cm deep into the cloaca until reading was stable for 3 seconds. T_c was systematically measured in first and as quickly as possible. We removed T_c values <36.5°C from our analysis as they represented outliers (≤1.25th percentile), and were likely the results of a non-deep enough insertion of the thermal probe.

Finally, we sampled blood directly after each respirometry trial, and after mid-term recovery (t_2, t_4). We sampled ~75µL of blood by brachial venipuncture using 26Gx$^1/_2$” needles (Agani^{TM}; Terumo®) and heparinized capillary tubes (Hirschmann®). Plasma was placed in ice until centrifugation (10 minutes at 2.10^3G and 4°C) in the hour following the blood sample. All samples were frozen at -80°C until later analyzes.

3.2. Respirometry protocol

Birds were introduced into individual metabolic chambers at 11:00 (t_1), data acquisition started at 12:00 and lasted until 16:00. All chambers were 0.53L airtight polypropylene containers (Sistema®). Birds were kept in the obscurity. All metabolic chambers were placed inside a 55L temperature-controlled cabinet (Sable Systems International®). The temperature inside the cabinet was monitored continuously using a thermocouple and controlled by a PELT5 temperature controller (±0.5°C; Sable Systems International®). Temperature was set either at 30°C or 40°, and averaged 30.6±0.2°C or 40.0±0.2°C within metabolic chambers (Ibuttons^{TM}; DS1925L; Maxim Integrated®).

An eight-channel multiplexer (TR-RM4^{TM}, Sable Systems International®) coupled with a mass flow meter (Side Track 830 ^{TM}, Sierra®) were used to control the flow of air to each of the four chambers holding individual birds, and to the empty chamber used for baseline recordings. Baseline was established in an empty metabolic chamber during 6min before and after each measurement. Birds were recorded sequentially for a duration of 7.5min each during a cycle. One full cycle lasted 60min, and 4 cycles were conducted during the whole trial, representing a total of 30min of measurement for each bird. Air was pulled at a 500mL.min^{-1} flow rate within each chamber alternatively. Airflow through the chambers was maintained by the multiplexer even when the metabolic rates were not being measured. A layer of mineral oil was disposed at the bottom of each chamber to trap feces and excreta in order to prevent evaporation of any additional water from excretion, and birds were separated of this layer by a metal mesh. Fractional concentration of H_2O, and O_2 and CO_2 were measured using dedicated gas analyzers (RH-300^{TM}; Oxzilla FC-2^{TM}; CA-2A^{TM}; Sable Systems®). Excurrent air from the empty chamber had a baseline partial pressure of H_2O averaging 0.73±0.24kPa, and absolute humidity was 5.23 gH_2O.m^{-3} at 30°C and 4.98 gH_2O.m^{-3} at 40°C (30°C, RH=17.1%; 40°C, RH=9.9%; Campbell and Norman, 1998), representing typical dry desertic conditions (Freeman et al., 2024; Griffith et al., 2017b; Noakes and McKechnie, 2019; Powers, 1992; Walsberg, 2000)

We calculated both rates of CO_2 production (VCO_2), O_2 consumption (VO_2) and evaporative water loss (EWL) following Lighton (2008; Eqs. 11.7, 11.8, 11.9 respectively). Our respiratory quotient (RQ) was considerably low and differed significantly between 30°C and 40°C (30°C, RQ=0.62; 40°C, RQ=0.54; F=330.10, p<0.001). While reporting RQ in the 0.6 to 0.7 range is not rare for birds (Mellen and Hill, 1955; Walsberg and Wolf, 1995), such a low RQ is likely owed to the underestimation of CO_2, especially when water vapor pressure is higher (i.e. at 40°C due to increased EWL; Lighton, 2008). Moreover, Cooper et al (2020b) reported RQ to be similar at 30°C and 40°C for zebra finches. Since VCO_2 measurement is sensible to the ambient humidity, and because the estimation of metabolic rate from VCO_2 further vary depending on RQ assumption than when using VO_2 (Walsberg and Wolf, 1995), we decided to restrict our analyses to VO_2.

We calculated metabolic heat production (MHP) and metabolic water production (MWP) from VO_2 assuming a RQ of 0.72. We estimated evaporative heat loss (EHL) from EWL using a latent heat of vaporization of 2.4 J.mg^{-3} (Tracy et al., 2010). We report cooling efficiency (EHL/MHP) and relative water economy (RWE=MWP/EWL). MHP was calculated using an oxyjoule equivalent of [16+5.164*RQ] (i.e. MHP=[16+5.164*0.72]*VO_2]; Lighton, 2008), and MWP using a coefficient of 0.572 (i.e. MWP=[0.572*VO_2]; Withers et al., 2016). After 4 hours of food restriction, zebra finches were likely in a post-prandial state (Rutkowska et al., 2016). We assumed RQ to be 0.72 as it matched the food quotient, and because it represents the mean post-prandial RQ for non-heat acclimated birds (Black et al., 1986; Gavrilov and Gavrilov, 2019; Hall et al., 2019).

We estimated the weight loss and gain of H_2O through evaporation (M_{EWL}) and metabolism (M_{MWP}) during the whole respirometry trial using EWL and MWP respectively. We corrected M_{EWL} and M_{MWP} to represents the whole trial, i.e. from 11:00-16:00, rather than during data acquisition (12:00-16:00), so they matched with M_b. To do so, we assumed M_{EWL} and M_{MWP} in first hour of trial (11:00-12:00) to be similar to the 30°C condition, for both 30°C and 40°C exposure. We report the total water balance as $M_{H2O}=M_{EWL}-M_{MWP}$. We assumed total body water (TBW) to be 66% of M_b (Cooper et al., 2020a; Speakman, 1997). We estimated water intake during short-term recovery from M_b, correcting for blood sampling (0.075g) and M_b loss during fasting (0.36% of $M_b.h^{-1}$; Rutkowska et al., 2016).

3.3. Measures of blood markers

We measured blood cells concentration using a flow cytometer (BD Accuri™ C6 Plus; BD Biosciences®). We counted the total number of events in 50µL of $^1/_{500}$ diluted whole blood in PBS. Intraclass correlation (ICC) between duplicates was 0.66 (SE=0.056; CI: [0.535, 0.759]; p<0.001) and we excluded data when CV>10%. We measured plasma osmolality of 10µL of $^1/_2$ diluted plasma in ddH_2O using a vapor pressure osmometer (Vapro™; ELITechGroup®). We only measured standards in duplicates, and their mean CV was <1%.

3.4. Statistical analysis

All statistical analyses were conducted using R (Version 4.3.2). We used linear mixed models to take into account the longitudinal nature of our data [formula: measure ~ parameters+(1|Bird.Identity)+(1|Trial.Identity); Bates et al., 2015]. Trial identity designate the first or second trial. We used body mass as a covariate for all models on respirometry variables (i.e. VO_2, MHP, EHL, EWL, MWP) following Speakman (2013), but also reports our results as divided by individuals body mass to allow the comparison with other studies. Summary statistics of all models are available in supplementary material. Statistics for MHP, EHL and EHL/MHP are not reported since MHP and EHL are respectively direct conversion of VO_2 and EWL, and EHL/MHP is equivalent to RWE (MWP/EWL). We report marginal means and standard error calculated using the “emmeans” R-package (Lenth, 2024). We used the package “DHARMa” to assess model assumptions, and “rptR” to assess repeatability (Hartig, 2016).

4. Results

4.1. Body mass

Initial body mass (M_b at t_0) did not differed significantly between treatment (F=0.74, p=0.391), young and old individuals (F=0.61, p=0.438), or male and females (F=0.10, p=0.745). M_b loss during the experiment varied significantly depending on the treatment (Table 1; Figure 2; Time:Trmt, F=13.69, p<0.001), but the effect of time and treatment was not related with the age or sex the individuals (Time:Trmt:Age, F=0.09, p=0.967; Time:Trmt:Sex, F=0.25, p=0.859). Most notably, M_b loss during respirometry (t_1-t_2) was higher at 40°C compared to 30°C (t=-4.83, p<0.001). Additionally, individuals significantly gained weight during the short-term recovery after being exposed to 40°C (t=-6.13, p<0.001), but not to after exposure at 30°C (t=1.57 p=0.771).

Interactions between our treatment and age or sex where non-significantly related with M_b recovered 48h after exposure at 30°C or 40°C (Time:Trmt:Age, F=2.56, p=0.113; Time:Trmt:Sex, F=0.04, p=0.850). However, the interaction between time and treatment was significant (Time:Trmt, F=4.29, p=0.041), and individuals recovered their initial M_b (t_0) only after exposure at 30°C (30°C, t=0.29, p=0.991; 40°C: t=3.15, p=0.011). Overall, M_b 48h after heat exposure (t_4) represented 100.0% and 96.7% of the initial M_b for 30°C and 40°C respectively.

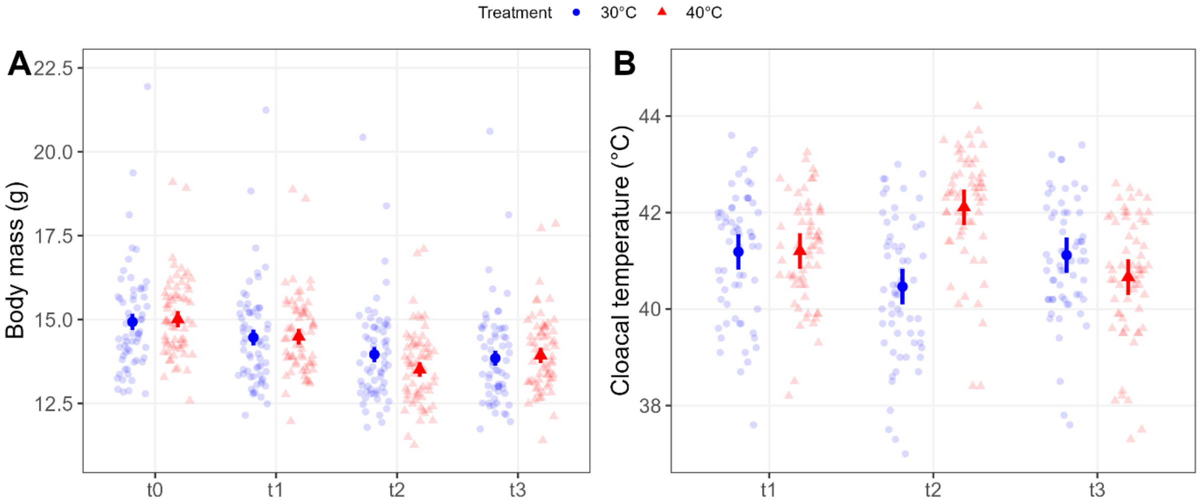

Figure 2. effect of time and heat exposure on (A) body mass and (B) cloacal temperature of captive zebra finches (*Taeniopygia guttata*). Blue circles: 30°C; red triangle: 40°C. Raw data is represented a semi-transparent while marginal means and standard errors are opaque. t0: initial capture (8:00); t1: before heat exposure (11:00); t2: after respirometry trial (16:00); t3: short-term recovery (17:30).

Table 1. Effect of heat exposure on body mass and cloacal temperature of captive zebra finches (*Taeniopygia guttata*).

Parameter	Treatment	t0	t1	t2	t3
M_b (g)	30°C	14.93 ± 0.24^{a}	14.47 ± 0.24^{b}	13.96 ± 0.23^{c}	13.85 ± 0.23^{c}

M_b loss (%)		–	(3.10%)	(6.50%)	(7.24%)
	40°C	15.01 ± 0.24^{a}	14.49 ± 0.24^{b}	13.51 ± 0.23^{d}	13.93 ± 0.23^{c}
		–	(3.45%)	(9.98%)	(7.17%)
T_c (°C)	30°C	–	41.19 ± 0.37^{a}	40.46 ± 0.37^{b}	41.12 ± 0.37^{a}
	40°C	–	41.20 ± 0.37^{a}	42.11 ± 0.37^{c}	40.66 ± 0.37^{ab}

We report marginal means±SE computed using the "emmeans" R-package. Values of each M_b or T_c with different superscript differ significantly ($p<0.05$). M_b: body mass; T_c: cloacal temperature; t0: initial capture (08:00); t1: before heat exposure (11:00); t2: after heat exposure (16:00); t3: short-term recovery (17:30).

4.2. Cloacal temperature

Cloacal temperature was significantly related with age (Age, F=4.72, p=0.034), with old individuals having a lower T_c than young individuals by 0.3°C across all times and treatments. Main effect of sex was not significant (Sex, F=0.17, p=0.686). Time and treatment did no significantly interacted with age or sex (Time:Trmt:Age, F=0.39, p=0.677; Time:Trmt:Sex, F=0.58 , p=0.559). However, interaction between the time and treatment was significant (F=28.39, p<0.001). T_c was significantly higher after exposure at 40°C compared to 30°C (t_2; t=-7.93, p<0.001; Table 1, Figure 1B). T_c significantly decreased during exposure at 30°C (t=3.49, p:0.007) while it increased during exposure at 40°C (t=-4.35, p<0.001). T_c returned to its pre-exposure value after short-term recovery (t_3), but tended to be slightly lower when exposed to 40°C (30°C, t=0.33, p=1; 40°C, t=2.71, p=0.096).

