

1 **Roasting in nest boxes: physiological, behavioural and fitness consequences of extreme heat in**
2 **cavity-nesting birds and mitigation strategies**

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16 **Abstract**

17 Artificial nest boxes are widely used to mitigate the loss of natural cavities caused by deforestation
18 and habitat degradation, and they have become an important tool in both avian conservation and
19 ecological research. However, the capacity of nest boxes to provide suitable microclimatic conditions
20 for breeding birds is increasingly challenged by climate change. In particular, more frequent and
21 severe episodes of extreme heat may expose developing embryos and nestlings to potentially harmful
22 thermal conditions and may also reduce parental food provisioning. In this review, we synthesised
23 current knowledge on the impacts of extreme heat on cavity-nesting birds breeding in nest boxes.
24 Following a mechanistic framework, we first examined thermoregulatory responses to high
25 temperatures, including evaporative cooling and facultative hyperthermia, together with dehydration
26 risk and cellular stress responses. We placed particular emphasis on the sublethal effects of early-life
27 exposure to extreme heat and their potential long-term fitness consequences. We further synthesised
28 evidence for behavioural responses of parents and nestlings, including changes in parental care, food
29 provisioning, and nestling behaviour, and considered their potential consequences for offspring
30 development, survival, and subsequent fitness. We also examined evidence for heat-related mortality
31 and potential population-level consequences, identifying ecological factors associated with variation
32 in vulnerability. Finally, we evaluated strategies for reducing harmful thermal exposure, including
33 changes in nest-box materials, wall thickness, surface reflectance, shading and placement. Integrating
34 species-specific thermal physiology with nest-box design and placement will be important for
35 maintaining the conservation value of artificial nesting structures under ongoing climate change.

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37 **Keywords:** cavity-nesting birds; climate change; extreme heat; nest box; thermal physiology;
38 thermoregulation; heat wave

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1. Introduction

Deforestation and habitat degradation have significantly contributed to the loss of natural structures used by animals for nesting and refuge, such as tree hollows, rock crevices and natural burrows (Cowan et al. 2021; Ke et al. 2023). Consequently, many species of vertebrates, in particular cavity-nesting birds, have experienced population declines attributable to the scarcity of suitable nesting sites (Lindenmayer et al. 1997; Cockle et al. 2011; Frick et al. 2020). A commonly implemented mitigation strategy is the deployment of artificial cavities, including nest boxes, bat boxes and artificial burrows, which are human-made structures designed to provide suitable nesting sites for cavity-dependent species. The installation of artificial cavities has progressively expanded since the early 20th century, facilitating ecological monitoring while increasing the availability of nesting sites and thereby supporting the recovery of declining populations (Lambrechts et al. 2010; Ruegger 2016; Woolley et al. 2024). Hereafter, we use the term ‘nest box’ to refer broadly to artificial nesting structures for cavity-nesting birds, including artificial burrows.

Nest boxes have been successfully used in bird conservation worldwide. For example, the occupancy and survival of forest insectivorous birds have been shown to increase with the provisioning of nest boxes in managed pine forests of Europe and North America (Thompson et al. 2023). Similarly, the deployment of nest boxes, in the form of artificial burrows, has successfully supported conservation programs for endangered African penguins (*Spheniscus demersus*; Pichegru et al., 2024). In Australia, nest boxes are used by several species of endangered birds as well as by small mammalian taxa (Goldingay et al. 2020). These examples demonstrate the capacity of nest boxes to increase the availability of suitable breeding sites and contribute to population persistence and recovery. However, their effectiveness can vary among species, habitats, nest box characteristics, and local environmental conditions (Cowan et al. 2021; Zhang et al. 2023a). In light of climate change and associated extreme events, understanding how nest box design and placement can be optimized is critical for maintaining their effectiveness as long-term conservation tools.

67 One key aspect of nest box suitability for breeding species is their capacity to buffer thermal
68 variability. Natural cavities nests may provide enhanced microclimatic buffering and are more
69 common than other enclosed nest types in arid and cold environments across both passerine and non-
70 passerine birds (Chia et al. 2026). However, studies comparing microclimates inside nest boxes and
71 natural cavities have generally reported lower thermal buffering capacity in artificial structures (Table
72 1). In particular, nest boxes may provide less stable thermal conditions during periods of extreme heat
73 (Sudyka et al. 2023; Corregidor-Castro et al. 2026).

74 Ongoing global climate change is driving an increase in the frequency, intensity and duration
75 of heat waves (Perkins-Kirkpatrick and Lewis 2020; Heinicke et al. 2026), which are generally
76 defined as periods of consecutive days during which temperatures rise substantially above the
77 seasonal average for a given region (Perkins and Alexander 2013). Although formal definitions of a
78 heat wave vary, they are inherently relative to regional temperature conditions. For example,
79 temperatures of ~30 °C may constitute a summer heat wave in Northern Europe but fall within the
80 normal summer range in Southern Europe. Therefore, to avoid ambiguity, we here refer more
81 generally to extreme heat which may expose birds occupying nest boxes to thermal conditions that
82 challenge their thermoregulatory capacity and, under severe conditions, threaten survival (McCowan
83 and Griffith 2021; Pattinson et al. 2022).

84 When environmental temperature (T_{air}) approaches or exceeds body temperature (T_b), heat
85 dissipation becomes increasingly constrained, requiring greater reliance on physiological evaporative
86 cooling mechanisms to dissipate metabolic and environmental heat loads (McKechnie and Wolf
87 2019). Accordingly, evaporative heat loss increases markedly under high temperature conditions,
88 particularly when operative temperature (T_e), which represents the combined effects of air
89 temperature, radiation, conduction, and convection on an animal's heat balance, approaches or
90 exceeds T_b (McKechnie 2022). Inside nest boxes, the T_e experienced by nestlings can differ markedly
91 from T_{air} . Maintaining water balance is therefore critical for birds exposed to high T_e , as evaporative
92 cooling can impose substantial water costs. Accordingly, a species' evaporative cooling efficiency,

defined as the maximum ratio of heat dissipated evaporatively to that generated metabolically, is a key determinant of heat tolerance (Smit et al. 2018; McKechnie et al. 2021a).

Even when not lethal, exposure to extreme heat may have sublethal consequences that ultimately reduce individual fitness (Conradie et al. 2019). Importantly, controlled increases in T_b can form part of an adaptive thermoregulatory response, whereas excessive or prolonged hyperthermia may become physiologically costly. Cellular responses to thermal stress, including antioxidant defence and increased production of heat-shock proteins, may themselves entail energetic costs and potentially contribute to trade-offs with growth, development, or other fitness-related processes (Stillman 2019; Nord et al. 2026). Such trade-offs may be further exacerbated by reduced foraging activity during extreme heat. In particular, parental feeding rates can be reduced during heat waves, such that nestlings confined to nest boxes simultaneously experience elevated T_e and reduced food provisioning (Molenaar et al. 2026). Understanding how these physiological and behavioural responses interact is therefore essential for assessing both the immediate and long-term fitness consequences of extreme heat in birds breeding in nest boxes.

In this review, we synthesise current knowledge of the physiological, molecular and behavioural mechanisms through which birds respond to extreme heat and integrate this knowledge with studies documenting effects of extreme heat on reproductive success, fitness-related traits and, ultimately, survival of cavity-nesting birds breeding in nest boxes. Following a mechanistic framework (Fig. 1), we first examine thermoregulation at high temperatures, focusing on thermoregulatory constraints, dehydration risk, and cellular stress responses, and discuss how sublethal effects may translate into long-term consequences for survival and fitness. We then explore how elevated temperatures alter parental care and nestling behaviour, including changes in incubation, provisioning and premature nest departure, highlighting their potential cascading effects on offspring development and recruitment. We further review documented mortality events and the ecological and evolutionary factors that may shape vulnerability to heat-related mortality. Next, we review strategies aimed at mitigating thermal stress in nest boxes, including modifications to nest box

119 design, materials, placement, shading and ventilation. Finally, we identify critical knowledge gaps
120 and outline priorities for future experimental and longitudinal studies that could improve the
121 effectiveness of nest box programmes under continued climate warming. More broadly, the
122 mechanisms and mitigation strategies discussed here are likely relevant to other endothermic
123 vertebrates using artificial refuges, including bats and small mammals, underscoring the broader
124 implications of thermal extremes for conservation in a warming world.

125 **2. Physiological and molecular responses to extreme heat**

126 As homeothermic endotherms, birds regulate T_b across a broad range of environmental temperatures.
127 Within the thermoneutral zone, T_b can be maintained without substantial increases in metabolic heat
128 production or evaporative cooling. When T_e approaches or exceeds T_b , the organism needs to spend
129 energy and body water to sustain thermoregulation, otherwise, it may enter a state of hyperthermia
130 with potentially lethal or sublethal consequences (McKechnie 2022). Compared to other endotherms
131 such as mammals, birds have a higher T_b during both rest and the active phase (Prinzinger et al. 1991).
132 Across bird species, T_b averages approximately 41 °C, but varies considerably among taxa, with
133 passerines generally maintaining higher T_b than other avian orders. Lethal T_b values of 46–48°C have
134 been reported for many birds (McKechnie 2022), although some species can tolerate T_b exceeding 48
135 °C (Freeman et al. 2020).

