

ADVANCED REVIEW

The impacts of heat stress on animal cognition: Implications for adaptation to a changing climate

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Abstract

With global surface air temperature rising rapidly, extensive research effort has been dedicated to assessing the consequences of this change for wildlife. While impacts on the phenology, distribution, and demography of wild animal populations are well documented, the impact of increasing temperature on cognition in these populations has received relatively little attention. Cognition encompasses the mental mechanisms that allow individuals to process information from the surrounding environment, respond accordingly, and flexibly adjust behavior. Hence, it is likely to be a key factor in allowing animals to adjust adaptively to climate change. Captive studies show that heat stress can negatively affect cognitive performance not only in the short-term but also in the long-term, by altering cognitive development at early life stages. Field studies indicate that cognitive performance may affect survival and reproductive success. However, the link between heat stress, cognition, and fitness in wild animals has yet to be formally established. We propose a comprehensive research framework for the collection of robust empirical datasets on heat stress and cognitive performance in the wild. We then suggest how knowledge of heat stress impacts on cognitive performance could be applied to population viability models and wildlife management actions. We believe that a joint research effort encompassing the fields of thermal physiology, behavioral ecology, comparative cognition, and conservation science, is essential to provide timely mitigation measures against the potential impacts of climate change on wildlife.

This article is categorized under:

Climate, Ecology, and Conservation > Observed Ecological Changes

KEYWORDS

cognition, conservation, fitness, heat stress, wildlife

1 | INTRODUCTION

Global surface air temperatures are rising at an accelerated rate, along with the frequency of extreme weather events (IPCC, 2018). In response, many wild animal populations are changing their phenology and distribution, for example,

shifting their range to higher latitudes or elevations (Pecl et al., 2017), emerging earlier from hibernation (Ozgul et al., 2010), or advancing the timing of migration (Hurlbert & Liang, 2012) and oviposition (Telemeco et al., 2009). The resulting changes in interspecific interactions and resource availability can affect survival rates and reproductive success, and consequently population demography (Kubelka et al., 2018; Ozgul et al., 2010; Renner & Zohner, 2018). Extinction risk is predicted to accelerate with increasing global surface temperature (Urban, 2015). Accordingly, the decline in abundance of bird and mammal populations has been more pronounced in areas where the warming rate has been higher (Spooner et al., 2018). These population-level changes ultimately depend on the response to increased temperatures occurring at the individual level (Johnston et al., 2019).

Exposure to high environmental temperatures induces physiological and behavioral regulatory responses: when the demands exceed regulatory capacities, the individual experiences heat stress (Bradshaw, 2003). Heat stress is quantified as the deviation from the normal homeostatic state, which if sustained can lead to death (Bradshaw, 2003). Massive die-offs of wild animals during heatwaves (Mao, 2019; McKechnie et al., 2012) are a dramatic example of the consequences of heat stress. Heat stress can also directly impact animals' ability to breed by altering gametogenesis (Alix et al., 2020; Hansen, 2009). Animals avoid heat stress by modifying habitat use and activity patterns to seek thermal refugia, but such behavioral adjustments may come at the cost of reduced mating opportunities, increased predation risk, and constraints on foraging or offspring provisioning (Bartholomew, 1964; Cunningham et al., 2021). For example, fiddler crabs (*Uca mjoebergi*) retreat into cool burrows as the sediment surface gets warmer (Munguia et al., 2017), but this prevents courtship display and mating, which can only happen on the surface (Darnell et al., 2020). During the hottest hours of the day, many terrestrial birds and mammals rest in the shade and dissipate heat through evaporative cooling, for example, panting or sweating, and resume foraging activity at sunset or during the night (Fuller et al., 2014; Funghi et al., 2019; Montgomery et al., 2019). However, foraging at night can increase the exposure to nocturnal predators. For example, in the presence of lions (*Panthera leo*) ungulates are more likely to forage during the day under suboptimal temperatures (Veldhuis et al., 2020). Foraging in the heat can be less efficient due to heat dissipation: in Southern pied babblers (*Turdoides bicolor*) when daily temperature exceeds 35.5°C, panting hinders digging behavior and prey manipulation, leading to body mass loss (du Plessis et al., 2012), and reduced provisioning rates (Wiley & Ridley, 2016). As a consequence, nestling mortality increases at high temperatures (Bourne et al., 2020a). Similar trade-offs between thermoregulation and foraging or parental care have been described for many species worldwide (e.g., Catry et al., 2015; Cunningham et al., 2021; Edwards et al., 2015; Ma et al., 2018). As the number of hot days increases, these sublethal effects are predicted to drive future population declines (Conradie et al., 2019). For example, recent evidence shows that the increased frequency of hot and dry summers is reducing interannual survival in an arid-zone bird (Bourne et al., 2020b).