4.3. Evaporative water loss and water balance

Evaporative water loss (EWL) was significantly higher at 40°C compared to 30°C (Table 2; Figure 2A; 3-fold higher; F=570.43, p<0.001). However, EWL was not related with age (Age, F=0.45, p= 0.450) or sex (Sex, F=1.97, p=0.167), and there was no significant interaction between age or sex with the treatment (Trmt:Age, F=0.02, p=0.882; Trmt:Sex, F=0.13, p=0.724). Metabolic water production (MWP) was significantly higher at 40°C compared to 30°C (Table 2; F=10.15, p=0.002), but relative water economy (RWE, i.e. MWP/EWL) was drastically lower at 40°C (Table 2; Figure 2B; 3-fold lower; F=549.15, p<0.001). There was no significant interaction between age and sex with the treatment, although sex tended to be significant (Trmt:Age, F=0.01, p=0.928; Trmt:Sex, F=3.83, p=0.055).

Estimated water loss during the whole respirometry trial ($M_{H2O}=M_{EWL}-M_{MWP}$; i.e. between t_1 and t_2) was 0.15 and 0.62 gH_2O at 30°C and 40°C, representing a loss of 1.04% and 4.25% of M_b, or 1.58% and

6.44% of total body water at t_1. Overall, M_{H2O} represented 27.95% and 69.28% of the total M_b loss during respirometry (ΔM_b between t_1 and t_2) at 30°C and 40°C respectively. Finally, estimated water intake during short-term recovery (from t_2 to t_3) was 0.05g and 0.58 gH_2O after exposure at 30°C and 40°C respectively, representing 95.54% of M_{H2O} at 40°C.

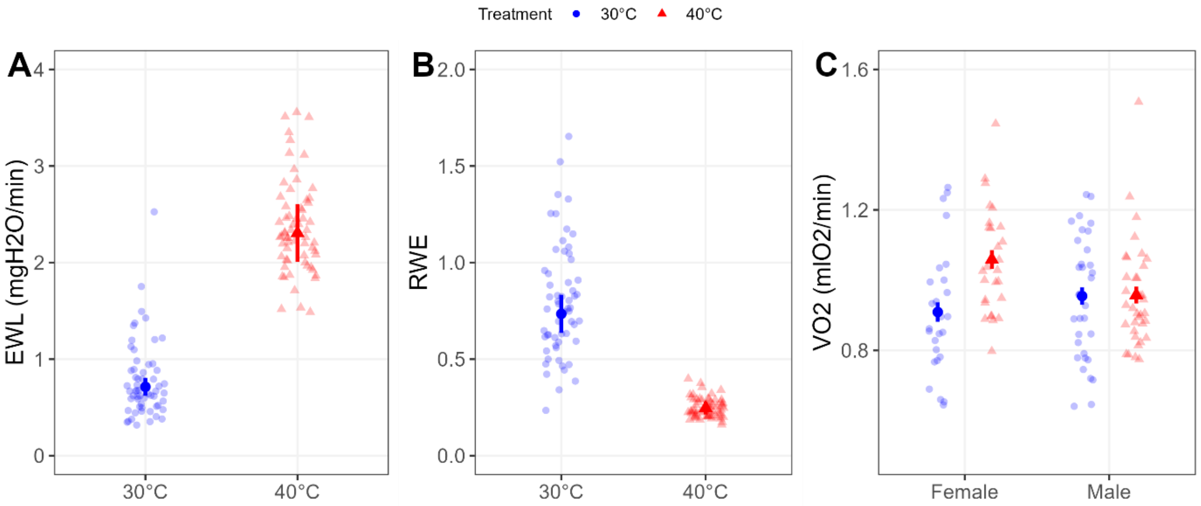

Figure 2. Effect of heat exposure on (A) evaporative water loss, (B) relative water economy and (C) oxygen consumption of captive zebra finches (*Taeniopygia guttata*). Blue circles: 30°C; red triangle: 40°C. Raw data is represented as semi-transparent while marginal means and standard errors are opaque. EWL: evaporative water loss; MWP: metabolic water production; RWE: relative water economy (MWP/EWL); VO_2: oxygen consumption rate.

Table 2. evaporative water loss and metabolism of captive zebra finches (*Taeniopygia guttata*) during heat exposure.

Parameter	30°C	40°C
EWL (mgH_2O/min)	0.71 ± 0.09^a	2.31 ± 0.30^b
EWL (mgH_2O/g/h)	2.96 ± 0.38^a	9.54 ± 1.24^b
MWP (mgH_2O/min)	0.53 ± 0.11^a	0.58 ± 0.10^b
RWE	0.73 ± 0.10^a	0.25 ± 0.03^b
VO_2 (mlO_2/min)	0.93 ± 0.02^a	1.01 ± 0.02^b
VO_2 (mlO_2/g/h)	3.84 ± 0.08^a	4.16 ± 0.08^b
MHP (W)	0.31 ± 0.01^a	0.33 ± 0.01^b
EHL (W)	0.03 ± 0.01^a	0.09 ± 0.01^b

EHL/MHP	0.10 ± 0.01^{a}	0.28 ± 0.04^{b}

We report marginal means±SE computed using the "emmeans" R-package. Values of each parameter in a row with different superscript differ significantly ($p<0.05$). EHL: evaporative heat loss; EWL: evaporative water loss; MHP: metabolic heat production: RWE: relative water economy (MWP/EWL); VO$_2$: oxygen consumption rate.

4.4. Oxygen consumption and heat flux

Rate of oxygen consumption (VO$_2$) was significantly related with the treatment, the age and the sex of the individuals. VO$_2$ was 0.06mLO$_2$/min lower in older individuals (i.e. ~6% lower; Age, F=4.91, p=0.031), but the interaction between age and treatment was not significant (Trmt:Age, F=0.14, p=0.707). Treatment was significantly related with VO$_2$ (Table 2; Trmt, F=10.15, p=0.002), and although the main effect of sex was not significant (F=1.05, p=0.310), there was a significant interaction between our treatment and sex (Figure 2C; Trmt:Sex, F=9.43, p=0.003). Post-hoc analysis highlighted that VO$_2$ increased significantly at 40°C compared to 30°C only for females (female, t=-4.17, p<0.001; male, t=-0.09, p=1). Metabolic heat production increase (MHP) while evaporative heat loss decreased from 30°C to 40°C (Table 2). Overall, EHL/MHP decreased by ~3 fold from 30°C to 40°C (Table 2).

4.5. Blood markers

Time was the only significant predictor of blood cells concentration (Table 3; Figure 3A; Time, F=50.50, p<0.001), meaning blood cell concentration was lower after 48h of recovery regardless of the treatment (Trmt, F=0.15, p=0.703; Time:Trmt, F=1.29, p=0.259), age (Age, F=1.62, p=0.209), sex (Sex, F=0.42, p=0.522), or their interaction (Time:Trmt:Age, F=3.16, p=0.078; Time:Trmt:Sex, F=0.07, p=0.792).

Plasma osmolarity (P$_{osm}$) differed significantly in function of the time and treatment (Table 3; Figure 3B; Time:Trmt, F=20.18, p<0.001). P$_{osm}$ was significantly higher after exposure at 40°C compared to 30°C (t$_2$; t=-4.06, p<0.001), but was not different after 48h of recovery (t$_4$; t=2.28, p=0.106). Age (Age, F=1.09, p=0.298), sex (Sex, F=0.06, p=0.812), or their interaction with time and treatment were not significant predictors of P$_{osm}$ (Time:Trmt:Age, F=0.07, p=0.796; Time:Trmt:Sex, F=0.08, p=0.781).

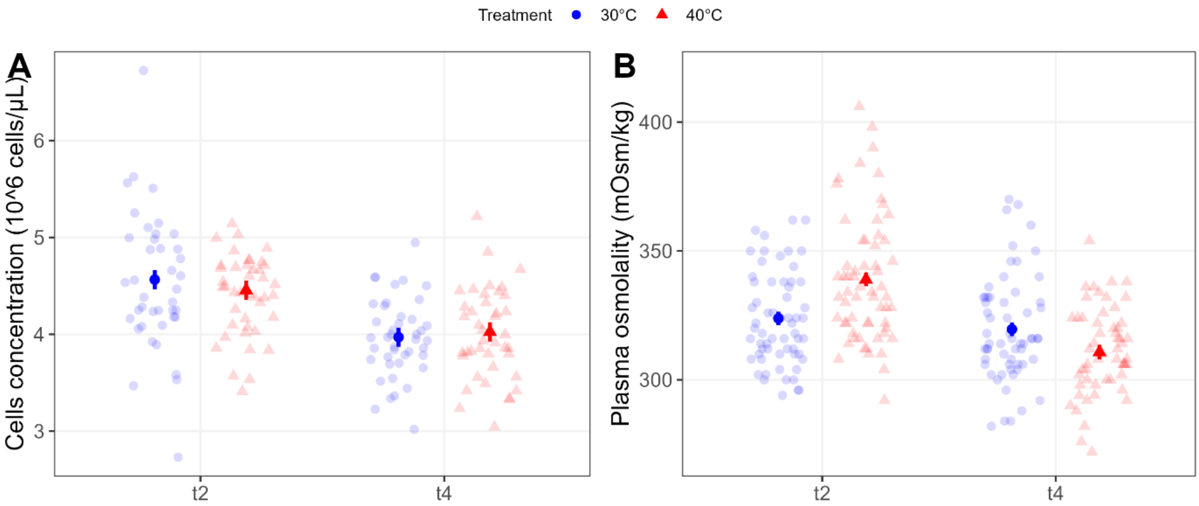

Figure 3. Effect of heat exposure on (A) blood cells concentration (B) plasma osmolality of captive zebra finches (*Taeniopygia guttata*). Blue circles: 30°C; red triangle: 40°C. Raw data is represented as semi-transparent while marginal means and standard errors are opaque. t2: after respirometry trial; t4: mid-term recovery (48h post-respirometry).

Table 3. Effect of heat exposure on hematological parameters of captive zebra finches (*Taeniopygia guttata*).

Parameter	After respirometry (t2)		After recovery (t4)	
	30°C	40°C	30°C	40°C
Cell concentration (10^{-6} cells/µL)	4.56±0.10^{a}	4.46±0.10^{a}	3.97±0.10^{b}	4.02±0.10^{b}
P_{osm} (mOsm/kg)	324±2.62^{a}	339±2.62^{b}	320±2.67^{ac}	311±2.81^{c}

We report marginal means±SE computed using the "emmeans" R-package. Values of each parameter in a row with different superscript differ significantly ($p<0.05$). P_{osm}: plasma osmolality. $P_{[compound]}$: concentration of a specific compound in the plasma. Na: sodium. UA: uric acid; TG: triglycerides.

5. Discussion

5.1. Dehydration risk

The observed increase in VO_2 is most likely associated with an increased respiratory water loss via panting (Wojciechowski et al., 2021). This is supported by the drastic increase in EWL and EHL when exposed to 40°C compared to 30°C (3-fold higher). Relative increase in EWL and EHL were in the same range as reported by others studies (Cade et al., 1965; Cooper et al., 2020a; Cooper et al., 2020b; Wojciechowski et al., 2021). Zebra finches EWL exceeded MWP both at 30°C and 40°C (RWE<1) and suggest a dependency on dietary water to maintain water balance. While zebra finches have been reported to be able to survive from a diet of dry seed only, their daily water intake represent ~24% of their body mass in standard rearing conditions (20-22°C, RH: 20-40%, water and food ad libitum), and only 50% of the individuals survived during the 3 months of water deprivation (Cade et al., 1965). RWE was drastically lower at 40°C compared to 30°C and metabolic water production could only compensate for ~25% of evaporative water loss at 40°C similar to (Cooper et al., 2020a).

Zebra finches lost approximately twice more M_b during the exposure at 40°C compared to 30°C. Estimated water loss (M_{H2O}) during respirometry represented most of the M_b loss at 40°C (~69.3%). Overall, we estimated that birds lost in average 6.4% of their total body water during exposure at 40°C, meaning individuals were likely dehydrated. This is further supported by the fact that birds only drank after exposure at 40°C during the short-term recovery. We estimated their water intake to be ~0.58g, representing 95.5% of M_{H2O}. Interestingly, this value match well with the maximum crop mass of ~0.60g reported by Meijer et al (1996). Whether birds aligned water intake with their previous loss, or drank up to their full crop capacity is thus yet to determine. In summary, exposure at 40°C promoted a significant water loss compared to 30°C mediated by an increased EWL, and individuals compensated for that loss by increasing their water intake during recovery. Individuals were thus likely dehydrated after heat exposure.