136 Species differ substantially in the maximum T_{air} they can tolerate while maintaining effective
137 thermoregulation. These differences are strongly influenced by pathways used for evaporative heat
138 loss and by the metabolic costs associated with them. In birds, evaporative cooling occurs primarily
139 through respiratory and cutaneous routes, with their relative contributions varying among species
140 (Smit et al. 2018; McKechnie et al. 2021a). Respiratory cooling commonly involves panting or gular
141 fluttering, whereas cutaneous and cloacal evaporation can provide additional routes for dissipating
142 heat (Hoffman et al. 2007; McKechnie et al. 2017). In Columbiformes, for example, greater reliance
143 on cutaneous evaporation contributes substantially to their ability to tolerate higher T_{air} , as this

144 pathway allows heat to be dissipated without the respiratory costs associated with panting or gular
145 fluttering (McKechnie et al. 2016). The avian bill can also contribute substantially to heat dissipation,
146 particularly in large-billed species such as toucans and hornbills, in which heat loss through the bill
147 can reach rates equivalent to approximately 400% of resting heat production (Tattersall et al. 2009;
148 Chaves et al. 2023; Coulson et al. 2024).

149 An important strategy that may contribute to heat tolerance is facultative hyperthermia,
150 whereby birds permit T_b to increase above normothermic levels during exposure to high T_{air} (Tieleman
151 and Williams 1999; Freeman et al. 2020). This response is not indicative of thermoregulatory failure,
152 rather, a controlled increase in T_b can reduce reliance on evaporative cooling and thereby conserve
153 water. In fact, increasing T_b reduces the inward thermal gradient between the body and the
154 environment, thereby limiting passive heat gain and reducing the reliance on evaporative cooling
155 (McKechnie 2022). Facultative hyperthermia may therefore contribute to water conservation by
156 allowing birds to tolerate higher T_b during periods of intense heat exposure, although uncontrolled
157 increases in T_b beyond physiological tolerance limits can ultimately become lethal. The functional
158 significance of this strategy, however, varies substantially among species. Facultative hyperthermia
159 appears to be more pronounced in passerines compared to other orders (Gerson et al. 2019), while
160 capacity for hyperthermia also varies among birds from different climatic environments (Freeman et
161 al. 2022).

162 Although facultative hyperthermia may reduce the energetic and water costs of evaporative
163 cooling, maintaining an elevated body temperature is not physiologically cost-free. At the cellular
164 level, excessive or prolonged hyperthermia can disrupt protein homeostasis, alter membrane and
165 mitochondrial function, and increase the production of reactive oxygen species (ROS), potentially
166 resulting in oxidative damage to proteins, lipids, and DNA (McKechnie and Wolf 2019; González-
167 Medina et al. 2026). Cellular responses include the upregulation of antioxidant defences and heat
168 shock proteins (HSPs), which contribute to maintaining redox balance and protein homeostasis but
169 may also entail resource costs (Fig. 1). Consequently, the benefits of tolerating elevated T_b through

170 facultative hyperthermia must be considered alongside potential cellular costs of maintaining redox
171 balance and protein homeostasis.

172 **2.1 Oxidative stress**

173 During early development, encompassing the embryonic and nestling stages, altricial birds are
174 confined to the nest environment. Therefore, during extreme heat, offspring have limited
175 opportunities to behaviourally avoid unfavourable thermal conditions within the nest. The capacity
176 of altricial nestlings for physiological thermoregulation varies markedly with developmental stage,
177 making cellular mechanisms that protect against thermal and oxidative damage particularly important
178 during early development (McKechnie and Wolf 2019).

179 Experimental studies across vertebrate taxa suggest that oxidative stress is an important
180 component of the physiological mechanisms underlying thermal tolerance (Kikusato et al. 2015;
181 Messina et al. 2023; Zhang et al. 2023b). In wild birds, while variation in evaporative cooling capacity
182 appears to be a primary determinant of acute heat tolerance, oxidative imbalance and cellular damage
183 may emerge as downstream physiological consequences when thermoregulatory capacity is
184 challenged (McKechnie 2022). In particular, species relying more heavily on panting and facultative
185 hyperthermia, such as many Passeriformes, could potentially experience greater oxidative challenges,
186 although direct links between specific thermoregulatory pathways and oxidative damage remain
187 poorly established. Consistent with a link between thermal stress and oxidative status, a recent
188 experimental study on great tits (*Parus major*) found that heat-exposed birds maintained a persistently
189 elevated body temperature (+0.2 °C) accompanied by increased levels of oxidative damage and
190 reduced antioxidant capacity (González-Medina et al. 2026).

191 Organisms can counteract oxidative challenges through a range of antioxidant mechanisms,
192 including enzymatic defences and endogenous and exogenous antioxidant compounds. Evidence
193 from wild birds suggests that antioxidant capacity may influence the physiological costs of heat
194 exposure. For example, nestlings of house wrens (*Troglodytes aedon*) developing in experimentally

195 heated nest boxes showed a context-dependent increase in body mass when supplemented with
196 vitamin E, suggesting that antioxidant availability may mitigate some of the negative effects of
197 elevated temperature on offspring development (Duncan et al. 2024). Similarly, tree swallow
198 (*Tachycineta bicolor*) nestlings exposed to experimentally elevated nest temperatures exhibited
199 widespread transcriptional changes associated with antioxidant defences (Woodruff et al. 2025).
200 However, maintaining antioxidant defences and repairing oxidative damage are themselves
201 energetically demanding, and the capacity to prevent or repair oxidative damage varies substantially
202 both among and within species (Pamplona and Costantini 2011; Messina et al. 2017). Because
203 excessive oxidative damage can impair physiological function and reduce fitness, variation in the
204 mechanisms regulating oxidative status may contribute to differences in physiological resilience and
205 vulnerability to thermal stress.

206 **2.2 Heat-shock proteins**

207 Another key cellular mechanism involved in vertebrate responses to elevated temperatures across life
208 stages is the upregulation of heat-shock proteins (HSPs) (Gao et al. 2014; Nord et al. 2026). HSPs are
209 a conserved family of molecular chaperones that play a critical role in maintaining cellular integrity
210 during thermal stress by facilitating the refolding of damaged or misfolded proteins (Woodruff et al.
211 2022; Galletta et al. 2022). HSP expression is often co-regulated with other physiological responses,
212 forming an integrated network that contributes to restoring homeostasis. In tree swallow, nestlings
213 exposed to short-term high temperature (mean = +4.5 °C) showed increased levels of HSP gene
214 expression in the blood, alongside widespread transcriptional changes related to antioxidant defences
215 and inflammation (Woodruff et al. 2025). Such molecular changes were accompanied by increased
216 panting and lower body mass in heat-exposed nestlings compared with controls, consistent with
217 substantial physiological costs of heat exposure.

218 The upregulation of HSPs, antioxidant enzymes, and other molecules involved in the response
219 to thermal stress requires cellular resources and may contribute to trade-offs with fitness-related traits.

Such allocation could potentially reduce resources available for other physiological processes, generating immediate or delayed fitness consequences (Fig. 1; Metcalfe 2025; Siepielski et al. 2026). Accordingly, adult zebra finches (*Taeniopygia guttata*) exposed to a sub-lethal temperature known to reduce fertility ($T_{\text{air}} = 43^{\circ}\text{C}$) increased their panting behaviour, which was negatively correlated with the expression of genes associated with sperm function and positively associated with expression of genes coding for HSPs in the testis (Lipshutz et al. 2022). These associations are consistent with a potential trade-off between cellular protection and reproductive function under thermal stress, although they do not by themselves demonstrate a causal reallocation of resources. Other negative effects of extreme high temperatures on fitness-related traits in zebra finches include reductions in cognitive abilities and motor performance (Danner et al. 2021). However, further studies are required to understand how these effects relate to panting behaviour and water loss, and whether these processes involve trade-offs with cellular self-maintenance.

2.3 Sublethal effects of early-life exposure to extreme heat

Early-life exposure to extreme heat may induce persistent effects on an individual's phenotype. On the one hand, short-term exposure can elicit phenotypic plasticity through physiological acclimation, including changes in thyroid hormones, HSPs and antioxidant activity, which may enhance the organism's capacity to cope with thermal stress in subsequent life stages (Nord and Giroud 2020; Wada and Coutts 2021). On the other hand, prolonged or repeated exposure to extreme temperatures, even when not lethal, can impair development and reduce adult fitness, negatively affecting traits such as fertility, fecundity, lifespan and body size (Fig. 1; Schou et al. 2021; Eastwood et al. 2022; Morosinotto et al. 2025). Developmental plasticity refers to reversible or persistent phenotypic adjustments arising during development in response to environmental conditions, whereas developmental damage occurs when environmental stress disrupts developmental processes and causes lasting impairments that reduce organismal performance or fitness. Given that nest boxes provide breeding sites for many species across different habitats, a better understanding of the

245 sublethal effects of high T_e on developing birds and their carry-over effects on adult fitness is needed
246 under ongoing climate change.