An underestimated sublethal effect of heat stress might be cognitive impairment (Danner et al., 2021). Cognition comprises the mental mechanisms by which an animal acquires, processes, stores and uses information from the surrounding environment; these include perception, learning, memory, and decision-making (Shettleworth, 2010). As such, cognition largely underpins behavioral plasticity: it allows animals to track environmental changes and formulate appropriate responses, and ultimately, to cope with new and challenging situations (Ducatez et al., 2020). Thus, cognition is likely to be a key factor in determining animal responses to climate change (Figure 1). While the behavioral responses to increased temperatures have been well studied, the effects of temperature on underlying cognitive processes have received little attention. Considering temperature-induced changes in cognitive mechanisms is critical, because they may alter behavior in a way that cannot be predicted by physiological changes alone (Abram et al., 2015).

Given that (a) climate change models predict sharp temperature increases (IPCC, 2018), and (b) cognitive performance can impact survival, reproduction (Ashton et al., 2018; Maille & Schradin, 2016; Raine & Chittka, 2008; Sonnenberg et al., 2019), and adaptation to changing environments (Ducatez et al., 2020; Shettleworth, 2010), there is urgent need to understand the relationship between heat stress, cognition, and fitness in animals. Here, we first introduce key concepts on thermal physiology and animal cognition, highlighting the potential links with fitness. Then, we review the evidence for heat stress effects on cognition. Finally, we establish a research framework to encourage the generation of empirical datasets quantifying variation in cognitive performance under different temperatures in the wild. Our goal is to stimulate interaction between scientists from different fields: a joint research effort may help predict wildlife adaptability to a changing climate and implement mitigation measures.