This is further supported by the variation in hematological parameters. Most notably, plasma osmolality (P_{osm}) was significantly higher after heat exposure. P_{osm} as been reported to be a reliable marker of dehydration and to scale with dehydration severity (Chapter 3). Moreover, it has been reported to increase with heat exposure in wild (Salaberria et al., 2014) and captive birds (Arad, 1985; Arad and Marder, 1983; Arad et al., 1989; Carmi et al., 1993; Itsaki-Glucklich and Arad, 1992). This is because an increase in P_{osm} is both a key mechanism allowing water retention during phases of antidiuresis, and one of the main consequences of an increased body water loss (Braun, 1982; Skadhauge, 1981). Blood cells concentration were similar to the one reported by Coughlan et al (2022). Blood cells concentration did not vary with heat exposure but only decreased after 48h due to the previous blood sampling. While blood cells concentration or hematocrit is likely to increase with dehydration because of plasma volume loss (Dawson et al., 1983; Stewart, 1972; Takei et al., 1988), it is not the most reliable markers of dehydration (Chapter 3). In the case of thermal dehydration more specifically, hematocrit has been reported to not vary (Arad et al., 1989; Carmi et al., 1993; Carmi et al., 1994; Itsaki-Glucklich and Arad, 1992; Maloney and Dawson, 1998) or even increase (Arad, 1983; Arad et al., 1987; Zhou et al., 1999). This is likely because birds are believed to be "plasma volume conservers", i.e. they maintain plasma volume through fluid movement from the intracellular or interstitial compartments (Arad et al., 1989; Carmi et al., 1993; Carmi et al., 1994; Dawson et al., 1983).

5.2. Hyperthermia risk

Heat exposure significantly increased T_c in zebra finches, with T_c reaching ~42.1°C after 4h of exposure at 40°C, and being ~1.7°C higher than after exposure at 30°C. This is within the range of other studies (Cooper et al., 2020a, 30°C: T_c=37.7°C, 40°C: T_c=42.5; Cooper et al., 2020b, 30°C: T_c=37.7°C, 40°C: T_c=42.5; Wojciechowski et al., 2021, T_b=41.0°C, 40°C: T_b=41.7°C), although the relative increase between 30°C and 40°C was lower than previously reported by Cooper et al (2020a, 2020b).

The EHL/MHP ratio represents the proportion of heat dissipated over the metabolic heat produced, and is often referred to as "cooling efficiency". We report comparable values than previously reported by Cooper et al (2020a, 40°C: EHL/MHP=0.39; 2020b, 40°C: EHL/MHP=0.24), but approximately 2-fold lower both at 30°C and 40°C than reported by other studies (Cade et al., 1965, 30°C: EHL/MHP=0.2, 40°C: EHL/MHP=0.7; Wojciechowski et al., 2021, 30°C: EHL/MHP=0.2, 40°C: EHL/MHP=0.6). This is because we measured a similar MHP, but an EHL approximately twice lower. Overall, zebra finches increased their EHL/MHP during exposure at 40°C but did not dissipate all MHP through evaporation (EHL/MHP<1).

Despite a significant increase in T_c, a mean value of 42.1°C after heat exposure still is within the natural range of T_b of active birds (e.g. Linek et al., 2021; Tapper et al., 2020; Tapper et al., 2021), and quite far from the estimated maximum T_b~45-47°C, (Freeman et al., 2020; Freeman et al., 2022). Moreover, facultative hyperthermia seems to be a strategy highly conserved between avian species and taxa (Gerson et al., 2019; Tieleman and Williams, 1999), and zebra finches were able to quickly recover their initial T_c. It is thus unclear whether this observed 'hyperthermia' is likely to have deleterious effects. However, our birds had very limited locomotor activity, were in a post-prandial phase and were maintained in obscurity. We could expect more drastic increases in T_b in more natural conditions and/or increased costs associated with the maintenance of T_b under harmful levels. While acute exposure to 40°C is not likely to promote lethal hyperthermia for zebra finches, it may limit their foraging in natura, via changes in activity patterns or a decreased cognitive and locomotor performance (Cooper et al., 2019; Danner et al., 2021b; Funghi et al., 2019; Wheeler et al., 2023).

5.3. Recovery

Only individuals exposed to 40°C drank water during the short-term recovery, and recovered in average ~2.8% of their initial M_b. Such a quick increased in water intake and body mass gain during rehydration has been similarly described in others studies (Arad, 1985; Arad et al., 1989; Itsaki-Glucklich and Arad, 1992; Takei et al., 1988). However, birds had recovered their initial M_b 48h after exposure at 30°C, but did not at 40°C (~3.3% M_b loss). As a comparison, chicken (*Gallus domesticus*) having loss ~15% of their initial M_b during water restriction were able to recover within 48h, but it took 6 to 8 days for varying species of quails (Koike et al., 1977; McNabb, 1969).

Water intake and osmotic excretion is believed to peak shortly after dehydration, especially during the first day of rehydration (Fleming et al., 2004; McNabb, 1969). P_{osm} was back to its initial value or to an intermediate value 1h after the start of the rehydration for chickens (Arad, 1985; Koike et al., 1977), and back to its initial value after 1h for different species of quails (Takei et al., 1988). It is this no surprise that P_{osm} was back to its initial value 48h after heat exposure in our experiment. However, it is worth noting than hormones levels may be still elevated 48h after rehydration, testifying of the mid-term response to such a stress (Koike et al., 1977; Takei et al., 1988). Finally, T_c was back at its initial level following the short-term recovery, similar to what has been previously described in chickens (Arad, 1985).

While non-significant, T_c following short-term recovery seemed slightly lower after exposure at 40°C, and may results from a compensation mechanism. This is also consistent with P_{osm} being slightly lower 48h after exposure at 40°C compared to 30°C. Overall, while individuals seem to have quickly recovered from heat exposure, there are some indications of slight costs and compensation mechanisms. Wild birds, in potentially less-optimal condition (no food and water ad libitum), may not be able to recover as well from such a stress, especially if heat exposure is sustained during multiple days. For instance, a variety of adults and nestlings have shown changes in activity patterns, decreased foraging efficiency and daily body mass loss during heat events in the Kalahari desert (Bourne et al., 2021a; du Plessis et al., 2012; Kemp et al., 2020; Oswald et al., 2021; Sharpe et al., 2019; van de Ven et al., 2019; van de Ven et al., 2020).

5.4. Influence of age and sex

Contrary to our initial hypothesis, heat response and subsequent recovery did not seem related with the age of the individuals. Still, it is worth noting that older individuals had a lower T_c and VO_2 regardless of the treatment. Metabolic rate is known to decrease with age across multiple taxa including varying avian species (reviewed by Elliott et al., 2015), and zebra finches are no exception (Berntsen and Bech, 2021; Moe et al., 2009; Rønning et al., 2014). Body temperature (T_b) has also been reported to decrease with age in humans (Geneva et al., 2019) and some avian species (Andreasson et al., 2020b; Zagkle et al., 2020). Contrary to other studies, body mass and blood cell concentration were not significantly lower in older individuals (M_b: ~1.7% lower; p=0.439; hematocrit: ~3.0% lower, p=0.102; Briga et al., 2019; Coughlan et al., 2022; Elliott et al., 2015). We do not exclude the possibility of some hidden costs associated with such a response, that we were either not able to detect, or that we did not measured (e.g. oxidative balance; HSPs genes; Xie et al., 2017). Most notably, there may be a selective disappearance of low-quality individuals with age, buffering the senescence pattern observed (e.g. Hämäläinen et al., 2014; Simons et al., 2016). Alternatively, many traits do not vary linearly in relation with age, and the greater decline in survival or performance is usually observed close to death (i.e. terminal decline; Cohen-Mansfield et al., 2018; Hammers et al., 2012; Simons et al., 2016). For instance, heat-related mortality risk seems to increase exponentially with age in humans (Gallo et al., 2024). Overall, there was limited support for age effects and further studies are needed to shed light on it.

There was a significant interaction between sex and treatment when predicting VO_2, and a tendency when predicting RWE (or MHP/EHL). Interestingly, only females increased their VO_2 when exposed to 40°C. While we did not find such results in the literature, some authors have reported sex-differences in metabolic rates and T_b across varying bird species (Nilsson and Nord, 2018; Rønning et al., 2014; Tapper et al., 2021). For zebra finches, captive females may to have a higher metabolic rate than male (Rønning et al., 2014). Reaction norm to heat exposure has also been reported to be sex-dependent in few studies (Jaarsveld et al., 2021; Pessato et al., 2023). Wild females may have a higher T_b, lower EHL and a lower EHL/MHP ratio when exposed to ambient temperatures exceeding 38°C (Pessato et al., 2023). Thus, thermoregulatory capacity of zebra finches may vary between sexes and represent exciting perspectives for future studies.

Theme 2. Discussion

Pied babbler (*Turdoides bicolor*) population in the Kalahari Desert is declining rapidly with the increased frequency of heatwaves (South Africa; Ridley et al., 2021). Photo from Macaulay Library (ML626032418).

1. Hyperthermia-dehydration trade-off

When exposed to high temperatures, birds usually increase their body temperature (Tb) and/or increase heat dissipation (McKechnie and Wolf, 2019). For most birds, evaporative heat dissipation represents the main way of active heat dissipation (e.g. via panting; McKechnie et al., 2021a). Increase in Tb despite environmental temperature (Te) not exceeding Tb is often referred to as "facultative hyperthermia", and seems to be a mechanism highly conserved across avian taxa (Figure 1; Gerson et al., 2019; Tieleman and Williams, 1999). This suggests a trade-off between hyperthermia and dehydration risk during heat exposure. In chapter 3, we briefly review literature on the hyperthermia-dehydration trade-off hypothesis. In laboratory settings, water-restricted birds show reduced evaporative heat dissipation at the expense of a higher increase in Tb during heat exposure, representing experimental evidence for the hyperthermia-dehydration trade-off (Figure 2; Arad, 1983; Arad et al., 1987; Greenwald et al., 1967; Maloney and Dawson, 1998; Zhou et al., 1999). Overall, birds usually use a combination of heat storage and increased heat dissipation, mostly through evaporative pathways, to achieve the most favorable thermal and osmotic balance. In chapter 4, we investigate the response to heat exposure in zebra finches. Heat exposure led to an increase in Tb and evaporative water loss (EWL), similar to other studies in captive and wild zebra finches (Cooper et al., 2020a; Cooper et al., 2020b; Wojciechowski et al., 2021). Heat exposure led to considerable body water loss, increase in plasma osmolarity and promoted thirst, representing physiological signs of dehydration.

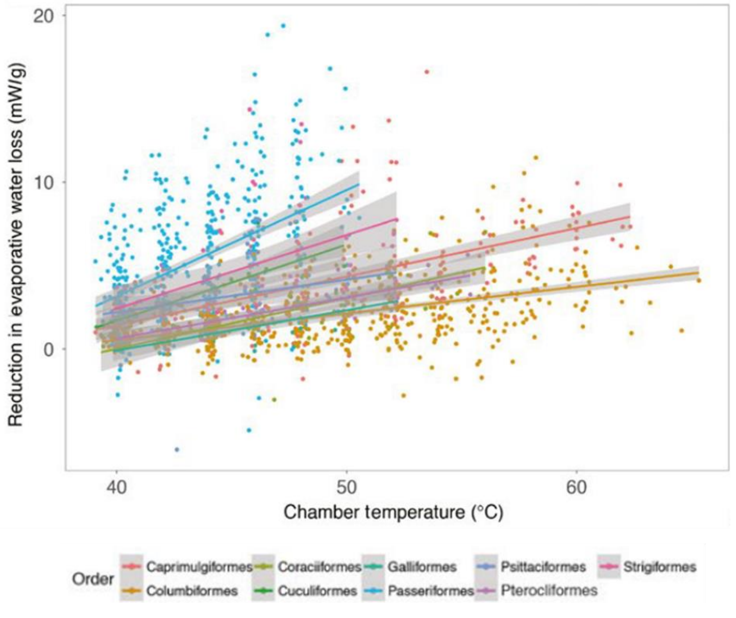

Figure 1. Hyperthermia reduce predicted evaporative water loss across varying avian orders. The reduction in the rate of evaporative water loss differs significantly among orders and species. The of hyperthermia differs strongly among broad phylogenetic groups, where doves (Columbiformes), sandgrouse (Pterocliformes) and nightjars (Caprimulgiformes) do not benefit as much as songbirds, owls and cuckoos after accounting for body size. Adapted from Gerson et al., 2019.