247 Fertility and fecundity are key drivers of population persistence because they are directly
248 linked to reproductive success. High-temperature stress impairs fertility and fecundity through a range
249 of physiological and molecular mechanisms, including effects on the quality and quantity of gametes
250 and reproductive fluids. These processes may be mediated by oxidative stress, activation of the heat-
251 shock response, and epigenetic mechanisms that alter gene expression (Snook et al. 2026). As
252 discussed above, high temperatures have been associated with impaired male reproductive function
253 in zebra finches (Lipshutz et al. 2022); however, reproductive disruptions can affect both sexes and
254 may persist across life stages (Hurley et al. 2018; Schou et al. 2021). Nevertheless, the sublethal
255 effects of heat on these critical reproductive traits in wild birds remain understudied (Walsh et al.
256 2019; Assersohn et al. 2021). Further studies are required to experimentally assess whether exposure
257 to extreme temperatures during development has carry-over effects on adult fertility and fecundity.

258 Telomere dynamics provide one potential biomarker of the long-term physiological
259 consequences of developmental stress (Roast et al. 2022). Telomeres are repetitive DNA sequences
260 at the ends of eukaryotic chromosomes that contribute to maintaining genome integrity (Reichert and
261 Stier 2017). They generally shorten with cell division, and oxidative damage can accelerate telomere
262 attrition (Chatelain et al. 2020). Elevated nest temperatures have been associated with shorter
263 telomeres in nestlings of purple-crowned fairy-wrens (*Malurus coronatus*) and great tits (Stier et al.
264 2021; Eastwood et al. 2022, 2026). In contrast, exposure to simulated heat waves during the first 12
265 days of life reduced telomere attrition in zebra finch nestlings compared with controls, suggesting an
266 age-dependent response to thermal stress (Ton et al. 2023). In barn swallows (*Hirundo rustica*), longer
267 telomers were associated with higher survival beyond the first year of life (Novelli et al. 2026).
268 Together, these findings suggest that heat exposure may negatively affect long-term survival, with
269 potentially species- and age-specific windows of sensitivity.

270 In birds, early-life exposure to extremely high T_{air} generally constrains nestling growth and
271 development (Salaberria et al. 2014; Van De Ven et al. 2020; Corregidor-Castro et al. 2023). Such
272 effects may arise directly through physiological trade-offs between growth and thermoregulation, as
273 suggested by an experimental study in which blue tit (*Cyanistes caeruleus*) nestlings raised in heated
274 nest boxes had significantly higher T_b and lower body mass than those raised in unheated nest boxes
275 (Andreasson et al. 2018). Alternatively, constraints on nestlings' growth and development may be due
276 to reduced food intake and assimilation efficiency, potentially through reduced intestinal integrity and
277 alterations in the gut microbiota, or from reduced nutrient metabolism as a mechanism to limit
278 endogenous heat production under heat stress (Cao et al. 2021; Olayiwola and Adedokun 2025).
279 Finally, thermal constraints on nestling development may be mediated indirectly by temperature-
280 induced changes in parental investment and foraging behaviour (Nord et al. 2026). Interestingly, an
281 experimental study on lesser kestrels (*Falco naumanni*) found that supplementary food provisioning
282 had positive effects on the body size of nestlings raised at higher T_{air} , despite parental provisioning
283 rates not differing among experimental groups (Corregidor-Castro et al. 2026). Disentangling these
284 direct and indirect pathways is therefore essential to understand how thermal stress experienced
285 during development translates into persistent phenotypic and fitness consequences.

286 **2.4 High temperatures and gut microbiota**

287 The gastrointestinal microbiota plays a vital role in maintaining host health by contributing to nutrient
288 uptake, detoxification and interactions with the immune system (Grond et al. 2018). In poultry, gut
289 microbial communities are closely linked to host growth, as several bacterial taxa contribute to the
290 digestion and assimilation of nutrients (Bodawatta et al. 2022). In wild birds, however, the functional
291 roles of specific gut bacterial symbionts remain largely unknown. The relationship between the gut
292 microbiome and its host is considered mutualistic, with gut microbes metabolizing dietary and host-
293 derived compounds and producing neuroactive metabolites. These metabolites can enter the
294 circulation or interact locally with the enteric nervous and immune systems, influencing physiological

processes mediated by the central nervous system, including behaviour and cognition (Cao et al. 2021). Consistent with this gut-brain connection, the first correlational evidence linking gut microbiome composition to cognitive performance in birds came from captive zebra finches, in which learning and memory performance was associated with gut microbiome beta-diversity, but not alpha-diversity (Slevin et al. 2020).

Heat stress is a potent modulator of the gut microbiome, as shown in poultry studies in which elevated temperatures reduced the microbial diversity and altered community composition of the hosts (reviewed in Ncho 2025). However, these effects have been poorly studied in wild birds. To our knowledge, only one field study has experimentally tested the impact of high nest temperature on the gut microbiota of wild nestlings. Experimental warming of nest boxes during development reduced gut microbial diversity in eastern bluebird (*Sialia sialis*) nestlings, but not in tree swallows, compared with unheated controls (Ingala et al. 2021). These contrasting responses suggest that microbiome responses to development heat exposure may be species-specific, although the mechanisms underlying this variation remain unknown. Further studies are therefore needed to determine how exposure to extreme temperatures during development affects the gut microbiome of wild birds, and whether alterations in microbial communities contribute to the physiological, developmental, and behavioural consequences of early-life heat stress. In particular, investigating these responses in nest boxes could help clarify how anthropogenic breeding sites affect host–microbiome interactions and whether these effects differ from those experienced in natural cavities.

3. Behavioural responses to extreme heat

The physiological and energetic challenges imposed by elevated temperatures can elicit behavioural adjustments that modify exposure to heat and its associated physiological costs. When T_{air} approaches T_b , both adults and nestlings may increase the frequency and duration of thermoregulatory behaviours such as panting and gular fluttering. However, whereas adults can modulate their activity levels and select more favourable microclimates to reduce thermoregulatory costs and water loss, nestling

320 survival depends strongly on both their physiological capacity to dissipate heat and the thermal
321 conditions of the nest because they are largely confined to the nest environment.

322 ***3.1 Parental care and food provisioning***

323 In breeding birds, elevated temperatures can alter incubation behaviour. In Cassin's auklets
324 (*Ptychoramphus aleuticus*), parents increased the frequency of egg turning in unshaded nest boxes,
325 where egg temperatures are elevated relative to shaded boxes, potentially enhancing heat
326 redistribution and helping to maintain suitable conditions for embryonic development (Kelsey et al.
327 2016). In collared flycatchers (*Ficedula albicollis*), parents reduced their time spent incubating eggs
328 in heated nest boxes and spent more time outside the nest (Arct et al. 2022). In pied babblers
329 (*Turdoides bicolor*), reduced nest attendance at high temperatures has been linked to increased
330 dehydration risk in attending adults (Bourne et al. 2021). In Carolina wrens (*Thryothorus*
331 *ludovicianus*) and prothonotary warblers (*Protonotaria citrea*), increased nest cavity temperature
332 during incubation reduced post-hatching begging by nestlings, indicating carry-over effects of
333 temperature during incubation on post-hatching development (Mueller et al. 2019). Whether reduced
334 begging reflects direct effects of developmental temperature or indirect effects mediated through
335 changes in offspring condition requires further investigation.

336 Reduced rates of food provisioning to nestlings during periods of extreme heat have been
337 documented in wild zebra finches, southern yellow-billed hornbills (*Tockus leucomelas*) and pied
338 babblers, three species inhabiting arid environments (Wiley and Ridley 2016; Van De Ven et al. 2020;
339 Wheeler et al. 2025). By contrast, no reduction in provisioning rates was observed in Mediterranean
340 lesser kestrels, despite reduced nestling survival in unshaded nest boxes (Catry et al. 2011;
341 Corregidor-Castro et al. 2026). These contrasting findings suggest that the effects of heat on parental
342 provisioning are context-dependent and may vary with environmental water availability, species-
343 specific thermal physiology, diet, body size and foraging ecology. Accordingly, Sloane et al. (2022)
344 reported that during a heat wave, bushtit (*Psaltiriparus minimus*) broods that survived were located in

345 closer proximity to water sources compared to those that perished. Although this association does not
346 identify the underlying mechanism, access to water could potentially reduce dehydration costs for
347 attending adults and thereby facilitate continued parental care during extreme heat. Experimental
348 studies are needed to determine whether water availability directly modifies the trade-off between
349 adult self-maintenance and parental investment. Moreover, this relationship may also be affected by
350 species-specific traits, such as body mass and diet, as indicated by a recent meta-analysis of
351 temperature-related changes in avian nestling provisioning (Molenaar et al. 2026).

