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The Complex Relationship Between High Temperatures and Avian Breeding Success: Insights From a Global Review

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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 the breeding success of wild birds. We focus on avian species, as they are widespread throughout the world and benefit from numerous long-term monitoring programs. 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 the effect of high temperatures. High temperatures were defined in regard to the average temperature recorded at the study site. The species thermoregulation was taken into account depending on the information available. We were able to extract the local climate type (i.e., arid, temperate, continental, polar, and tropical) for 135 studies. Temperate and continental climates were over-represented, and studies were more likely to investigate the relationship between hot events and breeding success in arid environments. The relationship between high temperatures and breeding success is highly complex, as it most likely involves a combination of "direct" effects (mediated through thermoregulation) and "indirect" effects (mediated through phenology, food availability, trophic interactions) and may vary depending on the system studied. Finally, we present some considerations for future studies, in particular regarding species' sensitivity at high temperatures.

1 | Introduction

Climate change emerges as one of the main drivers of the current biodiversity erosion (Maxwell et al. 2016). The main environmental changes associated with climate change are 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).

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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 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, see glossary; McKechnie and Wolf 2019). In ecological studies, different authors refer to "high temperature" as relative to the species sensitivity (e.g., thermoregulatory response and fitness costs) or to the local climate variability. Defining "high temperatures" in an ecophysiological context is a real challenge, especially when focusing on a global scale. First, studies that 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 thermoneutral zone (TNZ; Mitchell et al. 2024). Additionally, 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). Finally, 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 temperatures 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, Gerson, et al. 2021; Piatt et al. 2020) and complete breeding failures (McCowan and Griffith 2021; Romano et al. 2020; Sharpe et al. 2021) of various bird species. Overall, reproductive success is a key factor when assessing avian species population viability, and temperature seems to be an important mediator of reproductive success 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, Hegemann, et al. 2020), growth and development (Hepp et al. 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 and duration of the breeding season), abiotic factors (e.g., snow coverage and water availability) or trophic interactions (e.g., food availability, predation, parasitism, and competition). Finally, we briefly present perspectives and considerations for future studies, ranging from experimental design to data analysis and insist on the importance of disentangling relationships within a system.

2 | Material and Methods

2.1 | 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

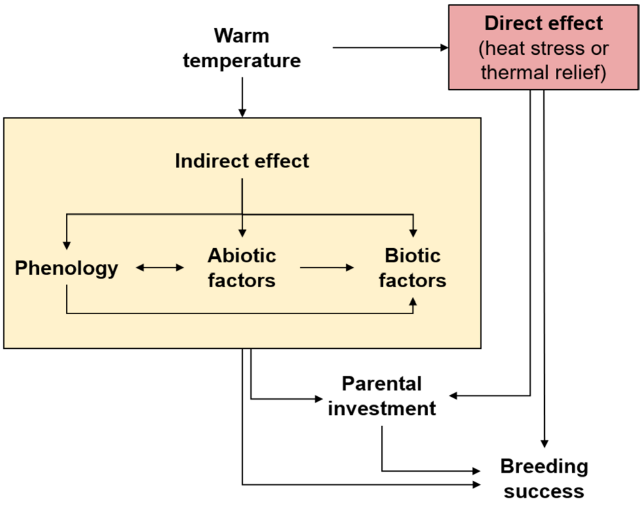

FIGURE 1 | Schematic representation of the mechanisms that potentially mediate the link between high temperature and breeding success. High temperature can influence breeding success through direct (i.e., via thermoregulation of parents and offspring) or indirect ways such as variation in phenology (e.g.,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

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, that is, 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, that is, 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"; and (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 (Data S1). 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 (Data S2).

We defined five 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.

2.2 | 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, behavioral 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).

2.3 | 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 100 km, or with a range exceeding 5000 km^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 climate 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 were conducted in QGIS (Version 3.16.16).

3 | Overview of the Studies

3.1 | 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 < 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%; $n = 165/229$), and 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 a 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).