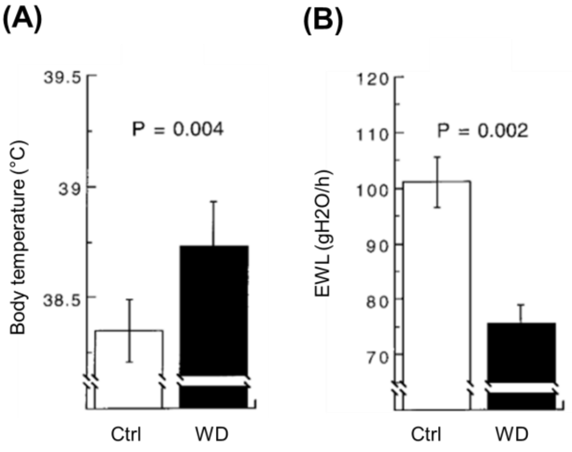

Figure 2. Hyperthermia and dehydration trade-off during heat exposure (Te=45°C) in water-deprived captive emus (*Dromaius novaehollandiae*). (A) Body temperature; (B) Evaporative water loss. EWL: evaporative water loss; Ctrl: hydrated individuals; WD: water-deprived individuals. Dehydrated individuals have a higher body temperature and EWL when exposed to Te=45°C. Dehydrated emus delayed panting initiation by 30 minutes compared to hydrated individuals during heat exposure, leading to further heat storage and ultimately a higher body temperature. Adapted from Maloney and Dawson (1998).

2. Inter-specific variation in the physiological response to heat exposure

While most birds seem to show some level of hyperthermia and evaporative heat dissipation when exposed to high temperatures, there is a high variation in the diversity of responses (Figure 3). Most notably, there is a high inter-specific variation in the diversity of responses and heat tolerance (McKechnie et al., 2021a; Smit et al., 2018). For instance, passerines seem to rely more on hyperthermia than other taxa (Gerson et al., 2019). This is likely explained by their reliance on panting, which is appears to be a relatively inefficient mechanism of heat dissipation due to its high metabolic heat production output (Figure 3; Figure 4). Passerines have a relatively high tolerance to hyperthermia, but seem to have a lower evaporative scope, evaporative cooling efficiency, UCT and HTL relative to other taxa (Figure 3; McKechnie et al., 2021). Moreover, they are predicted to have a higher dehydration risk due to their smaller body size (McKechnie and Wolf, 2010). These differences in thermoregulatory capacity may explain their over-representation in heat-related mortality events (Figure 5; McKechnie et al., 2021b). Additionally, birds UCT seems to scale with maximum temperature in their habitat, suggesting an adaptation to local thermal challenges (Qu and Wiens, 2020; Song, 2018).

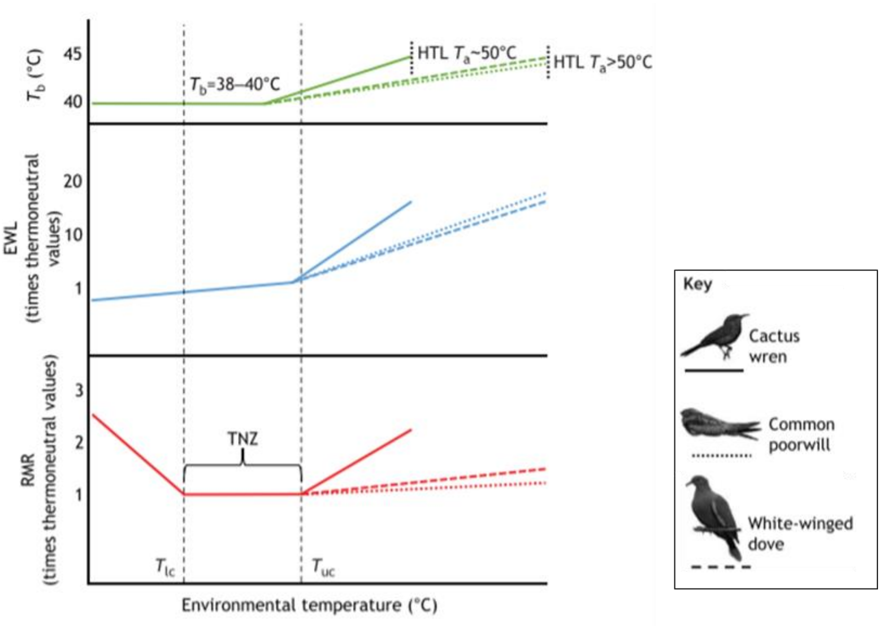

Figure 3. Integration of processes related to avian thermoregulation in the heat across functionally diverse taxa. In passerines (e.g., cactus wren), panting (continuous lines) is the primary pathway for evaporative heat dissipation, and the large metabolic cost adds significantly to the total evaporative demand. In addition, passerines show a steep hyperthermic response and modest heat tolerance limits at air temperature (Ta) ~50°C when Tb approaches lethal values. In Columbiformes (e.g., white-winged dove; dashed line), cutaneous evaporation provides a very efficient evaporative mechanism with modest metabolic costs and hyperthermic responses, and heat tolerance limits may occur at Ta exceeding 60°C. Finally, in the Caprimulgiformes (e.g., common poorwill; dotted lines), evaporative water loss occurs primarily via gular flutter and associated metabolic costs are minimal, allowing for a modest hyperthermic response and heat tolerance limit (HTL) which may exceed Te=60°C. Thermoneutral RMR and EWL can vary substantially among taxa, and the patterns shown here

illustrate fractional changes rather than absolute values; TNZ, thermoneutral zone; adapted from McKechnie et al., 2021a.

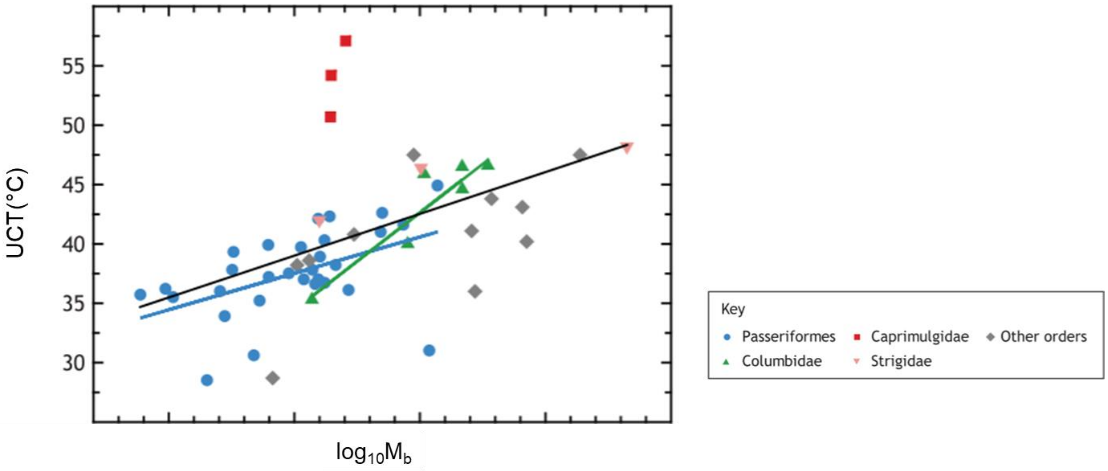

Figure 4. Scaling and phylogenetic variation of upper critical limit of thermoneutrality (UCT) in desert birds; adapted from McKechnie et al., 2021a.

3. Intra-specific variation in the physiological response to heat exposure

Finally, there is likely an inter-individual variation in reaction norm and tolerance to heat exposure. For instance, while red-billed quelea (*Quelea quelea*) have the highest maximum Tb measured among birds, maximum Tb exhibited substantial inter-individual variation (max Tb: 48°C; range: 46.4-49.1°C; Freeman et al., 2020). Tolerance to dehydration is also likely to vary between individuals (Bartholomew and Macmillen, 1960; Mulkey and Huston, 1967). Mourning doves (*Zenaida macroura*) survived 7 days of water deprivation on average, but survival time ranged from 3 to 11 days, and body mass loss at death ranged from ~25% to ~45% (Bartholomew and Macmillen, 1960). Such inter-individual variation is likely to have implications on individual fitness in natura (Figure 5A; e.g. “why did these individuals died and not others”). On one hand, thermoregulation traits are plastic and have been reported to show acclimation in controlled conditions and acclimatization in natural conditions after repeated heat exposure (e.g. Cooper et al., 2020a; Cooper et al., 2020b; Noakes et al., 2016). On the other hand, inter-individual variation may be related to other biological variables such as age, sex or pathological state (Cramer et al., 2022; Fernández-Peña et al., 2023).

Yet, very few studies investigate biological drivers of such inter-individual variation in birds (e.g. Jaarsveld et al., 2021; Mulkey and Huston, 1967; Pessato et al., 2023). In humans, humans, age and sex of the individuals may influence their reaction norms to heat exposure and mortality risk (Cramer et al., 2022; Gallo et al., 2024). Older humans have a reduced ability to dissipate heat through evaporation, as well as lower hyperthermia tolerance, leaving them at higher risk of mortality during heat events (Figure 5B; Gallo et al., 2024). In 1967, Mulkey and Huston reported that "as the bird ages heat stress becomes more severe" when studying heat exposure on domestic fowl (*Gallus domesticus*). In this thesis, we explored the reaction to heat exposure and the subsequent recovery depending on the age or sex in captive zebra finches. Similar to other studies, older individuals showed lower body temperature (Andreasson et al., 2020b; Zagkle et al., 2020) and metabolic rate (Berntsen and Bech, 2021; Moe et al., 2009; Rønning et al., 2014), but reaction norm and recovery to heat exposure did not vary with age. However, reaction norm to heat exposure varied between sexes. Only females increased their metabolic rate during heat exposure. There are some other reports of sex-differences in reaction to heat, but underlying mechanisms are unknown and would need further investigation (Jaarsveld et al., 2021; Pessato et al., 2023). In humans, females seem to have a lower maximal sweat rate than males, and core body temperature varies with sexual hormones while it is maintained constant in males (Cramer et al., 2022; Fernández-Peña et al., 2023).

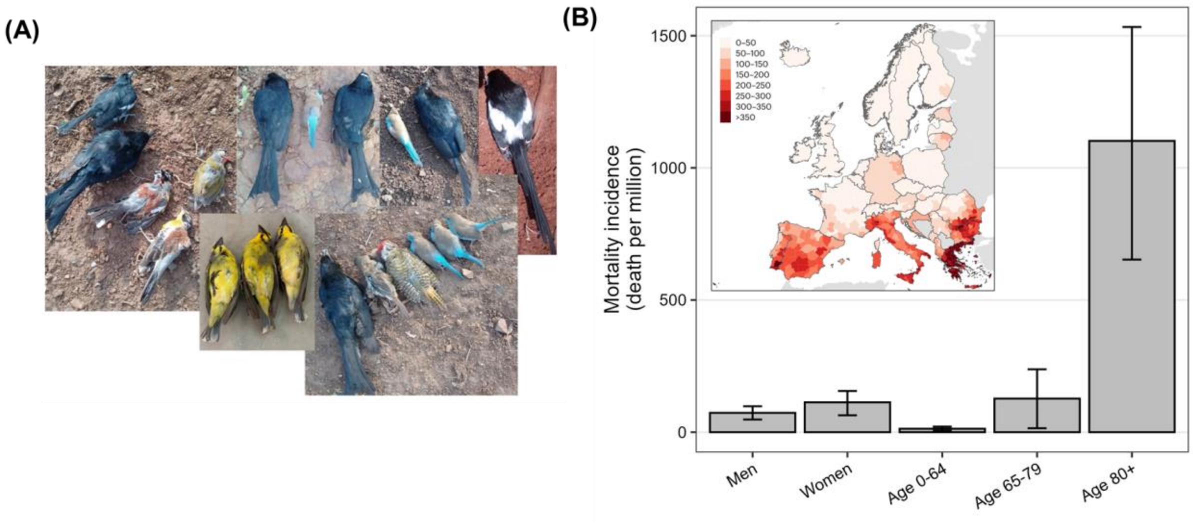

Figure 5. Heatwave related mortality in birds and humans (A) mass-mortality event of birds in 2020 (South Africa). 47 birds of 14 species were found dead, and passerines represented ~79% of avian species impacted by this mortality event. Such extreme events highlight difference in response to heatwaves between taxa (e.g. "why are passerines over-represented?") and individuals (e.g. "why did

these specific individuals died?”). From McKechnie et al., 2021b (B) Mortality incidence in humans across 35 European country during 2023 depending on sex and age of the individuals. Mortality incidence seemed to increase with age, and was drastically higher in the older age class (>80-year-old). Histogram represented mean±95% confidence interval. Adapted from Gallo et al., 2024.

While we were not able to identify any effects of ageing on reaction norm to heat exposure and recovery, we do not exclude the possibility of hidden responses and costs that we did not detect or measured (e.g. gene expression, oxidative balance; Finger et al., 2018; Huang et al., 2015; Xie et al., 2018). Perhaps most importantly, we did not assess physiological traits of tolerance to heat exposure (e.g. heat tolerance limit, dehydration tolerance), and we could expect to see differences during exposure at higher temperatures (i.e. “is our protocol severe enough?”). Moreover, we expect age-related effects to increase non-linearly with age (e.g. Lemaître et al., 2020). For instance, heat-related mortality seems to increase exponentially with age in humans, highlighting the question “are our individuals old enough?” (Figure 5B; Gallo et al., 2024). Individuals were older than the mean zebra finch lifespan, and senescence patterns have been described in zebra finches of similar ages to our individuals, but some were not statistically different among our study (i.e. body mass, hematocrit; Briga et al., 2019; Coughlan et al., 2022). Additionally, we used a cross-sectional experimental design, which do not account for a potential selective disappearance of lower-quality individual with age (Hämäläinen et al., 2014; Simons et al., 2016). In summary, further studies using longitudinal design and assessing tolerance to heat exposure are needed to shed light on this topic (Cam et al., 2002; Nussey et al., 2008).