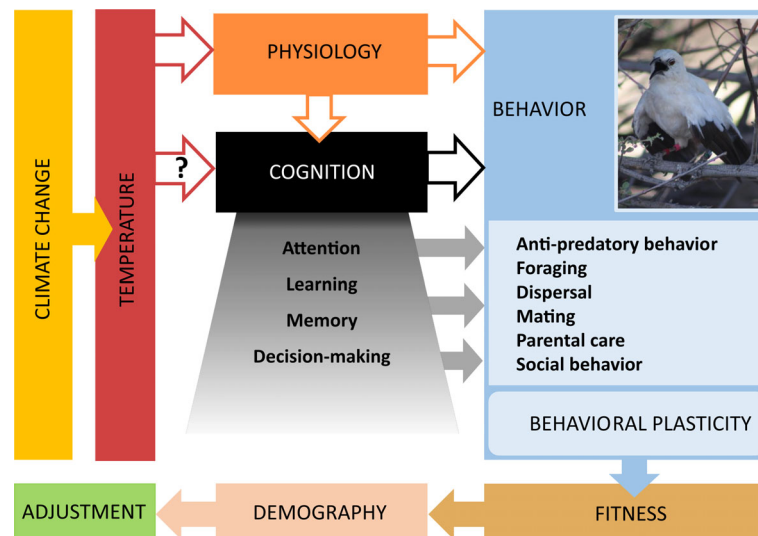


FIGURE 1 The proposed relationship between cognition and animal response to climate change. The same cognitive mechanisms (attention, learning, memory, and decision-making) regulate multiple behaviors in different contexts. Despite cognition and behavior being intrinsically linked, cognition is not the only cause of changes in behavior: The physiological response to increasing temperatures can directly modify behavior, for example by inducing heat dissipation behaviors and changing activity levels. A key piece of missing information is how increasing temperatures may impact animals' ability to process environmental information, that is cognition itself. This knowledge gap is important because cognition determines behavioral plasticity: It allows individuals to adjust their behavioral responses when conditions change or a behavior stops being successful. Ultimately, cognition can affect an animal's survival and reproductive success (proxies of fitness), which in turn determine population demography and the potential for adjustment to climate change
Source: Photo: Southern pied babbler (*Turdoides bicolor*) panting and wingspreading to dissipate heat (photo credit: Nicholas B. Pattinson)

2 | THE STATE OF KNOWLEDGE

2.1 | Thermal tolerance and heat stress

Understanding when and how heat stress may occur is a prerequisite to investigate how it may impact cognition. Animal species differ greatly in their thermal tolerance and thermoregulatory mechanisms. Here we briefly describe what defines the thermal environment and species' thermal tolerance, and indicate how heat stress may be measured empirically in different species.

Metabolism produces heat that is exchanged with the surrounding environment through the body surface by conduction, convection, and radiation (Gates, 1980). Substrate temperature, air or water temperature, and solar radiation determine the thermal environment. The structure of the environment, for example, vegetation cover and type of substrate, regulates the extent to which each component is involved in heat exchange with the animal and thus determines the microclimate (Mislán & Helmuth, 2008).

In endotherms, the range of temperatures in which the temperature gradient between the body surface and the environment suffices to dissipate metabolic heat defines the thermoneutral zone (Scholander et al., 1950). Above this zone, terrestrial endotherms can cool evaporatively (e.g., panting, sweating); this is sustainable as long as the water intake is increased accordingly (Mitchell et al., 2018). As temperature further increases from the onset of evaporative cooling, metabolic rate increases due to a temperature-dependent increase in the speed of biochemical reactions (Q_{10} effect; Mitchell et al., 2018), which may translate into a higher energy expenditure. As the resources available to the animal are depleted, body temperature rises, eventually damaging cellular function (e.g., protein denaturation), and causing death (Velichko et al., 2013).

Unlike endotherms, which possess physiological specializations that allow internal regulation of body temperature, in ectotherms body temperature is largely determined by external heat sources (Cowles, 1962). Hence, ectotherms thermoregulate behaviorally by moving in the thermal landscape. For this reason, instead of referring to normothermic body temperature, two measures of thermal tolerance are used: (1) optimal environmental temperature, that is, temperature that optimizes measures of locomotor performance or fecundity (Angilletta et al., 2002; Cooper et al., 2010); and

(2) preferred body temperature range. The preferred body temperature range is defined as the temperature selected by individuals in the absence of constraints for thermoregulation (Camacho & Rusch, 2017). This is measured by recreating a thermal gradient in a laboratory setting and allowing the animal to move freely within this gradient. The upper limit of the preferred body temperature range corresponds to the voluntary thermal maximum (VTM), which is the temperature at which active avoidance of heat sources occurs by changes in body position or in microhabitat selection (Camacho et al., 2018).¹ A more complex model of thermal tolerance applies to aquatic ectotherms. In water environments, increased temperatures reduce oxygen solubility, and oxygen supply can be further reduced by high CO₂ concentration. Therefore, thermal tolerance in aquatic ectotherms is defined with reference to the capacity of the animal to supply oxygen to tissues to meet the demand (oxygen-limited and capacity-limited thermal tolerance; Pörtner et al., 2017).