3.2 | 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. First, 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 authors generally do not regard hot events as potential drivers 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). Second, birds in cold climates may be less likely to

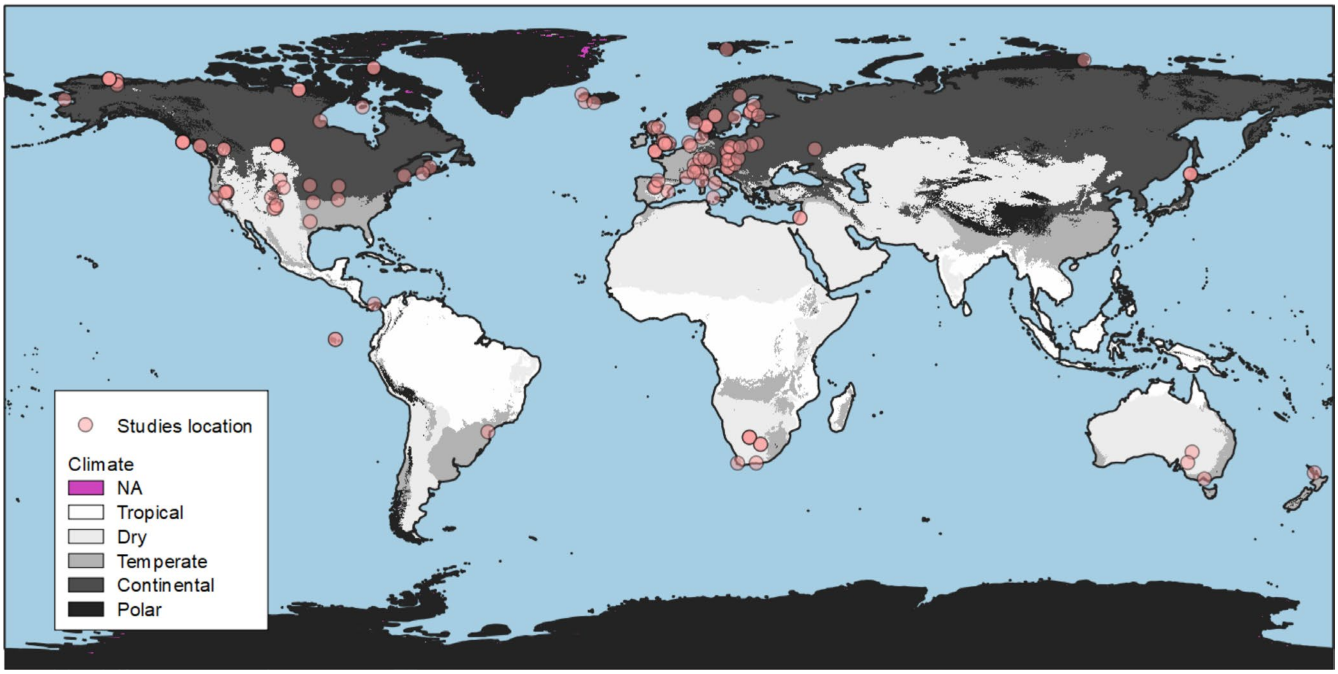

FIGURE 2 | Global map of the study locations ($n=135$). Symbols and colors represent the associated correlation sign between high air temperature and overall breeding success. The Köppen-Geiger climate classification is represented in shades of gray, and studies location as dots. Location with multiple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

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)

Note: T_a: air temperature. *Hot events: T_a likely to promote heat stress (behavioral signs of heat dissipation, signs of dehydration or hyperthermia, T_a > UCT), hot days (e.g., 90th percentile of the hottest days) or based on authors description (e.g., "heatwave"). 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)

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

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 investigating trophic factors (i.e., food availability, predation or competition) highlight the need to study relationships between breeding success and weather effects at the ecosystem level.

4 | Mechanisms Underlying the Relationship Between Temperature and Breeding Success

4.1 | Direct Effects: Thermal Environment and Parental Care

4.1.1 | 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 behaviors (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. 2022). 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).