4. **Implication for wild birds population**

Cooling requirement, hyperthermia and dehydration risk are expected to increase with climate warming (e.g. Albright et al., 2017; Cabello-Vergel et al., 2022; Conradie et al., 2020; McKechnie and Wolf, 2010). Yet, relatively few studies directly assess either behavioral and physiological markers of heat exposure on wild birds (e.g. time and energy budget, heat dissipation behavior, body temperature, hydration status). There has been recent progress on biologging allowing measurement of body temperature in field settings (Linek et al., 2021; Williams et al., 2021), but as far as we are aware, there are only few studies assessing hydration status (Ardia, 2013; Goldstein and Zahedi, 1990; Sabat et al., 2009; Salaberria et al., 2014). We consequently review physiological markers of avian dehydration. Measuring body water represents the most direct way of assessing dehydration. However multiple logistical constraints limit its suitability for field studies. Similar to other taxa, plasma osmolarity appears to be the gold-standard marker for assessing hydration status in birds (Bekkevold et al., 2013; Brusch and DeNardo, 2017; Cheuvront and Kenefick, 2014). Increasing plasma osmolarity predicted dehydration, and plasma osmolarity scaled with dehydration severity. Other markers such as hematocrit, hormones levels, nitrogenous compounds or characteristic of the excreta may also be relevant as complementary ways to assess hydration status. However, water-balance homeostasis is a dynamic process, and levels of markers such as plasma osmolarity vary during anti-diuresis, but do not necessarily predict dehydration per se. Dehydration threshold are yet to be identified for birds and represent great perspectives for future studies. Finally, assessing fitness cost associated with repeated heat exposure necessitates to investigate other markers of physiological stress (e.g. glucocorticoids, immunity markers, oxidative balance) and performance (e.g. foraging or breeding success). Lethal exposure and sublethal costs of heat exposure are expected to increase with climate warming, potentially shaping population dynamic and community composition (Figure 6; Conradie et al., 2019; Riddell et al., 2019; Riddell et al., 2021).

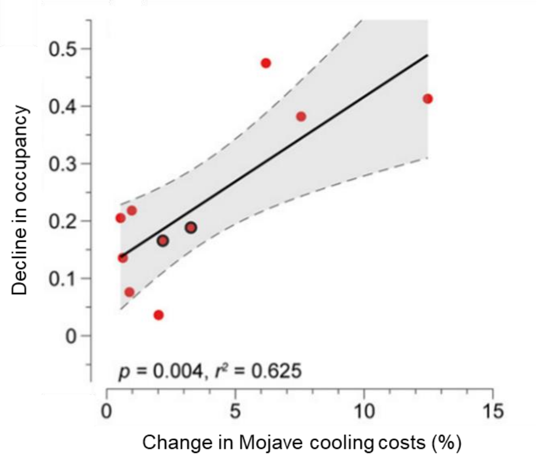

Figure 6. increase in cooling costs is positively associated with avian specie decline in the Mojave Desert; adapted from Riddell et al., 2019.

GENERAL DISCUSSION

King penguin (*Aptenodytes patagonicus*) dissipating heat via panting. Highlight that birds can experience heat stress even in polar climates. From Noiret et al., 2024.

1. Thesis summary

Climate change is one of the key drivers of the current biodiversity loss, and its impact on biodiversity is predicted to increase. Climate change is most notably characterized by increasing global temperatures, and increasing exposure to heatwaves. In this context, we aimed to investigate the effect of high temperatures on avian species, ranging from the physiological response to ecological consequences. In the first chapter of this thesis, we review the association between high temperatures and breeding success at a global scale. The association between high temperatures and breeding success was most likely multifactorial, and potentially driven by direct effects mediated through species thermoregulation (i.e. heat stress or thermal relief), or indirect effect mediated by changes in biotic and abiotic factors (e.g. phenology and trophic interactions). Exposure to high temperatures may be more likely to have deleterious effects on birds reproduction in hot and arid biomes, presumably because it can trigger heat stress (i.e. physiological and behavioral adjustment to maintain body temperature and water homeostasis). Alternatively, results seem to be more contrasted in colder biomes, probably because some breeding birds may benefit from a thermal relief (i.e. decreased heating requirements). Improving our knowledge on species exposure and response to high temperature depending on their local thermal environment should be an important focus for future research.

In the second chapter, we assessed the importance of weather on great tits (*Parus major*) breeding success in a temperate biome and across a gradient of urbanization. High temperatures and breeding timing were respectively positively and negatively associated with breeding success. However, the association between temperature and breeding timing with reproductive success seemed to be contrasted between the urban and forest environment. These contrasted results are likely to be driven by differences in individual and environmental quality. In future studies, disentangling direct and indirect effects would necessitate to improve the monitoring of the thermal environment (e.g. nest temperature), trophic interactions (e.g. food availability) and parental behavior (e.g. nest attentiveness, thermoregulatory behaviors). Ultimately, there are inherent limits to correlative approaches and testing these hypotheses would necessitates to conduct field experiments, such as manipulation of the nest box temperatures.

Overall, understanding and predicting climate change impact on birds populations necessitates to develop and implement ways to disentangle direct and indirect effects. We consequently focused the second theme of this thesis on the direct effects on birds, as the physiological response to heat exposure (i.e. temperature eliciting behavioral or physiological adjustment to maintain body temperature and water homeostasis). Most notably, during heat exposure most birds seem to face a trade-off between hyperthermia and dehydration. In chapter 3, we highlight the need to monitor hydration status in field studies, and provide ways to do so. Measurement of total body water are the gold standard to assess dehydration but are often not suitable to working in field environments. Plasma osmolarity emerges as a reliable marker of dehydration severity as it scales with body mass loss during water restriction. Other blood or excreta characteristics represent complementary ways to assess hydration status. However, most of these markers would need further validation.

Thermoregulatory response and tolerance to heat exposure show inter-specific, intra-specific and inter-individual variation. Despite substantial inter-individual variation, drivers of this variation seem to be underlooked in the literature. In the fourth chapter of this thesis, we assessed the response and recovery to an acute heat exposure in an arid-adapted passerine, the zebra finch, depending on the sex and age of individuals. Heat exposure promoted hyperthermia and dehydration, and individuals did not fully recover their initial body mass 48h after heat exposure. Heat response did not vary with the age of the individuals despite differences in body temperature and metabolic rates. We report sex-specific differences in heat response, with only females increasing their metabolic rates during exposure. While this is not the first report of sex-differences in heat response, only few studies investigated it, and results are contrasted. Mechanisms underlying these differences are currently unknown and would benefit from further research effort.

Finally, the relationship between climate warming and biodiversity response is complex. Improving our understanding of population vulnerability necessitates to study organism responses at different scales and using a variety of approaches (Figure 1). The prevailing negative effect of high temperature in hot and arid habitat, and predicted increases in thermoregulatory costs suggest that “desert birds persist near the edge of their physiological limit” (Iknayan and Beissinger, 2018). Yet, bird responses in other biomes are more contrasted and highlight a need to model species ecological niches, especially in regard with thermoregulation. At the individual level, characterizing response and tolerance to thermal challenges in laboratory and field setting should be of high priority. Heat exposure and response are likely to influence individual performance and fitness, shaping in turn population responses. In the following sections, we discuss limits of our works and perspectives for future studies.

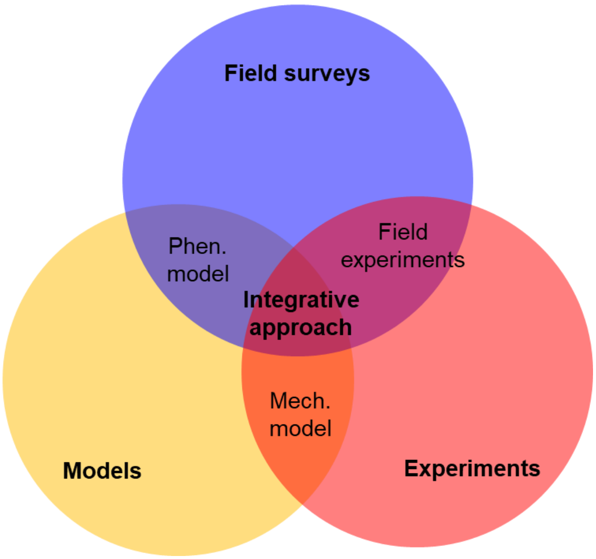

Figure 1. Classes and combinations of approaches used to investigate the ecological consequences of climate change via experiments, models, and field surveys. The inter-sections between classes are: mechanistic models of abiotic and biotic components based on theory and physiological knowledge; phenomenological models based on empirical observations; field experiments; adapted from Stewart et al., 2013.

2. Critical views and perspectives

2.1. High temperature, heat exposure and thermoregulatory costs

When reviewing breeding success association with high temperatures we were not able to restrict analysis to studies assessing the effect of hot events, representing a strong limitation of our study. This is because few studies tested for potential effect of high temperature, and because studies that did were heavily biased towards desert climates. Most importantly, extreme temperature based on the environmental stochasticity do not equate to heat exposure (Figure 2). There is consequently a need to put local climate variability into perspective with meaningful biological thresholds (Cunningham et al., 2013b).

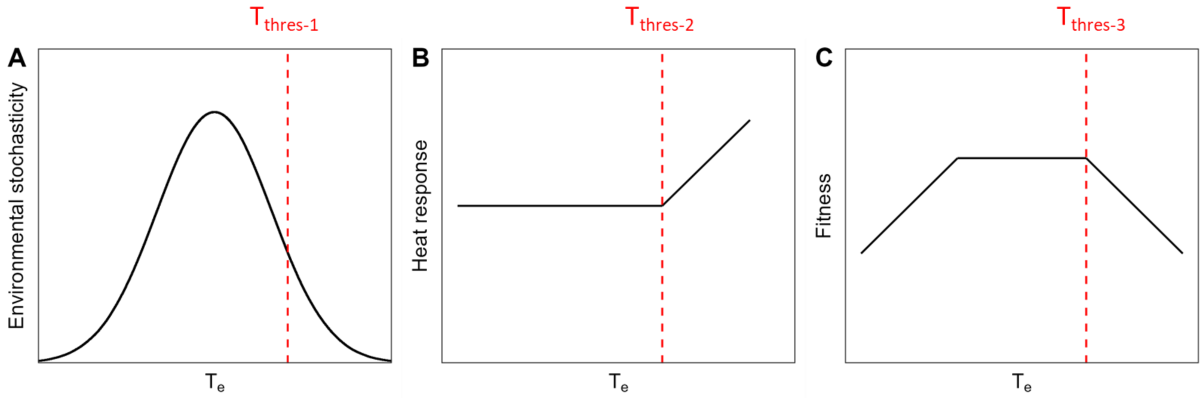

Figure 2. Environmental temperature (Te) stochasticity, species response and associated temperature thresholds (A) Threshold of high environmental temperature (e.g. hot days). In this example, we define $T_{thres-1}$ as the 90th percentile of Te (e.g. Pipoly et al., 2022); (B) Threshold eliciting a heat response (i.e. physiological or behavioral adjustment). For instance, wild zebra finches (*Taeniopygia guttata*) start panting at air temperature of ~34°C (Funghi et al., 2019); (C) Threshold promoting a decreased fitness (e.g. breeding success, survival). For instance, common fiscal (*Lanius collaris*) fledging growth was impaired when exposed to air temperature exceeding 33°C (Cunningham et al., 2013a).

Defining "high temperatures" from an ecophysiological standpoint is a complex task and should be an important focus for future studies. While air temperature (Tair) does not equal environmental temperature (Te). Improving monitoring and modelling of Te represents an important step for understanding thermal challenges in field settings (Conradie et al., 2023; Kearney et al., 2020; Maclean et al., 2021; Mitchell et al., 2024). For instance, the propensity of king penguin (*Aptenodytes patagonicus*) to exhibit heat-dissipation behavior is driven by solar radiation, wind speed, air temperature and their interactions with air temperature, but air temperature itself was a poor predictor of it (Noiret et al., 2024, in prep). While using a mechanistic approach to model exposure to heat events provides great insight on bird potential heat exposure (i.e. based on experimental studies; e.g. days with Te>UCT), it has some limitations. Response of captive birds to heat exposure is not fully representative of wild birds response (e.g. food and water ad libitum, non-heat acclimated birds) and the TNZ has limited applicability to real-life scenario (e.g. fasted and inactive birds; Clusella-Trullas et al., 2021; Mitchell et al., 2018). Phenomenological studies represent necessary and complementary approaches, highlighting the need to monitor behavioral and physiological monitoring of breeding birds and offspring (i.e. based on field observations; e.g. panting behavior, body temperature, hydration status). Ultimately, assessing species and populations response to high temperatures and climate warming requires to relate heat exposure and fitness-related traits (e.g. breeding success; Figure 3).