352 Reduced provisioning is likely driven by multiple interacting mechanisms, including
353 thermoregulatory constraints on adults, increased risk of dehydration, and reduced foraging
354 efficiency. In tree swallows, females with experimentally enhanced heat-dissipation capacity
355 maintained higher provisioning rates at high temperatures than control females, providing
356 experimental evidence that thermal constraints can limit parental care (Tapper et al. 2020). However,
357 Heft et al. (2026) found that male provisioning declined with increasing temperature regardless of
358 experimentally enhanced heat-dissipation capacity, suggesting that responses to thermal stress may
359 be sex-specific. High temperatures may also increase evaporative water loss, potentially further
360 constraining parental activity. Because small-bodied passerines have higher mass-specific rates of
361 evaporative water loss (Albright et al. 2017), they may be particularly vulnerable to dehydration under
362 extreme heat, potentially limiting their ability to sustain provisioning at the nest. However, direct
363 evidence linking adult dehydration to reduced provisioning remains limited. Finally, heat can alter
364 foraging conditions by affecting prey activity and detectability (Carter et al. 2025), such that reduced
365 foraging efficiency, rather than declining prey abundance alone, may contribute to lower provisioning
366 rates (Levillain et al. 2025).

367 ***3.2 Behavioural trade-offs in nestlings***

368 One behavioural strategy available to older nestlings during extreme heat is premature nest departure,
369 which can reduce exposure to high nest temperatures (Mueller et al. 2019; Sloane et al. 2022).

370 However, this response is likely associated with significant fitness costs. Catry et al. (2011) observed
371 that, among lesser kestrel nestlings that left nests prematurely, some succumbed to starvation while
372 others were preyed upon. Another high-risk behavioural response observed in lesser kestrels during
373 heat waves is increased time spent outside the nest box (Corregidor-Castro et al. 2025). By remaining
374 outside the nest, nestlings avoided elevated temperatures in unshaded nest boxes and gained
375 preferential access to parental food provisioning, thereby obtaining thermal and nutritional benefits
376 at the cost of increased exposure to predators.

377 Importantly, the costs and benefits of leaving the nest during hot conditions are likely to
378 depend strongly on nest-site configuration. In the study system of Corregidor-Castro et al. (2025)
379 nestlings could easily re-enter the nest because nest boxes were placed on the floor of a flat roof. This
380 may not be possible when nest boxes are mounted high on buildings or when nests are located in
381 inaccessible cavities, where nestlings that leave may be unable to return and may become more
382 vulnerable to predation or starvation (Catry et al. 2015). Therefore, nest box design and placement
383 should be considered as potential components of mitigation strategies, particularly for species in
384 which temporary nest departure is likely during extreme heat.

385 ***3.3 Longer-term behavioural consequences: cognitive performance***

386 Recent experimental studies reported impaired cognitive abilities in birds exposed to simulated or
387 natural extreme heat (Danner et al. 2021; Blackburn et al. 2022; Soravia et al. 2023, 2025). Because
388 cognitive processes such as learning, memory and decision-making contribute to foraging, predator
389 avoidance and behavioural flexibility, heat-related cognitive impairment could have important fitness
390 consequences (Szabo et al. 2022; Ducatez et al. 2020).

391 Exposure to high temperatures during early life can have persistent effects on cognitive
392 performance into adulthood, with potentially negative effects for fitness (Soravia et al. 2021). For
393 example, pied babblers raised at higher temperatures took three times longer to learn as adults an
394 association between a colour cue and a food reward than birds raised at lower temperatures (Soravia

et al. 2024). The observed cognitive impairment could reflect several non-mutually exclusive pathways, including nutritional stress resulting from reduced provisioning and direct effects of heat exposure on neural development.

Evidence from animal models indicates that oxidative stress can impair learning and memory, whereas antioxidant supplementation can improve cognitive performance under some conditions (Cram 2022). Oxidative damage may therefore represent one mechanism through which heat exposure affects cognitive performance. Poultry studies show that heat stress is associated with increased oxidative damage in the brain of young chickens and broilers (Chowdhury et al. 2014; Feng et al. 2026), although whether similar responses occur in wild birds and contribute to heat-related cognitive impairment remains unknown. Heat-induced alterations of the gut microbiota represent another potential, but as yet poorly understood, pathway linking thermal stress to cognitive function (Zhuo et al. 2025).

4. Survival and mortality during extreme heat

Bird reproduction may be particularly sensitive to periods of extreme heat because eggs and nestlings are confined to the nest throughout much of their development. For species that use nest boxes, microclimatic conditions experienced by developing offspring are affected by the characteristics and placement of the box as well as by the surrounding environmental conditions. If the thermal buffering capacity of nest boxes is poor, high T_{air} may result in elevated T_e inside the nest, imposing substantial thermal challenges on developing birds. Avian embryos and recently hatched birds are particularly vulnerable to extreme temperatures because their capacity for endogenous thermoregulation is absent or poorly developed. In altricial species, endothermic capacity develops progressively after hatching, with the timing and rate of development varying among species and with body size and developmental stage (Sirsat et al. 2016; Ton et al. 2023).

4.1 Hatching success

419 In developing embryos, prolonged exposure to temperatures above the optimal range can impair
420 development and, under severe conditions, lead to embryonic mortality (Peterka et al. 1996; Krausova
421 and Peterka 2007). These effects may arise from heat-induced alterations in cell proliferation and
422 apoptosis, oxidative stress, and activation of cellular heat-shock responses (Buckiová et al. 1998; Du
423 and Shine 2022). For example, experimental exposure of zebra finch embryos to temperatures ranging
424 from 37.5 to 45 °C induced upregulation of several HSP genes, consistent with a role for the heat-
425 shock response as an important mechanism of cellular protection against thermal stress (Galletta et
426 al. 2022). In zebra finches, nest temperatures can frequently exceed the optimal range for embryonic
427 development, with elevated nest temperatures accelerating embryonic development (Griffith et al.
428 2016). However, in a wild nest box population of zebra finches in Australia, no embryo survived
429 cumulative exposure of ≥ 20 h to 40.5 °C during incubation, and a heat wave resulted in complete
430 mortality in 23 of 25 clutches (McCowan and Griffith 2021).

431 Reduced hatching success in response to intense heat has also been documented in lesser
432 kestrels breeding in nest boxes in southern Italy (Corregidor-Castro et al. 2023). In this study, hatching
433 failure exceeded 50% when maximum nest temperatures around hatching exceeded 44 °C, while
434 experimental nest cooling substantially reduced nest temperatures and improved hatching success.
435 These findings suggest that the consequences of thermal stress may depend strongly on embryonic
436 developmental stage, with exposure close to hatching potentially having particularly severe effects
437 on embryo viability. This developmental sensitivity may partly reflect ontogenetic variation in
438 cellular protective mechanisms, including heat-shock responses. Although such mechanism has not
439 been directly demonstrated in wild embryos exposed to extreme nest temperatures, HSP expression
440 in avian embryos is known to vary with temperature and developmental stage (Leandro et al. 2004;
441 Galletta et al. 2022). Thus, elevated temperatures during critical developmental windows may have
442 disproportionately large effects on hatching success compared with similar thermal exposure
443 occurring during other stages of incubation. Further experimental studies manipulating the timing,
444 intensity, and duration of thermal exposure are needed to test this hypothesis.

445 **4.2 Nestling survival**

446 Following hatching, nestlings of altricial birds remain highly vulnerable to extreme temperatures
447 because their capacity for thermoregulation develops progressively during early post-hatching life
448 (Price and Dzialowski 2018). As nestlings develop, they progressively acquire endothermic capacity,
449 but exposure to high T_e can impose substantial physiological and energetic costs, particularly when
450 thermal conditions exceed their capacity for effective thermoregulation.

451 As previously discussed, one of the main consequences of exposure to high T_e is an increased
452 risk of dehydration through increasing evaporative water loss. Nestlings exposed to extreme heat may
453 be unable to fully offset metabolic heat production through evaporative cooling, resulting in
454 substantial water loss and an elevated risk of dehydration (Diehl et al. 2023). This limited capacity
455 for cooling may create a trade-off between maintaining heat balance and conserving body water,
456 particularly under conditions of prolonged or intense heat exposure. Evidence from cavity-nesting
457 species further suggests that thermal stress can impose trade-offs among thermoregulation, water
458 balance, and growth. In spotless starlings (*Sturnus unicolor*), nestlings exposed to high temperatures
459 in nest boxes showed increased dehydration, accompanied by reduced body mass and wing length
460 (Salaberria et al. 2014). Similarly, higher nest temperatures were associated with impaired nestling
461 growth in great tits, crimson rosellas (*Platycercus elegans*) and lesser kestrels and, in some cases,
462 with reduced post-fledging survival, indicating that thermal stress during development can have both
463 lethal and sublethal consequences (Larson et al. 2015; Rodríguez and Barba 2016; Corregidor-Castro
464 and Jones 2021; Corregidor-Castro et al. 2023).