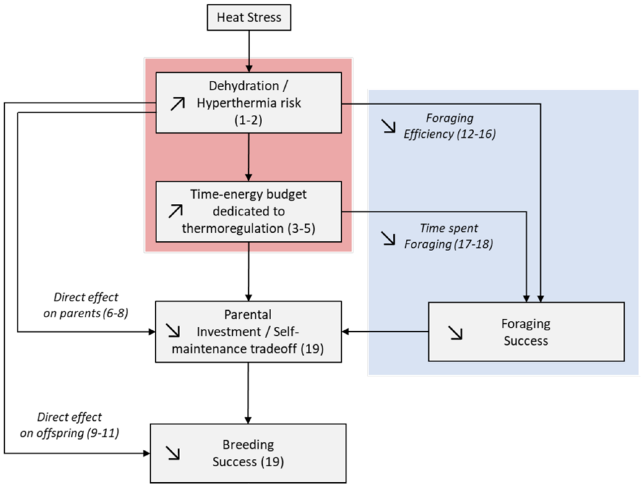

FIGURE 3 | Schematic representation of the direct mechanisms (i.e., through thermoregulation) that mediates the link between heat stress and breeding success. The red and blue boxes correspond respectively to increased expenses and decreased resources. References: (1) Gerson et al. (2019) (2) McKechnie 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, Ridley, McKechnie, et al. (2021) (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.

Decreased breeding frequency and probability of second brooding have been reported during warm periods (e.g., Chambers, Gibbs, et al. 2008; Marques-Santos et al. 2021; Mastrantonis et al. 2019). Clutch sizes were smaller when breeding season was reported to be warmer in several studies (e.g., Chambers, Quin, et al. 2008; 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), including some reports of catastrophic egg loss (McCowan and Griffith 2021; 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, Ridley, McKechnie, et al. 2021; 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, Ridley, McKechnie, et al. 2021; 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, Ridley, McKechnie, et al. 2021; 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, Ridley, Spottiswoode, et al. 2021; 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 a decreasing nestling provisioning rate at high temperatures (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 proportion of time to thermoregulatory behaviors, and hyperthermia may constrain offspring provisioning even for temperate birds (Andreasson, Nilsson, and Nord 2020; Tapper et al. 2020a, 2020b). This could ultimately lead to a reduction in nestling growth and survival (Bourne, Ridley, Spottiswoode, et al. 2021; 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, Martin, et al. 2013).

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 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 were related to decreased growth and reduced fledging and first-year survival for the Southern pied babbler (Bourne et al. 2020a, 2020b). 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).

4.1.2 | 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°C–40°C range, it is thought to be optimal in much narrower ranges (Durant et al. 2013; Webb 1987). For instance, the optimal range of incubation temperature is ~35°C–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). Consequently, the energy expenditure of parents during incubation can be as high as during chick rearing (Williams and Vézina 2001). Additionally, nestlings reach thermo-independence during post-natal development, although the extent to which they are dependent on parental warming varies alongside the precocial-altricial continuum (Ducatez and Field 2021; Price and Dzialowski 2017; Starck and Ricklefs 1998). Overall, breeding birds usually show increases in energy expenditure compared to non-breeding individuals, and the energetic cost of incubation seems 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. 2009; Bryan and Bryant 1999). For instance, the 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.

4.2 | Indirect Effects: Phenology and Trophic Interaction

4.2.1 | 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, that is, 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 favor 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 is 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.

4.2.2 | Trophic Interactions

4.2.2.1 | Food Availability. Temperature may drive breeding success through variation in food availability or quality, but multiple mechanisms may underlie 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 diets 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 underlie 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).

4.2.2.2 | 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 an alternative prey.

4.2.2.3 | 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 (*Tachycineta bicolor*) nests peaked at 25°C and decreased at both higher and lower temperatures (Dawson et al. 2005). The density of blowfly larvae was also more abundant around 23°C–25°C in Blue Tits (*Cyanistes caeruleus*) nests, 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.