When we reviewed avian breeding success in response to high temperature, studies in continental and temperate climate were over-represented, and studies in tropical biomes were lacking. This represents a strong limitation of our study, as our results are heavily biased towards studies in North-America and Europe. Increasing research effort in less studied environments, especially in tropical climate were avian diversity is the richest, represents a necessary step when assessing species vulnerability to global changes (Loiseau et al., 2020; Monge et al., 2023). Exposure to high temperatures were strongly associated with negative effects on breeding success in deserts, and multiple studies report signs of heat stress during hot days in such study sites (e.g. Bourne et al., 2021; Sharpe et al., 2019; Sharpe et al., 2021; van de Ven et al., 2020). Conversely, results were more contrasted in cooler biomes, and reports of heat stress seemed less common in the literature. Consequently, we hypothesize that thermal constrains during breeding may differ between biomes. More specifically, the propensity to being heat exposed during breeding, potentially leading to fitness costs (e.g. decreased breeding success) is likely the highest in deserts, and potentially increase with the local temperature maximum on a global scale (Figure 3A). Improving our knowledge on thermal requirements and potential heat exposure would beneficiates from the modelling of ecological and physiological niches of birds (Bennett et al., 2019; Gaston et al., 2009; Kearney and Porter, 2009; Porter and Kearney, 2009). Overall, desert birds seem to “live near the edge of their physiological limits”, potentially explaining their high vulnerability to climate warming (Figure 3B; Iknayan and Beissinger, 2018). Monitoring and modelling of heat exposure in various populations and species on a global scale in necessary to answer these questions, and should represent a major focus for future research.

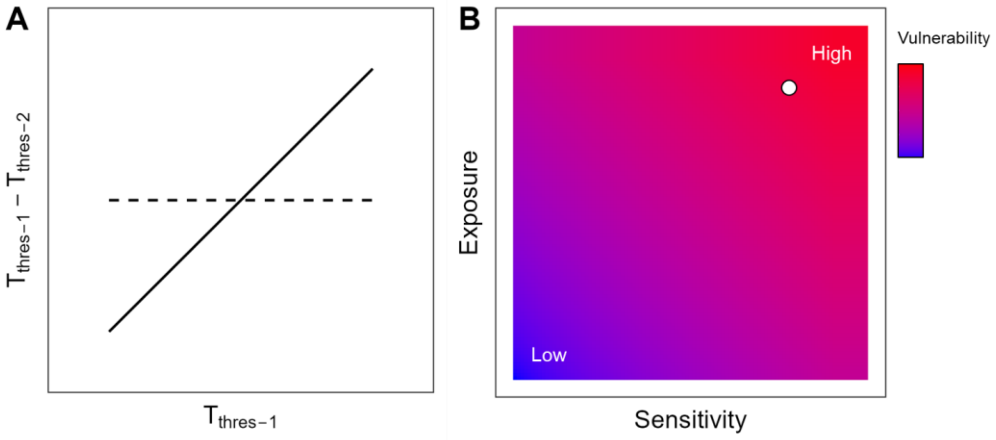

Figure 3. Theoretical representation of species heat exposure and vulnerability to hot events (A) heat exposure in function of the local thermal environment. Heat exposure represents the propensity to be exposed to environmental temperatures eliciting a heat response (e.g. behavioral and physiological adjustments). In this example, heat exposure is illustrated as '$T_{thres-1}$ - $T_{thres-2}$'; dashed line represents a theoretical scenario where species or populations are similarly adapted to their thermal environments, while the solid line represent a theoretical scenario where heat exposure ('$T_{thres-1}$ - $T_{thres-2}$) increase with local temperature extremes ($T_{thres-1}$). Avian UCT increases with local temperature testyfing of a specie adaptation to their thermal environment (Qu and Wiens, 2020; Song, 2018). Yet, there is little variation in UCT compared to LCT, and thermal mismatch between UCT and maximum air temperature in the environment is highest at low latitudes (Araújo et al., 2013; Khaliq et al., 2014). Consequently, species exploiting hotter environments may have a higher propensity to be exposed to environmental temperatures eliciting a heat response; (B) species vulnerability as a function of heat exposure and sensitivity; sensitivity represents the fitness consequences associated with heat exposure. White dot represents a population with high exposure and sensitivity, and therefore high vulnerability to climate warming. For instance, southern yellow-billed hornbills (*Tockus leucomas*) in the Kalahari Desert exhibit heat dissipation behaviors when Tair>34.5°C (50% likelihood of panting; van de Ven et al., 2020). The number of days exceeding 34.5°C has been increasing with climate change at this study site, and exposure to such temperature has deleterious impact on breeding success, predicting a rapid population decline and high risk of local extinction (Pattinson et al., 2022).

Finally, across this thesis, we focused on the potential effects of high temperature on heat response and cooling costs, especially in regard to a potential increase in maximum temperature with climate change. Yet, climate warming is likely to be associated with an increase in minimum (i.e. winter or night-time temperatures). Consequently, understanding and forecasting birds response to climate warming would necessitates to investigate changes in the thermal environments on avian population and thermoregulatory costs as a whole (i.e. heating and cooling costs). We may expect increased cooling costs to be compensated by decreased heating costs to some degree (Figure 4; Levy et al., 2019). For instance, dovekies (*Alle alle*) are expected to see their thermoregulatory costs decrease with climate warming due to reduced cooling costs exceeding the potential increase in cooling costs (Beaman et al., 2024).

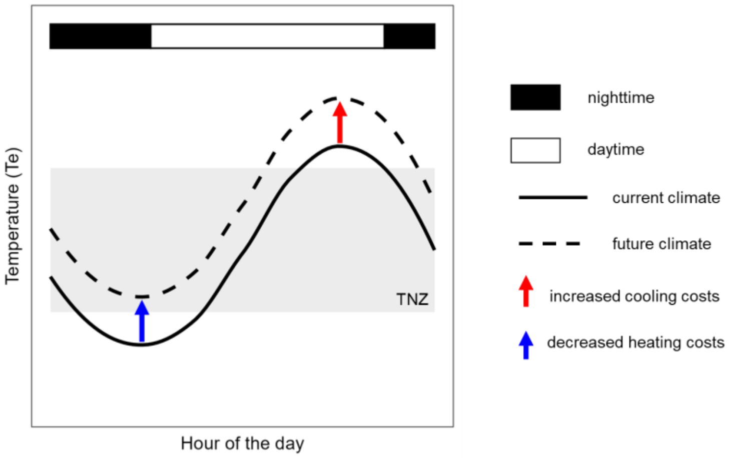

Figure 4. Daily temperature profile and thermoregulatory costs in a context of climate warming. Current and future climate are represented in solid and dashed lines respectively. Thermoneutral zone (TNZ) is represented in grey. Daytime is represented as a white band, and nighttime as a black band. Increasing temperatures may decrease heating cost (blue arrow) and increase cooling costs (red arrow). In this example, we represent daily temperature profile. However, similar relationship may be expected for yearly temperature profile (i.e. warmer winter and summer). Adapted from Levy et al., 2019.

2.2. Dehydration definition and diagnostic

As aforementioned, cooling costs are expected to increase with climate warming, and multiple studies have modelled under current and future climate warming scenarios (Albright et al., 2017; Conradie et al., 2019, 2020; McKechnie and Wolf, 2010). Dehydration is defined as a deficiency in body water, and these studies used varying thresholds of body mass loss to predict ‘moderate’, ‘severe’ or ‘lethal’ dehydration (e.g. loss of 11%, 15% or 22% of body mass). Yet, there is little guidance on the reliability of such dehydration thresholds. Multiple studies report captive birds losing more than 15% of their body mass during water restriction without direct effects on survival (e.g. Arad et al., 1987; Bartholomew and Macmillen, 1960; Mulkey and Huston, 1967; Skadhauge, 1974; Withers, 1983). In chapter 4, we estimated zebra finches to have lost ~6.4% of their total body water during heat exposure. Heat exposure also promoted an increase in plasma osmolarity (~4.6% increase) and promoted thirst, suggesting that individuals were likely dehydrated. However, plasma osmolarity is not only symptom of dehydration but also a key mechanism allowing water conservation. Homeostasis is a dynamic process, and there is a fine line between physiological adjustment and actual dehydration. Experimental studies are therefore needed to identify water-deficit thresholds eliciting a physiological response (i.e. thirst, variation in levels of physiological markers), and thresholds for impaired performance (cognitive, locomotor), health or survival (Figure 5). We measured mitochondrial superoxide production (i.e. a reactive oxygen species), and we isolated red blood cells to potentially assess other markers of the oxidative balance or gene expression in future analyses (e.g. Heat shock proteins; Xie et al., 2017; Xie et al., 2018).

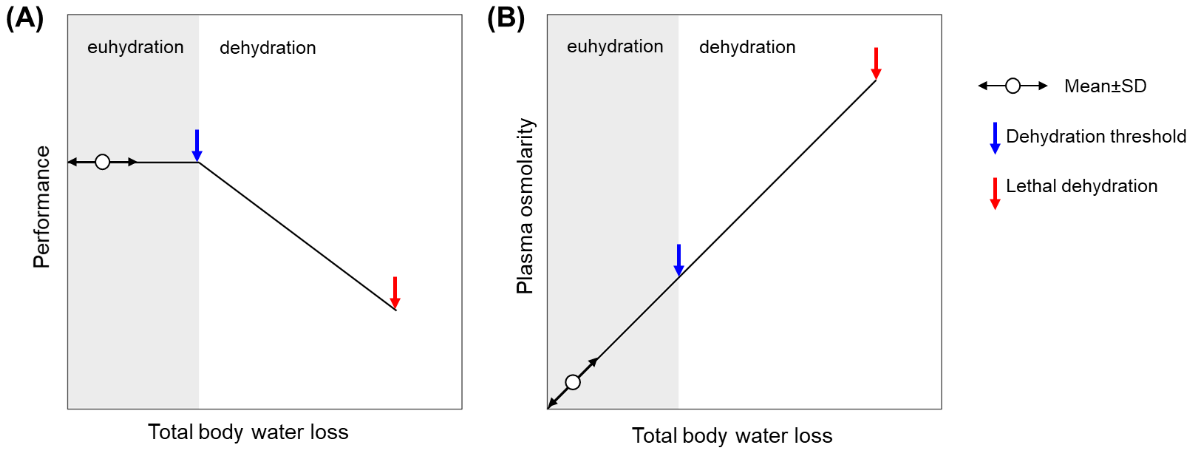

Figure 5. Dehydration threshold and theoretical relationships between total body water loss and (A) performance or (B) plasma osmolarity in birds. Dehydration is defined as a deficiency in total body water. However, improving our diagnostic of dehydration require to identify biologically meaningful thresholds (e.g. dehydration and lethal dehydration threshold). In humans, a TBW loss exceeding 2% impairs performance, promote anti-diuresis and thirst, testifying of a state of dehydration (Cheuvront and Kenefick, 2014; Cheuvront et al., 2010; Cheuvront et al., 2013; Villiger et al., 2018). Current consensus in humans is that a plasma osmolarity exceeding 300mOsm predicted a TBW loss exceeding 2% and thus dehydration (Lacey et al., 2019). Such thresholds are yet to be identified in birds. In chapter 3, we identify plasma osmolarity to be a reliable marker of dehydration for birds. Moreover, plasma osmolarity likely seemed to scale linearly with body water loss in birds.

2.3. Limitation of correlative approaches

In this thesis, we assessed the association between weather, breeding timing and breeding success. Air temperature was positively correlated with breeding success while breeding timing was negatively correlated with it. However, using a correlative approach comes with inherent limitations, as correlation does not imply causation. Moreover, breeding timing and temperature were negatively correlated, therefore representing confounding effects. For future statistical analysis, we will explore statistical procedure to detrend temperature from the calendar date (e.g. difference from mean historic temperature for a specific period). However, dissociating temperature and breeding timing effects would require to experimentally manipulate either breeding timing (e.g. delayed breeding initiation; Verhulst and Nilsson, 2008) or nest temperature (e.g. heating or cooling; Andreasson et al., 2018; Ardia et al., 2009; Nilsson et al., 2008; Rodríguez and Barba, 2016). For future studies, we suggest to experimentally heat great tits nest boxes in both urban and forest environments (Figure 6).