465 Extreme temperatures can nevertheless result in direct mortality when nestlings are unable to
466 dissipate sufficient heat to maintain T_b within physiological limits. This risk is particularly
467 pronounced in nest boxes, where exposure to solar radiation, box design and limited thermal buffering
468 can result in nest temperature to substantially exceed T_{air} . Experimental evidence from lesser kestrels
469 provides a clear example of this effect. During heat waves, nestlings in unshaded nest boxes
470 experienced substantially higher mortality than those in shaded boxes, with mortality reaching 55%

471 in unshaded nests compared with 10% in shaded nests. Mortality was concentrated during periods
472 when maximum air temperatures exceeded approximately 37 °C, and nest temperature had a strong
473 positive effect on the probability of nestling death in unshaded nest boxes (Corregidor-Castro et al.
474 2023). More recent evidence further highlights the importance of nest box location in determining
475 nestling mortality risk. In lesser kestrels, the effects of nest boxes on nestling survival differed
476 markedly between two Italian populations, with lethal hyperthermia occurring only at the warmer site
477 (i.e, the city of Matera), where nest box temperatures exceeded 44 °C during heat waves (Corregidor-
478 Castro et al. 2026). Thus, the thermal consequences of nest box use are strongly context-dependent,
479 and local climatic conditions and nest-box placement may be a key determinants of nestling mortality
480 under extreme heat.

481 The effects of heat stress may also vary among nestlings within the same brood. In particular,
482 later-hatched nestlings may be disadvantaged by their smaller size and reduced access to parental
483 resources. Accordingly, lower-ranking nestlings had a higher probability of mortality during heat
484 waves in lesser kestrels (Corregidor-Castro et al. 2023), suggesting that extreme temperatures may
485 amplify pre-existing differences in competitive ability within broods. Size-dependent mortality could
486 therefore disproportionately affect the smallest and most vulnerable individuals, altering brood size
487 and composition. If such differential mortality is recurrent, it could have consequences for recruitment
488 and potentially generate selection on traits associated with heat tolerance. However, whether these
489 effects translate into population-level change or evolutionary adaptation remains unknown.

490 ***4.3 Drivers of variation in heat-related mortality***

491 The negative impacts of extreme heat on survival have been documented worldwide across a wide
492 range of avian taxa (Stillman 2019; McKechnie et al. 2021b; Kotz et al. 2025). In general, desert birds
493 are particularly challenged by extreme heat because T_{air} can often exceed their normothermic T_b .
494 Under these conditions, birds increasingly rely on evaporative cooling to dissipate heat, resulting in
495 substantial water loss and an elevated risk of dehydration and lethal hyperthermia (McKechnie and

496 Wolf 2010; Thompson et al. 2018; Conradie et al. 2020; McKechnie et al. 2021a). Accordingly, a nest
497 box population of southern yellow-billed hornbills in the Kalahari Desert showed declines in breeding
498 attempts and reproductive success between 2008 and 2019, associated with increasing periods of
499 extreme heat and drought (Pattinson et al. 2022). However, vulnerability to extreme heat is not
500 restricted to arid environments. For example, in wet tropical regions the intensification of heat
501 extremes, combined with elevated humidity, has been associated with substantial declines in bird
502 populations (Kotz et al. 2025).

503 Extreme heat is also a major driver of mass mortality events and population declines in
504 seabirds (Holt and Boersma 2022; Clark-Wolf et al. 2023; Lavers et al. 2026). Many seabird species
505 have evolved morphological and physiological adaptations that minimize heat loss in cold aquatic
506 environments. For example, cold-adapted birds may have a narrower, cold-shifted thermoneutral zone
507 (Choy et al. 2021), potentially increasing their susceptibility to heat stress when breeding on land
508 under unprecedented high temperatures (Oswald and Arnold 2012; Noiret et al. 2026). African penguins
509 and little penguins (*Eudyptula minor*) can breed in nest boxes designed to function as artificial
510 burrows, whose thermal buffering properties have been relatively well characterized (Pichegru et al.
511 2024). Although some studies have highlighted the potential risk of thermal stress in penguins
512 breeding in nest boxes (Lei et al. 2014; Welman and Pichegru 2023; Clitheroe et al. 2025), there
513 remains a paucity of research directly assessing the effects of nest box thermal conditions on
514 reproductive success and chick physiology.

515 Many birds breeding in nest boxes located in anthropogenically modified habitats, such as
516 urban environments and intensive agricultural landscapes, may also be particularly exposed to
517 thermal stress (Sumasgutner et al. 2023; Lauck et al. 2023; Hari et al. 2026). Urban environments can
518 retain and re-radiate more solar energy than surrounding vegetated landscapes, resulting in higher
519 temperatures (Li et al. 2024; Jambhekar et al. 2025). Similarly, intensive agricultural landscapes may
520 provide less thermal and hydric buffering than traditional agricultural systems or natural habitats,
521 increasing exposure to heat and drought (Lin et al. 2008; De Frenne et al. 2019; Williams et al. 2020).

522 We previously referred to substantial heat-related nestling mortality in a nest box population of lesser
523 kestrels in the Italian city of Matera (Corregidor-Castro et al. 2023, 2026), while elevated mortality
524 during heat waves has also been reported in a population breeding in cereal crops in Portugal (Catry
525 et al. 2011).

526 The effects of extreme T_{air} on survival are not only determined by the T_e experienced at the
527 nest, but they also depend on species-specific physiological capacity for evaporative cooling and heat
528 tolerance. For example, whereas 36% mortality was recorded among lesser kestrels during a heat
529 wave in Portugal, no mortality was observed among sympatric European rollers (*Coracias garrulus*;
530 Catry et al. 2015). Differences in heat-dissipation capacity may provide one possible explanation for
531 this contrast. Comparative work has shown that lilac-breasted rollers (*Coracias caudatus*) have
532 particularly high evaporative cooling efficiency and heat tolerance (Smit et al. 2018). Although direct
533 physiological measurements are lacking for European rollers, their close phylogenetic relationship
534 with lilac-breasted rollers suggests a testable hypothesis that efficient evaporative cooling may
535 contribute to their apparent resilience to extreme heat.

536 More broadly, the evidence for heat-related mortality in birds highlights that the thermal risk
537 associated with nest box breeding emerges from the interaction between T_{air} , nest microclimate and
538 species-specific physiological tolerance, rather than from T_{air} alone. Further comparative studies of
539 evaporative cooling capacity and maximum tolerable T_b are needed to better predict which species
540 will be most vulnerable to increasingly frequent and intense thermal extremes across regions.

541 **4.4 Effects of air humidity on evaporative cooling capacity**

542 Air humidity is a critical factor that interacts with T_{air} to determine the maximum environmental
543 temperature birds can tolerate. High humidity constrains evaporative heat loss, reducing
544 thermoregulatory performance during hot weather and increasing the risk of lethal hyperthermia
545 (Gerson et al. 2014; McKechnie et al. 2021b). Experimental evidence shows that maximum
546 evaporative water loss can decrease by ~26% to ~39% under humid compared with dry conditions

547 across birds from arid, lowland, and montane habitats (Freeman et al. 2024). Because high humidity
548 constrains evaporative cooling, greater tolerance of elevated T_b has been proposed as a potential
549 adaptation to hot, humid environments (Weathers 1997; Freeman et al. 2022, 2024). Consistent with
550 this hypothesis, red-billed queleas (*Quelea quelea*), an African ploceid weaver, maintained similar
551 maximum tolerable T_b and heat tolerance limits across humidity treatments, despite reduced
552 evaporative cooling capacity (Freeman et al. 2025). Much less is known about the effects of humidity
553 on thermoregulatory physiology in temperate birds. In tree swallows, increased humidity reduced
554 evaporative water loss but had little effect on T_b , while the energetic costs of thermoregulation were
555 ~8% higher under humid than under dry conditions (Porter et al. 2024). Indirect evidence from a
556 long-term study of great tits suggests that combined exposure to extreme heat and heavy rainfall
557 during early development may impair offspring condition, reducing fledging mass by up to 27%
558 compared to more favourable environmental conditions (Satarkar et al. 2026). Although this pattern
559 may reflect interacting thermal and nutritional constraints, the relative contributions of humidity,
560 thermoregulation and reduced food provisioning remain unresolved.

561 Climate projections indicate that thermal extremes and air humidity will increase across large
562 parts of the tropics, subtropics, and mid-latitudes (Douville et al. 2022; Li and Tamarin-Brodsky
563 2026). Consequently, the number of species exposed to potentially lethal environmental conditions
564 may increase (Coulson et al. 2025; Kotz et al. 2025). Species breeding in nest boxes may be
565 particularly vulnerable, as artificial cavities can alter thermal and humidity conditions and expose
566 birds to microclimates that differ substantially from those of natural cavities. It is therefore important
567 for nest box conservation programmes to understand how nest boxes affect temperature and humidity,
568 particularly during periods of extreme heat, to reduce the risk of mortality caused by thermoregulatory
569 failure. In temperate deciduous forests, nest boxes were more humid than natural cavities in the
570 presence of actively thermoregulating nestlings (Sudyka et al. 2023). In a tropical lowland forest,
571 humidity within hornbill nests was extremely high, sometimes exceeding 99% in both artificial and
572 natural cavities. However, marked differences were observed in thermal conditions since internal

temperatures in natural cavities ranged from 22.5 to 27.5 °C and were slightly lower than or similar to local T_{air} in the forest, while nest boxes exhibited significantly higher temperatures, reaching maxima of up to 35 °C (Kaur et al. 2018). These findings highlight the importance of considering humidity, alongside thermal buffering, when assessing the suitability of nest boxes for bird conservation programmes, as both factors may interact to shape the thermoregulatory conditions experienced by adults and nestlings.