The thermal tolerance of individuals is affected by multiple factors: body mass (e.g., Mitchell et al., 2018), sex and life stage (e.g., Blanckenhorn et al., 2014), as well as seasonality and body condition (e.g., Turko et al., 2020). In addition, animals show physiological plasticity. The temperature conditions experienced by the individual during development can shape its thermal tolerance as adult (Refsnider et al., 2019). Even in adulthood, a process of acclimation can significantly increase thermal tolerance, by altering the expression of allozymes, modifying the cellular environment, increasing vascularization, and altering the structure of the epidermis or cuticle (Angilletta et al., 2002). For this reason, unpredictable heat extremes are more likely to cause heat stress than gradual seasonal changes (Cooper et al., 2019).

To determine whether increased temperature affects cognitive performance we need to: (a) measure environmental temperature at a relevant spatial scale (see Section 3.2.2), (b) measure exposure duration, (c) record individual traits, such as body mass, sex, age or reproductive status, that may influence the heat stress response and cognitive performance, and (d) if possible, consider temperature conditions experienced by individuals during development. Additionally, knowledge of the physiological specializations of the study species is important because, for example, species performing facultative hyperthermia (controlled elevation of body temperature to reduce water loss; Gerson et al., 2019) do not experience heat stress when body temperature increases within a certain range. For the purpose of comparing studies in this review, we will express heat stress as degrees of difference in water or air temperature relative to normothermic body temperature for endotherms, and to the VTM for ectotherms, unless otherwise stated. However, the large interspecific variation in thermal tolerance (McKechnie et al., 2021) means that comparisons of heat stress levels across species should be interpreted with caution.

2.2 | Cognitive mechanisms

An animal constantly acquires information from the environment through sensory mechanisms. In all contexts from foraging to mating or parental care, an animal must then process the acquired information to reduce uncertainty and make behavioral decisions: these require multiple cognitive mechanisms (Dukas, 2004). First, as the brain can only process a limited amount of information, animals need *attentional mechanisms* to select relevant stimuli from the environmental background (Bagheri et al., 2020; Dukas, 2002). They then need *learning mechanisms*, for example to associate stimuli and form predictions about their occurrence. An animal may experience the odor of a predator associated with the odor of injured conspecifics, and learn that the odor of a predator predicts an attack (Ferrari et al., 2015; Morand-Ferron, 2017). The new information will be stored through *memory*. Finally, *decision-making* mechanisms are used to determine the appropriate behavioral response. These may require *inhibitory control*. For example, a hungry animal might need to inhibit the response of attacking inedible prey and continue its search for an edible one (Lucon-Xiccato & Bertolucci, 2019). Each species will rely on learning, memory and decision-making over fixed, stimulus-response reflexes to different extents depending on its ecology and evolutionary history (Bond et al., 2007; Rosati et al., 2014; Shultz & Dunbar, 2006; Szabo & Whiting, 2020).

2.3 | The interplay between thermal physiology, cognition, and behavior

Temperature affects behavior in two interconnected ways (Figure 2):

- a. *Top-down*, where thermal information is processed to produce a thermoregulatory response;