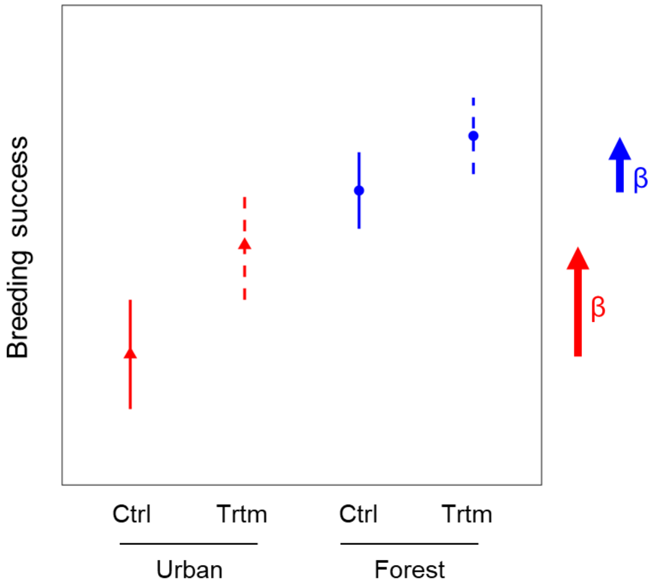

Figure 6. Expected results of a nest warming experiment on great tits breeding success in an urban and forest environment. In this example, we assume an increase of 2°C in heated nests compared to control nests. We expect nest warming to improve breeding success in our system and/or alleviate parental load (e.g. energy expenditure; Bryan and Bryant, 1999). We expect the positive effect of nest warming to be stronger in the forest due to the lower parental and environmental quality (i.e. lower food intake, lower parental quality; Seress et al., 2020). We expect higher variance for urban nests (Thompson et al., 2021). We represent mean ± standard error; Red triangle: urban nest; blue circle: forest nest; solid line: control nests; dashed line: treated nests; arrow: effect size (β).

There are also limitations to the monitoring protocol used. Most specifically in the monitoring of environmental factors (e.g. temperature, food availability and quality, pollution) and parental traits (e.g. behavior, quality). Prey abundance was monitored in 2015 and 2016, but has not been evaluated since (Saulnier et al., 2022). We hypothesize that food availability and synchrony between food abundance and energy requirements represent a key driver of reproductive success in our system. Assessing food abundance in time and space represents a high research effort but is ultimately necessary, and we emphasize the need to develop efficient ways to assess it. Understanding temperature effects would benefit from characterizing the thermal environment with a higher resolution and at the individual level (i.e. outside-nestbox temperature, inside-nestbox temperature and clutch temperature). Some models can be used to estimate microclimate but would need validation from field measurement (Kearney and Porter, 2017; Kearney et al., 2020; Maclean et al., 2021). Nests at our study site are being progressively equipped with temperature loggers, allowing the measurement of nest temperature (Figure 7). As aforementioned, nest temperature is regulated by the 'bird-nest unit' (Deeming, 2004). Assessing costs associated with nest thermoregulation would ultimately require to monitor parental time and energy budget (e.g. energy expenditure, nest attentiveness), physiological state (e.g. body temperature, hydration status) and nest characteristics (e.g. composition, thickness). Smart devices allowing to monitoring parental activity are currently under development, and will hopefully be tested on the field next season.

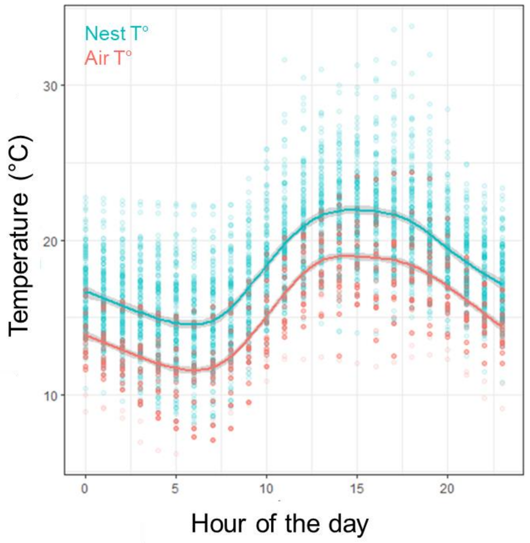

Figure 7. Great tits nest temperature as a function of atmospheric air temperature during nestling rearing at our study site. Nest and air temperature are correlated (p-value<0.001; nest temperature = air temperature*0.96+3.45). Data are from 11 nest in urban and forest environment during the 2023 season.

We made several decisions when analyzing the great tits database. Firstly, we excluded second broods from the data-analysis. This is because reproductive investment (e.g. clutch size) and breeding success are considerably lower in second broods, and second broods have been monitored only since 2021 in our system. Yet, we expect second brood to experience lower food availability and higher temperatures, potentially leading to deleterious effects on great tits breeding success. For instance, clutch size was depressed with warmer temperature only for second broods in barn swallows (*Hirundo rustica*; Møller, 2011). Assessing weather effect on second brood therefore represent interesting perspectives for future analyzes. Secondly, we qualitatively dissociated “urban” and “forest” nests. However, there is considerable variation between nesting environments, especially within the urban environment (e.g. nest in the city center, suburbs or urban parks). Future analysis will use an urbanization index, allowing to consider the degree of urbanization rather than encoding environments as “urban” or “forest”. Finally, individuals breed in artificial nest boxes at our study sites, which likely have different thermal properties and predation risk compared to nests in natural cavities. Moreover, the proximity of our forest site to an urban environment (~20 km). Overall, this raises the question of whether our study system accurately reflects natural conditions. Research project comparing reproduction of great tits between different urban and forest sites across France are currently being coordinated, and will provide an estimation of the quality of our system relative to others.

2.4. Limitation of experimental approaches

In this thesis, we conducted an experiment to assess zebra finch response to an acute heat exposure and subsequent recovery. However, there are multiple limitations to such experiment. Firstly, we used captive birds that had ad libitum access to food and water, meaning their body and physiological condition was likely different from wild birds. Moreover, these birds were maintained at 20-22°C, meaning they were not acclimated birds to heat exposure, which could influence our results (Cooper et al., 2020a; Cooper et al., 2020b). Secondly, there is limited applicability of such an experiment to a natural scenario. Although zebra finches are likely to be exposed 4h at an environmental temperature of 40°C in the wild, respirometry settings are not representative of wild conditions (i.e. individual are in post-absorptive state with very limited locomotor activity). We tried to improve ecological relevance by adjusting the protocol to minimize food restriction, and ensuring that heat exposure coincided with the hottest part of the day. While wild zebra finches decrease their foraging activity during hot events, they seem to increase their water intake, resulting in the maintenance of water homeostasis (Cooper et al., 2019). Future studies are needed to assess costs of exposure to such hot events, and to characterize the thermal environment in wild settings (i.e. environmental temperature rather than air temperature; Cunningham 2021).

One of the main goals of this experiment was to investigate inter-individual variation in heat response, more specifically between age classes and sex. We discuss hereafter limitations of our experimental design and data analysis. Firstly, while we did not report age-related differences in reaction norm to an exposure at 40°C, we did not assess non-evaporative heat dissipation, nor did we dissociate pathways of evaporative heat dissipation (cutaneous and respiratory evaporation), which could potentially reveal differences in responses (e.g. in humans, cutaneous evaporative heat dissipation decrease with age; Cramer et al., 2022). Estimation of dry and wet thermal conductance would provide valuable information on evaporative and non-evaporative heat dissipation (Cooper et al., 2020a; Tattersall et al., 2012). Use of specifically designed respirometry masks would allow to dissociate cutaneous and respiratory evaporative heat dissipation (e.g. Wojciechowski et al., 2021). Secondly, we did not assess heat tolerance limits during this experiment. While we do not report age-specific response to heat, ambient temperature of 40°C do not represent extreme temperature as the heat tolerance limit approximate ~45°C in zebra finches (HTL; i.e. maximum ambient temperature that individuals can tolerate during acute exposure; Cade et al., 1965). Future experiments are needed to assess whether old individuals have a lower heat tolerance. We suggest to evaluate individuals HTL, maximum body temperature, maximum evaporative water loss (EWL) and evaporative scope (i.e. difference between minimum and maximum EWL).

Finally, our individuals were divided into two age classes (<2 year-old versus ≥5 year-old). While senescence patterns have been identified for individuals of that age in zebra finches, the decline in performance commonly varies non-linearly with age, and our individuals may not be “old enough” to highlight differences in heat response (Lemaître et al., 2020). Additionally, we used a cross-sectional experimental design which allow the assessment of senescence at the population level only (Figure 8; Cam et al., 2002; Nussey et al., 2008). Quoting Nussey et al (2008): “Ageing is a within-individual process and the accurate measurement of within-individual changes in phenotype across ages is therefore crucial to its study”. Future studies should therefore prioritize the use of a longitudinal design when possible.

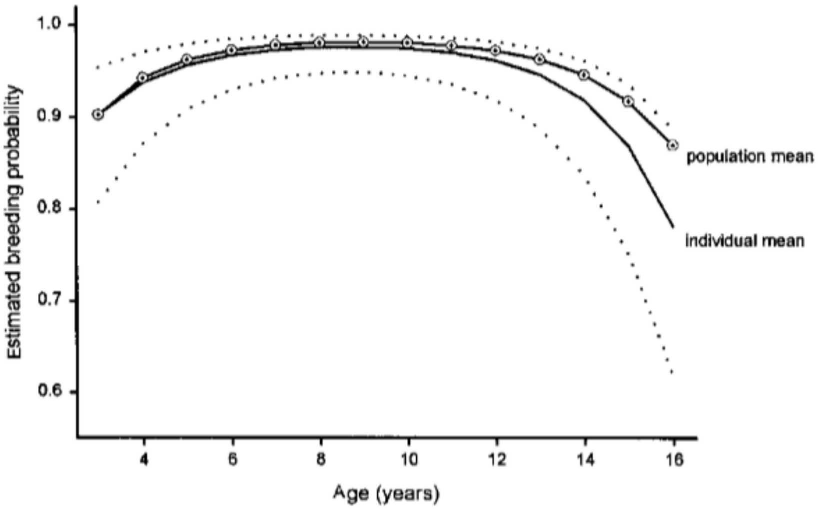

Figure 8. Influence of age on breeding probability in black-legged kittiwakes (*Rissa tridactyla*). Group-specific rate (circled data points) correspond to the pattern observed at the population level. Individual-specific rates (the mean is indicated by the solid line and the quartiles by the dashed lines) describe the influence of age within individuals. Breeding probability (after recruitment) increases in younger individuals, levels off, and declines at advanced ages. The population-level breeding rate underestimates the decline in older age classes expressed at the individual level. From Cam et al., 2002.

2.5. Long-term responses

In this thesis, we focused on the response of birds to high temperatures from the physiological response to heat exposure to ecological consequences such as breeding success. Understanding species responses would benefit from an increased knowledge on adaptation and plasticity to thermal challenges. There are several reports of acclimation or acclimatization of the thermal physiology in avian species (Cooper et al., 2020a; Cooper et al., 2020b; González-Medina et al., 2023; Noakes et al., 2016), and birds seem adapted to their local thermal environment (Khaliq et al., 2014; Song, 2018; Sunday et al., 2019). For instance, thermal environment varies greatly within great tits geographical range of distribution, and whether great tits show intra-specific adaptation to local thermal challenges is currently unknown (Figure 9). Moreover, early-life exposure to thermal challenges may influence life-trajectory and thermoregulatory performance at the adult stage (Figure 10; Al Amaz and Mishra, 2024; Khalil et al., 2024; Nord and Giroud, 2020). In summary, assessing adaptation and plasticity to thermal challenges represent exciting perspectives for future studies.

Climate change has been associated with changes in several phenotypic traits, such as birds morphology or phenology (e.g. Charmantier and Gienapp, 2014; Weeks et al., 2019). Evaluating whether changes in phenotypic traits are adaptative is of main importance when predicting population and species response to climate change (Radchuk et al., 2019). At our study site, temperature increased with time, great tits seem to breed earlier in warmer season, and breeding success was correlated with breeding timing (earlier breeders had a higher breeding success). Assessing whether great tits breed earlier with time, whether phenological advancement increases of buffers potential environmental mismatches (e.g. with weather or food availability), and the resulting fitness consequences are key perspectives for future studies. Finally, future studies should focus on integrating reproductive success into broader demographic processes, providing insights into population dynamic (Kentie et al., 2018; Ridley et al., 2021b).