Overall, these studies indicate that heat-related mortality in nest boxes cannot be predicted from T_{air} alone, but emerges from interactions among nest microclimate, humidity, developmental stage and species-specific thermoregulatory capacity.

5. Potential mitigation strategies

Compared with natural cavities, nest boxes often provide less effective thermal buffering (Table 1). Consequently, during periods of extreme heat, the thermal environment within nest boxes may result in elevated T_e , increasing the thermoregulatory demands on developing birds and potentially exceeding the thermoregulatory capacity of nestlings. As shown in previous sections, elevated temperatures within nests can reduce reproductive success and impair offspring development. As extreme heat events become more frequent and intense with ongoing climate change (IPCC 2023), improving the thermal performance of nest boxes is therefore an increasingly important conservation consideration.

Structural modifications represent one important mitigation strategy, particularly for nest box programmes at the design stage. Increasing wall thickness can enhance insulation and thermal inertia and thereby reduce diurnal temperature fluctuations inside the nest box. Nest boxes constructed from thick hardwood generally exhibit greater thermal buffering than thin plywood designs, which show greater coupling between external and internal temperatures (Maziarz et al. 2017). However, the thermal performance of different materials depends on nest-box design and ecological context. Nest boxes designed to mimic natural burrows for seabirds can be constructed from timber, fibreglass,

598 cement or ceramic. Available studies suggest that, in some systems, ceramic nest boxes can maintain
599 lower internal temperatures during thermal extremes than boxes constructed from alternative
600 materials (Table 1; Lei et al. 2014; Welman and Pichegru 2023; Johns et al. 2023).

601 Reducing solar radiation load is another key consideration. Because direct solar exposure is
602 an important driver of overheating, increasing surface reflectance through the use of light-coloured
603 nest boxes can reduce heat absorption. Griffiths et al. (2017) experimentally demonstrated that dark-
604 green (low reflectance) nest boxes exhibited higher mean and maximum daytime temperatures than
605 light-green (medium reflectance) and white (high reflectance) nest boxes. Another approach for
606 reducing conductive and radiative heat transfer to nest boxes is the installation of external shading
607 structures, which reduce direct solar exposure while creating an air gap around the nest box. Such an
608 approach was implemented by Corregidor-Castro et al. (2023) for brick nest boxes placed on roof
609 terraces. Shading reduced mean nest temperature during heat waves by 3.9 °C and increased survival
610 of lesser kestrel nestlings. Importantly, this study provides evidence that thermal mitigation can
611 improve not only nest microclimate but also reproductive outcomes.

612 Beyond nest box design, placement decisions can strongly influence thermal conditions.
613 Mounting nest boxes under vegetative or structural shade can reduce direct solar exposure and may
614 provide more favourable thermal conditions. For example, owls have been shown to select shaded
615 and thermally buffered refugia during diurnal resting periods (Barrows 1981; O'Connor et al. 2018).
616 Consistent with a potential role of shading, occupation rates of nest boxes by barn owls (*Tyto alba*)
617 were highest in nest boxes mounted on trees, intermediate in those placed on shaded poles, and lowest
618 in nest boxes exposed to direct sunlight (Charter and Rozman 2022). Orientation relative to solar
619 exposure may also contribute to reducing heat load (Ardia et al. 2006). Catry et al. (2011), for
620 example, reported that north-facing nest boxes had significantly lower daily maximum temperatures
621 than west-, east-, and south-facing nest boxes. However, the effect of orientation on mean nest box
622 temperature appears to be relatively modest overall (Table 2), with mean differences between the
623 warmest and coolest orientations generally ranging from approximately 0.3 to 1.5 °C. Orientation

624 may nevertheless be more relevant to short-term maximum temperatures than mean temperatures,
625 and its importance is likely to depend on latitude, season, surrounding vegetation and local patterns
626 of solar exposure. When evaluating mitigation measures, reductions in mean nest temperature should
627 therefore not be considered in isolation. Because acute mortality may be driven by short periods of
628 extreme heat, mitigation strategies should also be evaluated in terms of their effects on maximum
629 temperatures, the duration and frequency of exposure above biologically relevant thresholds, and
630 ultimately reproductive outcomes.

631 For existing nest-box programmes, where replacement of box material or design may be
632 impractical, relatively simple interventions such as adding external shade, increasing surface
633 reflectance or, where appropriate, relocating highly exposed boxes may offer practical short-term
634 approaches to reducing thermal exposure. Where natural cavities provide an appropriate reference,
635 nest box design should aim to approximate their thermal buffering and broader microclimatic
636 conditions rather than simply minimizing internal temperature. Enhanced thermal buffering may
637 reduce reproductive costs during extreme heat, particularly when it limits the increase in nest box T_e
638 relative to T_{air} . Further paired comparisons of natural and artificial cavities are needed to establish
639 appropriate microclimatic benchmarks for nest box design. Importantly, there is no universally
640 optimal nest box design. Instead, nest box design and placement should be tailored to the biological
641 and ecological requirements of the target species, local climatic and habitat conditions, and projected
642 climatic changes. Mitigation should therefore focus not on making nest boxes uniformly cooler, but
643 on reducing exposure to harmful thermal extremes while maintaining microclimatic conditions
644 appropriate for the target species.

645 **6. Perspectives and future directions**

646 In this review, we synthesised current knowledge on the effects of extreme heat on the physiology,
647 behaviour and survival of birds breeding in nest boxes, highlighting how the consequences of thermal
648 extremes depend on interactions among nest microclimate, developmental stage, species-specific

649 physiology and behaviour. Several important knowledge gaps nevertheless limit our ability to predict
650 vulnerability and design effective mitigation strategies. Here, we outline key directions for advancing
651 our understanding of the effects of extreme heat on birds and improving the effectiveness of nest box
652 programmes under climate change.

653 ***6.1. Integrating physiology, microclimate and fitness***

654 Simultaneous measurements of T_b , T_e , and T_{air} , humidity, and water balance under natural conditions
655 are needed to better capture how nest microclimate affects avian thermoregulation. Where direct
656 measurements of T_e are not feasible, studies should characterize the components of the nest
657 microclimate needed to estimate biologically relevant thermal exposure rather than relying on T_{air}
658 alone. Particular attention should be given not only to mean conditions but also to maximum
659 temperatures and the duration and frequency of exposure above physiologically relevant thresholds.
660 Combining these physiological and microclimatic measurements with reproductive outcomes and
661 other fitness traits in birds breeding in natural and artificial cavities would improve our mechanistic
662 understanding of how extreme heat affects individuals and potentially scales up to population-level
663 consequences. Future research should also investigate how elevated T_{air} interacts with other
664 environmental stressors, including drought, extreme rainfall, habitat degradation and anthropogenic
665 disturbance, to determine whether their combined effects on bird physiology, behaviour, and fitness
666 are additive, synergistic, or antagonistic. Linking individual thermal responses and reproductive
667 outcomes to demographic data will ultimately be necessary to determine whether heat-related effects
668 observed at nests translate into changes in recruitment and population growth.

669 ***6.2. Expanding taxonomic and ecological coverage***

670 Expanding research across a wider diversity of taxa and ecological contexts will improve our
671 understanding of variation in physiological and behavioural responses to extreme heat and refine
672 predictions of species vulnerability. For example, in cavity-nesting precocial birds such as the wood
673 duck (*Aix sponsa*), incubation temperature affects duckling performance during nest exodus (Hope et

al. 2019). Given that early-life heat exposure can impair locomotor and cognitive performance in vertebrates (Danner et al. 2021; Messina et al. 2025), future work should examine whether extreme heat during development affects nest exodus success in cavity-nesting ducks. Owls may warrant particular attention because, as nocturnal birds, they generally do not drink during the day, potentially limiting rehydration capacity during extreme heat (O'Connor et al. 2018). More generally, comparative studies should examine whether differences in activity patterns, body size, diet, access to water, developmental mode and evaporative cooling capacity predict vulnerability to extreme heat. Comparative studies across taxa and environments will help identify both shared and species-specific mechanisms underlying responses to extreme heat and support the development of more effective and species-appropriate conservation strategies under climate change.