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

5 | Summary

Our knowledge seems spatially confined to specific areas of the globe, mainly North America and Europe. It is crucial to increase research effort in overlooked areas and biomes, especially in tropical environments. Studies vary widely in their data acquisition and analysis, highlighting the need to establish guidelines for future studies. Most notably, the proportion of studies investigating hot events effects was considerably higher in arid environments. In such environments, authors may be more likely to use the terms “heatwaves”, “extreme events”, or “hot days”. High temperature is defined as relative to the species thermoregulation (i.e., likely to promote heat stress) in some studies and relative to the local temperature variability (e.g., hot days as 90th percentile of hottest days) in others. These definitions are, of course, not equivalent since a hot day does not necessarily promote heat stress and may even alleviate thermoregulatory costs depending on the system studied. Surprisingly, very few studies examined behavioral or physiological markers of heat exposure alongside reproductive success, resulting in limited insights into the potential occurrence of heat stress. Finally, multiple studies report complex and multifactorial relationships, with high temperature influencing breeding success through its interaction with phenology or trophic relationships. Overall, understanding and predicting the effects of high temperatures on avian breeding success require identifying the main drivers of reproductive performance, characterizing thermal constraints during reproduction, and evaluating their potential interactions. We hereafter present considerations for future studies.

6 | Considerations for Future Studies

Potential effects of high temperature on avian breeding success and underlying mechanisms may vary depending on the local climate. High temperatures seem to be consistently linked with negative effects on desert bird reproduction (e.g., McCowan and Griffith 2021; Pattinson et al. 2022; Ridley et al. 2021), while results seem more mixed in cooler climates (e.g., Pipoly et al. 2013, 2022). This is supported 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). Furthermore, while reproductive success has been positively associated with elevation in hot desert, a negative association is commonly reported in continental climates, suggesting different thermal constraints depending on the system studied (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 UCT. Although avian UCT has been reported to scales with the temperature in their habitat, it appears to be relatively conserved across species (Araújo et al. 2013; Qu and Wiens 2020; Song 2018; Sunday et al. 2019). For instance, in average, desert passerines seem to have a similar UCT as temperate passerines (desert: average UCT ~37.6°C across 30 species, McKechnie, Rushworth, et al. 2021; temperate: 37.7°C across 26 species, Cabello-Vergel et al. 2022; Pollock et al. 2021; Data S3). Thus, desert birds may “persist near the edge of their physiological limit” (Iknayan and Beissinger 2018). Overall, hot events may be more likely to promote heat stress in deserts, and 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. 2021).

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 an artifact 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 behavior (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 represents 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. In some instances, 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 (e.g., Conrey et al. 2016; Cunningham, Martin, et al. 2013). 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, Kruger, et al. 2013; Cunningham, Martin, et al. 2013). In addition, water availability most likely interacts 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 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 environmental stochasticity does 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, Kruger, et al. 2013). We strongly recommend systematically reporting temperature variables and summary statistics (e.g., mean temperature, average of maximum or minimum) and putting 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), and 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, Ridley, Spottiswoode, 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, Gerson, et al. 2021).

Author Contributions

Adrien Levillain: conceptualization (equal), data curation (lead), formal analysis (lead), investigation (lead), methodology (equal), supervision (supporting), validation (supporting), writing – original draft (lead), writing – review and editing (equal). **Sophie Reichert:** conceptualization (equal), funding acquisition (equal), methodology (equal), project administration (equal), supervision (equal), validation (equal), writing – review and editing (equal). **Sylvie Massemin:** conceptualization (equal), funding acquisition (equal), methodology (equal), project administration (equal), supervision (equal), validation (equal), writing – review and editing (equal).

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

Data are available as supporting information.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Data S1.** Dataset of articles screened for eligibility. **Data S2.** Dataset of all studies retained. **Data S3.** Dataset of passerines UCT.