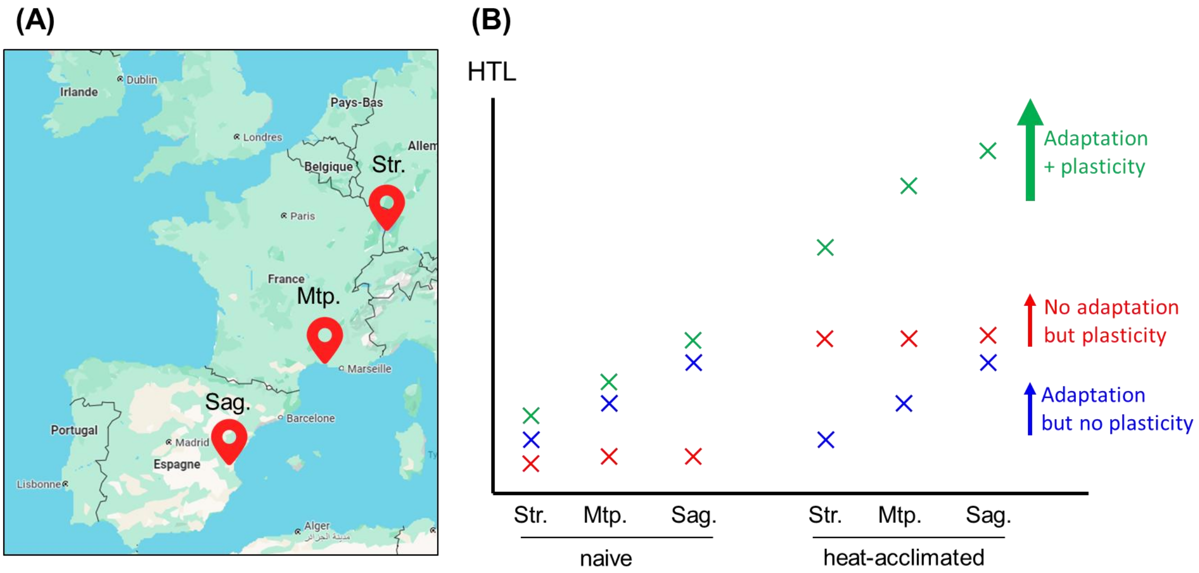

Figure 9. Example of a common garden experimental design to assess adaptation and plasticity to heat exposure in great tits (*Parus major*). (A) Eggs would be sampled from monitoring programs in Strasbourg, Montpellier and Sagunto; all eggs would experience the same artificial incubation and hand-feeding during growth; (B) Predicted heat tolerance limit (HTL) before or after repeated heat exposure in various scenario. HTL represent the maximum ambient temperature individuals can tolerate during an acute exposure.

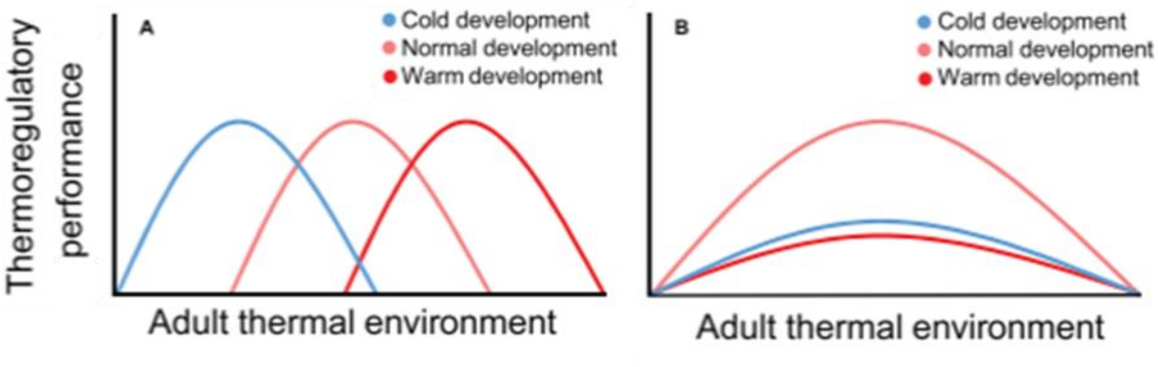

Figure 10. Possible effects of the thermal environment during development on thermoregulatory performance in adulthood. Under the environmental matching hypothesis (A), adult performance is better when the thermal environment matches that in which the individual developed. Under the silver spoon hypothesis (B), both colder-than-normal and warmer-than-normal developmental temperatures act suppressively on the pre- and/or postnatal phenotype, such that individuals that developed in non constraining thermal regimes (here, "normal") consistently perform better than cold- and warm-reared individuals as adults. Adapted from Nord and Giroud, 2020.

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RÉSUMÉ EN FRANCAIS

Le changement climatique est l'un des principaux facteurs de la perte actuelle de biodiversité. Le changement climatique se caractérise notamment par une augmentation des températures globales mais aussi augmentation de la fréquence et intensité des vagues de chaleur. Dans ce contexte, nous avons cherché à étudier les effets des températures élevées sur les oiseaux, de la réponse physiologique jusqu'aux conséquences écologiques. Nous nous focalisons sur les oiseaux car ils sont considérés comme « espèce sentinelles », c'est-à-dire qu'ils intègrent les changements environnementaux au niveau individuel et populationnel (e.g. comportement, physiology, reproduction, démographie).

Dans le premier chapitre de cette thèse, nous examinons l'association entre les températures élevées et le succès de la reproduction chez les oiseaux à l'échelle globale. L'association entre les températures élevées et le succès de la reproduction est probablement multifactorielle, et potentiellement motivée par des effets directs médiés par la thermorégulation des espèces, ou par des effets indirects médiés par des changements dans les facteurs biotiques et abiotiques (e.g. via phénologie et les interactions trophiques). L'exposition à des températures élevées semble être plus susceptible d'avoir des effets délétères sur la reproduction des oiseaux dans les biomes chauds et arides, probablement parce qu'elle peut induire un stress thermique. En revanche, les résultats semblent plus contrastés dans les biomes plus froids, probablement parce que certains oiseaux reproducteurs peuvent bénéficier d'une diminution de l'énergie dédié à la thermogénèse (i.e. « thermal relief »). L'amélioration de nos connaissances sur l'exposition et la réponse des espèces aux températures élevées en fonction de leur environnement thermique local représente un axe de recherche important pour de futures études.

Dans le deuxième chapitre, nous avons évalué l'importance des conditions météorologiques sur le succès de la reproduction des mésanges charbonnières (*Parus major*). Pour cela, nous avons analyser une base de données à long-terme sur la reproduction des mésanges long d'un gradient d'urbanisation à Strasbourg. Les températures élevées semblent corréler positivement avec succès reproducteur. En revanche, cela semble être l'inverse pour la date de ponte ou d'éclosion, qui semble corréler négativement avec le succès reproducteur, les nids les plus tardifs ayant le plus faible succès. Cependant, l'association entre la température et la date de ponte avec le succès de la reproduction semble être contrastée entre les environnements urbains et forestier. Ces résultats contrastés sont probablement dus à des différences de qualité individuelle et environnementale. Démêler les effets du timing de la reproduction et de la température nécessite d'améliorer le protocole de suivi de ces populations, notamment en améliorant le suivi météorologique et en mesurant la disponibilité alimentaire au cours de la saison. Finalement, il existe des limites inhérentes aux approches corrélatives, et la vérification de ces hypothèses nécessiterait la réalisation d'expériences sur le terrain, telles que la manipulation des températures des nichoirs.

Globalement, pour comprendre et prévoir l'impact du changement climatique sur les populations d'oiseaux, il est nécessaire de développer et de mettre en œuvre des moyens de distinguer les effets directs et indirects. Nous avons donc axé le deuxième thème de cette thèse sur les effets directs sur les oiseaux, en tant que réponse physiologique à l'exposition à la chaleur. Plus particulièrement, lors d'une exposition à la chaleur, la plupart des oiseaux semblent être confrontés à un compromis entre l'hyperthermie et la déshydratation. Au chapitre 3, nous soulignons la nécessité d’évaluer l'état d'hydratation dans les études sur le terrain et nous proposons des méthodes pour y parvenir. La mesure de l'eau corporelle totale est la méthode référence pour évaluer la déshydratation, mais n'est facilement adaptable aux études de terrain. L'osmolarité plasmatique apparaît comme un marqueur fiable de la sévérité de la déshydratation, car elle corrèle avec la perte de masse corporelle lors d'une période de restriction hydrique. D'autres caractéristiques du sang ou des excréments représentent de potentiels moyens complémentaires afin d'évaluer l'état d'hydratation. Toutefois, des études supplémentaires sont nécessaires afin d’évaluer leur fiabilité.

La réponse thermorégulatrice et la tolérance à l'exposition à la chaleur présentent des variations interspécifiques, intraspécifiques et interindividuelles. Malgré une variation interindividuelle substantielle, les facteurs de cette variation semblent être négligés dans la littérature. Dans le quatrième chapitre de cette thèse, nous avons évalué la réponse et la récupération à une exposition aiguë à la chaleur chez un passereau adapté à l'aridité, le diamant mandarin, en fonction du sexe et de l'âge des individus. Après exposition à la chaleur, les individus étaient hyperthermiques et déshydratés, et ces individus n’avait pas complètement récupéré leur masse corporelle initiale après 48h. Heat response did not vary with the age of the individuals despite differences in body temperature and metabolic rates

La réponse à la chaleur était indépendante de l’âge des individus, malgré le fait que les individus plus âgés aient une température corporelle et une activité métabolique plus faible. Seules les femelles augmentant leur activité métabolique pendant l'exposition à la chaleur, ce qui semble souligner des différences de physiologie de la thermorégulation en fonction du sexe chez les diamants mandarins. Bien qu'il ne s'agisse pas du premier rapport sur les différences de réaction à la chaleur entre les sexes, seules quelques études ont examiné cette question et les résultats sont contrastés. Les mécanismes sous-jacents à ces différences sont actuellement inconnus et bénéficieraient d'un effort de recherche supplémentaire.

Enfin, la relation entre le réchauffement climatique et la réponse de la biodiversité est complexe. Pour mieux comprendre la vulnérabilité des populations, il est nécessaire d'étudier les réponses des organismes à différentes échelles et en utilisant diverses approches. Les vagues de chaleurs semble avoir des effets négatifs marqués chez les populations exploitant des milieux désertiques, et les augmentations prévues des coûts de thermorégulation suggèrent une forte vulnérabilité de ces populations. Les réponses des oiseaux dans d'autres biomes sont plus contrastées et soulignent la nécessité de modéliser les niches écologiques des espèces, en particulier selon de prisme de la physiologie de la thermoregulation. Au niveau individuel, la caractérisation de la réponse et de la tolérance aux vagues de chaleurs en laboratoire et sur le terrain devrait être une priorité. L'exposition et la réponse à la chaleur sont susceptibles d'influencer les performances et la condition physique de l'individu, façonnant les réponses au niveau populationnel.

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Adrien LEVILLAIN

Influence of high temperatures on avian species: from physiological responses to ecological consequences

Abstract

Climate change emerges as one of the main drivers of the current erosion of biodiversity. In this thesis, we study birds response to high temperatures, from the physiological mechanisms to the ecological consequences. We review the influence of high temperature on avian breeding success on a global scale. Effect of high temperature on breeding success is likely multifactorial, and reproduction in desert seems strongly depressed during high temperature events, highlighting the vulnerability of desert species to climate warming. Potential impact of climate change are likely to interact with urbanization. We consequently assessed weather effects on great tit (*Parus major*) reproductive success in a temperate climate across an urbanization gradient. Breeding initiation advanced with warmer temperature and reproductive success seem to increase with temperature, but results were contrasted between urban and forest systems. Overall, cooling requirements, hyperthermia and dehydration risk are predicted to increase with climate change. We review, identify and highlight the need to monitor physiological markers of avian dehydration. Finally, we assess zebra finches (*Taenopygia guttata*), and arid-adapted bird, response to an acute exposure. Response to heat was sex-dependent, and ultimately promoted hyperthermia and dehydration. This work underscores the need for a multi-scale and integrative approach to better understand and predict climate change impacts on birds.

Keywords: Ecology, Physiology, Ecophysiology, Climate change, Climate warming, Avian, Bird, Heat stress, Thermoregulation, Reproduction, Breeding success.

Résumé

Le changement climatique apparaît comme l'un des principaux de l'érosion actuelle de la biodiversité. Dans cette thèse, nous étudions la réponse des oiseaux aux températures élevées, des mécanismes physiologiques aux conséquences écologiques. Nous examinons l'influence des températures élevées sur le succès de la reproduction des oiseaux à l'échelle globale. L'effet des températures élevées sur le succès reproduction est probablement multifactoriel, et la reproduction dans les déserts semble fortement impacté pendant les épisodes de températures élevées, soulignant la vulnérabilité des oiseaux désertiques au réchauffement climatique. L'impact potentiel du changement climatique étant susceptible d'interagir avec l'urbanisation, nous avons évalué les effets des conditions météorologiques sur la reproduction de la mésange charbonnière (*Parus major*) le long d'un gradient d'urbanisation. L'initiation de la reproduction est plus précoce lorsque la température est plus élevée et le succès de la reproduction semble augmenter avec la température, mais les résultats sont contrastés entre les systèmes urbains et forestiers. A travers une revue de la littérature, nous soulignons la nécessité de surveiller les marqueurs physiologiques de la déshydratation et identifions des marqueurs adaptés. Enfin, nous évaluons la réponse à une vague de chaleur simulé chez une espèce désertique, le diamant mandarin (*Taenopygia guttata*). L'exposition au stress thermique induit une hyperthermie et déshydratation chez le diamant mandarin, mais la réponse semble dépendre du sexe. Ce travail souligne la nécessité d'une approche multi-échelle et intégrative pour mieux comprendre et prévoir les impacts du changement climatique sur les oiseaux.

Mots-clefs: Ecologie, Physiologie, Ecophysiologie, Changement climatique, Réchauffement climatique, Aviaire, Oiseau, Stress thermique, Thermoregulation, Reproduction, Succès reproducteur.