6.3. *Identifying critical developmental windows and exposure thresholds*

Lethal and sub-lethal effects of extreme heat likely depend on the intensity and duration of thermal exposure, and the developmental stage at which the organism is exposed. For example, zebra finch nestlings exposed to elevated T_{air} showed lower telomere attrition during the first 12 days of life compared with controls, illustrating that physiological responses to developmental heat exposure are not necessarily uniformly negative and may vary with developmental stage (Ton et al. 2023). Identifying critical windows of sensitivity, together with the intensity and duration of exposure, and the physiological mechanisms underlying thermal responses, will be key to understanding the extent and limits of developmental plasticity under climate change.

6.4. *Quantifying long-term and sublethal consequences*

Detecting sublethal effects of early-life exposure to extreme temperatures is essential for fully assessing long-term fitness consequences. Future studies should quantify consequences for fertility, fecundity, survival, senescence and lifespan. Longitudinal studies should also examine the mechanisms linking early-life thermal exposure to later-life phenotypes, including persistent changes in oxidative status, cellular stress responses and, as an emerging area of research, the gut microbiome.

699 Evidence that heat-induced changes in the microbiome have consequences for cognition, behaviour
700 or fitness in wild birds remains particularly limited and warrants further investigation.

701 ***6.5. Testing the effectiveness of mitigation strategies***

702 The effectiveness of nest box mitigation strategies should be evaluated by considering both their
703 effects on nest microclimate and their consequences for breeding birds. Future experiments should
704 test alternative nest box designs, materials and placement strategies across contrasting environmental
705 conditions, combining microclimatic metrics, particularly maximum temperatures, humidity, and the
706 duration and frequency of exposure above physiologically relevant thresholds, with biological
707 outcomes such as reproductive success and offspring survival. Such studies should also assess
708 potential trade-offs to determine whether measures that reduce heat exposure during thermal extremes
709 may inadvertently reduce nest suitability outside periods of extreme heat.

710 **7. Conclusions**

711 Evidence synthesised in this review indicates that nest boxes often provide less effective thermal
712 buffering than natural tree cavities or burrows during periods of extreme heat, although the
713 consequences for breeding birds depend strongly on nest box design and placement, local
714 environmental conditions, and species-specific characteristics. Nest microclimate reflects interactions
715 among multiple environmental factors, including T_{air} , solar radiation, wind speed and humidity, such
716 that birds occupying the same habitat may experience substantially different thermal conditions
717 among nest boxes. Assessment of nest box suitability during extreme heat should therefore consider
718 microclimatic conditions beyond temperature alone, particularly humidity because of its influence on
719 evaporative cooling capacity.

720 The effects of extreme heat on reproductive success and other fitness-related traits are likely
721 to arise from interactions among the thermal environment, developmental stage, species-specific
722 thermoregulatory capacity, and physiological and behavioural responses. At high temperatures,
723 increased reliance on evaporative cooling increases water loss, while heat exposure can also alter

724 parental care, food provisioning and offspring behaviour. Together, these responses can influence
725 offspring development and survival, emphasizing that T_{air} alone may not adequately capture the
726 biological consequences of extreme heat.

727 More broadly, our review highlights the value of integrating thermal physiology into the
728 design and deployment of nest boxes. Nest box design and placement should aim to reduce exposure
729 to harmful thermal extremes while maintaining microclimatic conditions appropriate for the target
730 species across the range of environmental conditions experienced during breeding. The effectiveness
731 of mitigation strategies should therefore be evaluated by considering both their effects on nest
732 microclimate and their consequences for breeding birds. Integrating species-specific thermal
733 physiology and ecological requirements with nest box design and placement may therefore help
734 maintain the conservation value of artificial nesting structures under ongoing climate change.

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740 **Author contributions**

741 **SM** and **ME** conceived the ideas and designed methodology; **SM** led the writing of the manuscript.

742 All authors contributed critically to the drafts and gave final approval for publication.

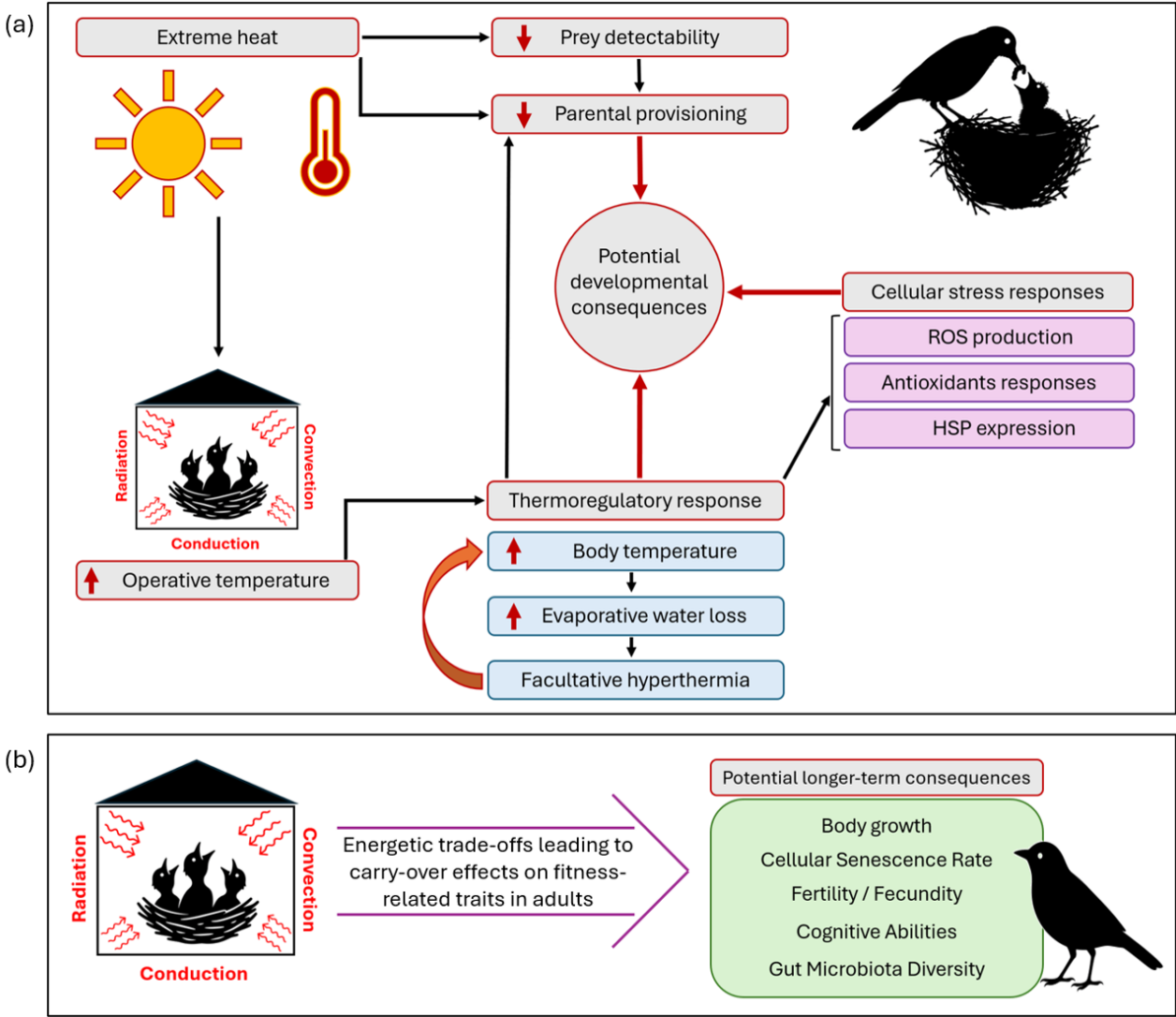
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744 **Conflict of interest**