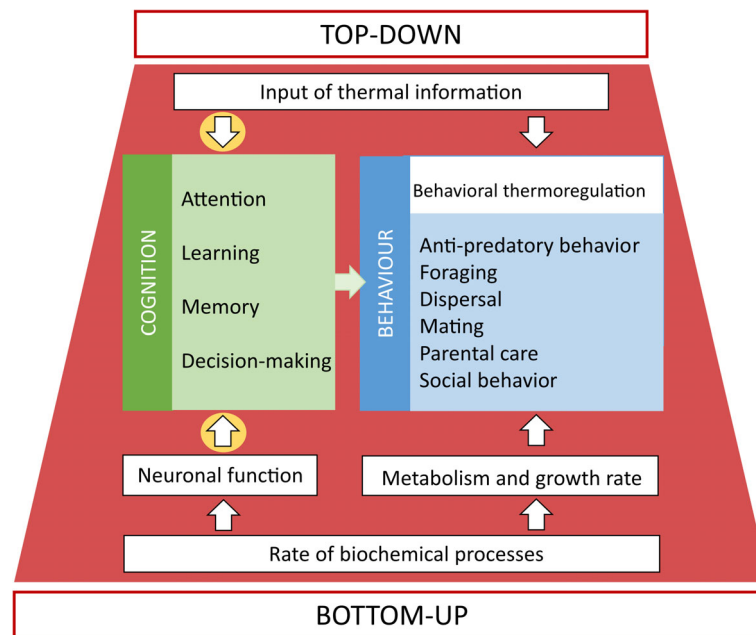


FIGURE 2 The proposed relationship between temperature, behavior, and cognition. Temperature affects animal behavior through *bottom-up* and *top-down* processes (Abram et al., 2017). The *top-down* effect of temperature refers to the processing of temperature information from sensory neurons to produce a thermoregulatory response (both physiological and behavioral). The *bottom-up* effect of temperature refers to the temperature-dependent rate of biochemical processes, which directly affects metabolism, growth rates, and neuronal function. Changes in metabolism can translate into behavioral changes, for example, altered feeding rates, without involving cognition. The present review focuses on how temperature may affect cognitive mechanisms (arrows highlighted in yellow). These include attention, learning, memory, and decision-making mechanisms, which allow selective filtering of environmental stimuli and modify behavior through experience (Shettleworth, 2010). The *bottom-up* highlighted arrow indicates that temperature-induced changes in neuronal function may lead to changes in cognitive performance, for example, impaired learning. The *top-down* highlighted arrow indicates that thermal information may reduce the cognitive capacity to process other competing external stimuli. Cognition regulates behavior in different contexts from foraging to predator avoidance, mate choice, and thermoregulation itself. Therefore, temperature-induced effects on cognition may translate into behavioral changes relevant for survival and reproductive success in the wild

- b. *Bottom-up*, where the temperature-dependent rate of biochemical reactions, and thus metabolism and growth rates, directly modifies behavior (Abram et al., 2017).

The *bottom-up* effect of temperature means that temperature variations can cause behavioral changes without requiring cognitive processing (Abram et al., 2017). For example, Moroccan bushcrickets (*Eugaster spinulosa*) produce song with shorter syllables as temperature increases, likely because higher temperatures directly increase the velocity of muscle contraction in the song-producing apparatus (Arias et al., 2012). Similarly, a higher metabolic rate induced by increased temperatures can cause a higher feeding rate in response to hunger level (Frances & McCauley, 2018; Walker et al., 2020). Finally, the functioning of sensory receptors can also be temperature-dependent, and therefore modify the quality of the information acquired from the environment and the following behavioral response, even if the underlying cognitive processes remain unchanged (Bakken et al., 2018).² Separating these mechanistic effects of temperature on perception from cognitive effects is likely to require controlled laboratory studies to complement field results. Potential avenues include psychophysical studies investigating an animals' ability to discriminate between stimuli under different temperatures, and electrophysiological studies assessing the electrical response of sensory neurons to a given stimulus under changing temperature conditions (Shettleworth, 2010).

The *top-down* response to temperature involves: (1) the input of thermal information from sensory neurons and integration in the central nervous system, and (2) the resulting production of a thermoregulatory response, which can be both physiological and behavioral, such as hormone release, regulation of peripheral blood flow, movement, induction of a specific posture (Angilletta et al., 2019). These behavioral changes are mainly stimulus–response reflexes. For example, small mammals spread saliva over their body surface to cool evaporatively, and both salivation and

subsequent grooming behavior can be directly elicited by increasing temperature in areas of the hypothalamus (Madden & Morrison, 2019).