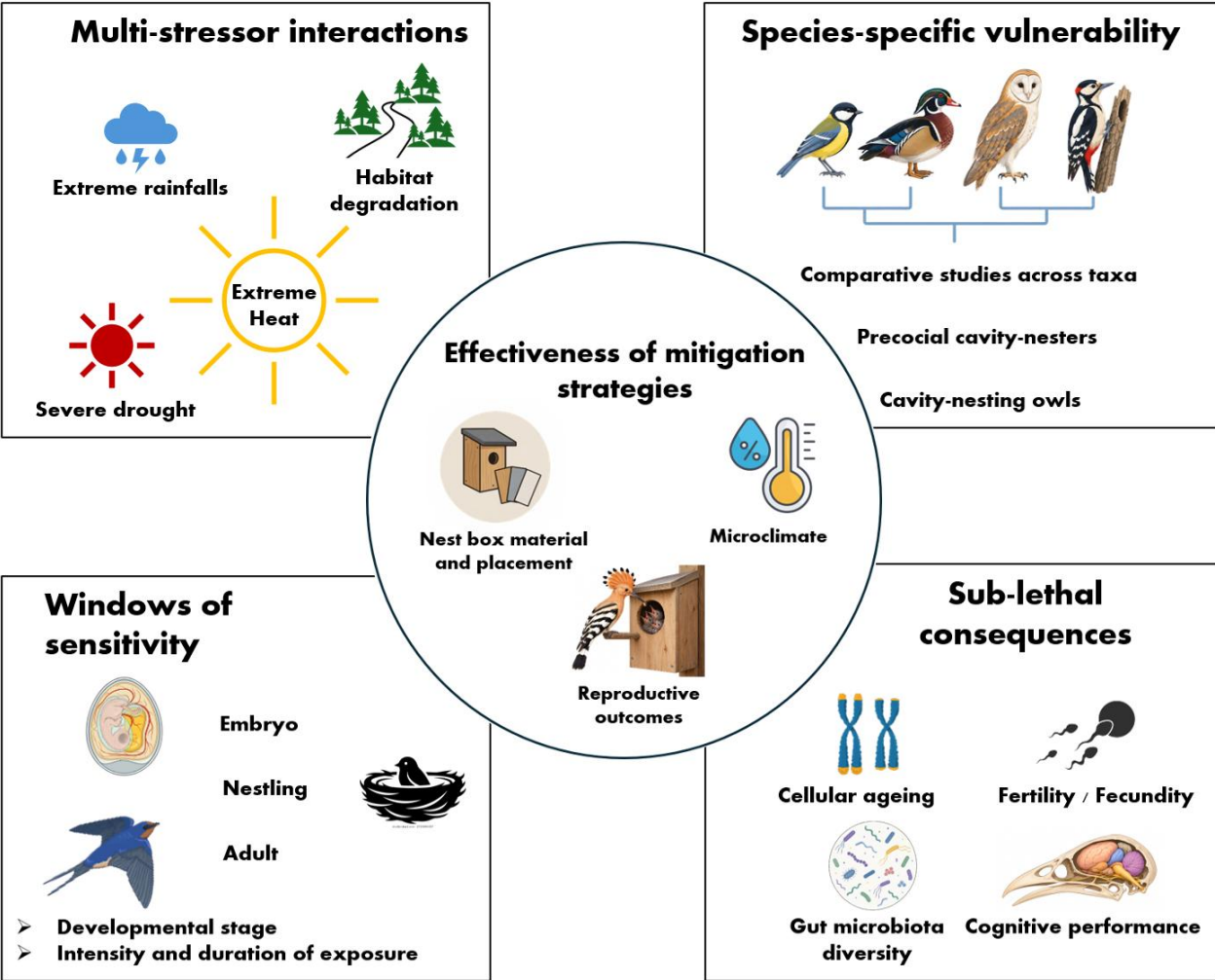
745 The authors declare no conflicts of interest.

746 **Figures and Tables**

747 Figure 1 – Conceptual framework illustrating potential pathways through which extreme heat may
748 affect nestling development and fitness-related traits. (a) Extreme heat can create thermal conditions
749 within nest boxes that result in elevated operative temperature, which integrates the effects of air
750 temperature, radiation, convection, and conduction on an animal’s heat balance, eliciting
751 physiological and behavioural thermoregulatory responses. When thermoregulatory responses are
752 sufficient, body temperature can be maintained within tolerable limits, whereas excessive increases
753 in body temperature may result in tissue and organ damage and, under severe conditions, mortality.
754 Heat exposure may also induce cellular stress responses and alter parental provisioning and energy
755 intake, with potential consequences for offspring development. (b) Early-life exposure to high nest
756 temperatures may have longer-term consequences for fitness-related traits, although the magnitude
757 of these effects may depend on the intensity, duration and developmental timing of exposure.



760 Figure 2 – Conceptual overview of key research priorities for advancing understanding of extreme
 761 heat impacts on cavity-nesting birds and enhancing the effectiveness of nest box programmes under
 762 climate change.



765 Table 1 Studies reporting temperatures measured in bird nest boxes and natural cavities or burrows, or
766 comparing different types of artificial nest structures. When available, mean maximum temperatures were
767 preferred over mean daily temperatures. If mean temperature data were not provided in the text, tables,
768 supplementary materials, or figures, the study was excluded from the table. Because temperature metrics and
769 sampling periods differed among studies, values should not be compared quantitatively across studies.

Study ID	Taxa	Country	Temperature measured (°C)	Nest type	Mean (°C) ± SD
García-Navas et al. (2008)	<i>Passer montanus</i>	Spain	Mean maximum temperature	Wooden nest boxes	25.4 ± 1.0
				Woodcrete nest boxes	28.3 ± 1.5
Catry et al. (2011)	<i>Falco naumanni</i>	Portugal	Mean maximum temperature on the hottest days	Wooden nest boxes	47.2 ± 7.4
				Stone cavities	38.2 ± 0.7
				Adobe cavities	37.9 ± 1.2
				Concrete cavities	41.1 ± 0.7
				Clay pots	44.6 ± 4.0
Lei et al. (2014)	<i>Spheniscus demersus</i>	South Africa	Mean maximum temperature	Natural burrows	26.0 ± 1.0
				Cement nest boxes	31.8 ± 0.6
				Fibreglass nest boxes	32.0 ± 0.7
Kelsey et al. (2016)	<i>Ptychoramphus aleuticus</i>	USA	Mean temperature	Natural burrows	14.5 ± 1.5
				Unshaded nest boxes	15.0 ± 3.3
				Shaded nest boxes	14.0 ± 2.2
Bueno-Enciso et al. (2016)	<i>Parus major</i> and <i>Cyanistes caeruleus</i>	Spain	Mean maximum temperature	Wooden nest boxes	20.6 ± 2.4
				Woodcrete nest boxes	21.2 ± 2.2
Combrink et al. (2017)	<i>Bucorvus leadbeateri</i>	South Africa	Mean maximum temperature	Natural cavities	27.7 ± 1.8
				Artificial nest boxes	40.8 ± 1.2
Fischer et al. (2018)	Procellariiformes	New Zealand	Mean maximum temperature	Insulated nest boxes	22.2 ± 2.0
				Burrows replica	22.3 ± 2.1
Schwartz et al. (2020)*	<i>Coracias garrulus</i>	France	Mean maximum temperature	Wooden nest boxes	33.3 ± 2.4
				Natural nests	30.2 ± 2.2
Scott-Baumann et al. (2022)	<i>Parus major</i> and <i>Cyanistes caeruleus</i>	United Kingdom	Mean temperature	Wooden nest boxes	12.6 ± 2.3
				Plastic nest boxes	12.5 ± 2.7
Corregidor-Castro et al. (2023)	<i>Falco naumanni</i>	Italy	Mean maximum temperature during heat waves	Unshaded nest boxes	45.7 ± 0.3
				Shaded nest boxes	41.8 ± 0.2
Sudyka et al. (2023)*	<i>Parus major</i> and <i>Cyanistes caeruleus</i>	Poland	Mean maximum temperature	Natural cavities	20.6 ± 3.9
				Woodcrete nest boxes	26.7 ± 3.1

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Welman and Pichegru (2023)	<i>Spheniscus demersus</i>	South Africa	Mean maximum temperature	Natural shaded burrows	29.3 ± 2.8
				Cement nest boxes	34.3 ± 2.0
				Ceramic nest boxes	27.5 ± 0.7
Niffenegger et al. (2024)	<i>Montifringilla nivalis</i>	Switzerland	Mean temperature	Natural cavities	8.9 ± 2.3
				Wooden nest boxes	10.5 ± 4.0
				Cavity in ski lift pylons	9.6 ± 5.0
Clitheroe et al. (2025)	<i>Eudiptula minor</i>	Australia	Mean maximum temperature	Natural burrows	24.7 ± 3.6
				Wooden nest boxes	26.5 ± 3.5
Corregidor-Castro et al. (2026)	<i>Falco naumanni</i>	Italy	Mean maximum temperature	Natural cavities	28.1 ± 3.9
				Refractory bricks nest boxes	32.0 ± 4.0
		Italy	Mean maximum temperature	Natural cavities	32.7 ± 5.5
				Refractory bricks nest boxes	38.7 ± 5.8

*We reported only data referred to the period in which nestlings were in the nests.

Table 2 – Studies reporting temperature measurements (mean ± SD) in bird nest boxes as a function of orientation. When numerical data were not provided in the text or tables, values were extracted from figures.

Study	Species	Mean nest box temperature (C°)			
		N	E	S	W
Butler et al. (2009)	<i>Falco sparverius</i>	17.7 ± 1.7	18.1 ± 1.8	18.1 ± 2.0	17.4 ± 1.9
Goodenough et al. (2011)	<i>Parus major</i>	12.6 ± 0.3	13.3 ± 0.4	14.0 ± 0.2	13.8 ± 0.2
Lambrechts et al. (2020)	<i>Parus major</i>	9.5 ± 3.7	10.7 ± 4.1	10.5 ± 4.5	9.9 ± 3.9
Schwartz et al. (2020)	<i>Coracias garrulus</i>	26.6 ± 1.6	27.4 ± 1.3	25.8 ± 2.0	25.9 ± 1.8
			NE	SE	SW
Kamm and Reed (2020)	<i>Falco sparverius</i>		21.6 ± 1.9	21.9 ± 1.2	21.6 ± 1.6

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