Here, we focus on the cognitive mechanisms that allow selective filtering of environmental stimuli (attention) and determine lasting changes in behavior through experience (learning and memory) (Shettleworth, 2010). Temperature may impact these cognitive mechanisms through both a *top-down* and a *bottom-up* effect. First, *top-down* processing of thermal information may limit the processing capacity for competing environmental information and impair cognitive performance, even before a rise in body temperature (Gaoua et al., 2012). Second, a *bottom-up* effect of temperature may cause both short-term and long-term changes in neurotransmitter activity and neuronal function (e.g., Van Hook, 2020), which may in turn alter cognitive performance (Figure 2). Moderate temperature increases will not necessarily cause cognitive decline. Animals may have evolved adaptive compensatory responses to natural mild heat stress events (Robertson & Money, 2012). Moreover, a modest rise in temperature may support cognitive efficiency by accelerating the metabolic rate of oxygen in the nervous tissue (Schmit et al., 2017). Nonetheless, rapid anthropogenic warming and hot extremes may lead to cognitive impairment due to unpredictable, intense and prolonged heat exposure. For example, in zebrafish (*Danio rerio*), a 21-day exposure to 34°C (2°C above the species' VTM; Rey et al., 2015) reduced the production of synaptic proteins and neurotransmitters, leading to impaired learning (Toni et al., 2019).

Below we review the evidence for effects of elevated temperatures on cognition and discuss potential fitness implications. We refer the reader to other studies (Buchholz et al., 2019; Cunningham et al., 2021; Diele-Viegas & Rocha, 2018; Harvey et al., 2020; Stillman, 2019) for a review of the behavioral and physiological responses to increased temperatures.

2.4 | Cognitive performance and fitness

Cognitive processes cannot be observed directly, but must be inferred through experimentation. The behavioral responses of animals in particular tasks can thus give us measures of *cognitive performance* (Thornton et al., 2014). Recently, cognitive tasks have been employed to investigate the link between cognition and fitness in wild animals (Thornton & Boogert, 2019). Cognitive performance need not necessarily correlate positively with fitness (Madden et al., 2018; Rowe & Healy, 2014) because, for example, the investment in energetically costly brain tissue may be traded-off against other fitness-related traits (e.g., Burger et al., 2008). Nevertheless, numerous studies provide compelling evidence that higher cognitive performance can yield fitness benefits (reviewed in Boogert et al., 2018). Spatial memory has been the most investigated cognitive trait in this regard, because memory of shelter location, food sources, or territory borders is hypothesized to enhance survival. For example, mountain chickadees (*Poecile gambeli*) cache large quantities of food during the autumn, which they then retrieve during the harsh winter months. In this species, juveniles that perform better in a spatial memory task have higher survival chances (Sonnenberg et al., 2019). Analogously, male African striped mice (*Rhabdomys pumilio*) that perform well on long-term spatial memory tasks are more likely to survive during the dry season (Maille & Schradin, 2016).

Higher cognitive performance may also increase reproductive success. For example, male North Island robins (*Petroica longipes*) that perform better in a spatial memory task carry a higher proportion of large prey and spend less time flying when provisioning the nest, raising more offspring per brood (Shaw et al., 2019). Similarly, female Australian magpies (*Cracticus tibicen dorsalis*) that have higher general intelligence, a score combining performance in four cognitive tasks, raise more offspring to independence per year (Ashton et al., 2018). These studies show how survival and reproductive success in the wild may depend on individual cognitive performance. However, even in species where there is no evidence that higher cognitive performance is beneficial, cognitive performance below normal is likely to be detrimental.

When coping with challenging environmental conditions, such as food shortage and habitat modification, cognitive performance may become crucial. For example, after a heatwave reduced prey availability, bottlenose dolphins (*Tursiops aduncus*) that used a novel, socially-learned foraging behavior had lower mortality than dolphins that did not exhibit this behavior (Wild et al., 2019). Similarly, among bird species threatened by habitat destruction globally, those that are more likely to adopt novel feeding techniques have stable or increasing population trends (Ducatez et al., 2020). Therefore, behavioral flexibility and the propensity to innovate can increase wildlife resilience against environmental change.

2.5 | Cognitive performance and heat stress

Studies investigating the impact of heat stress on cognition have mostly focused on humans. Heat-mediated cognitive impairment is so common in humans that it is considered one of the most prevalent occupational health hazards globally (Hancock, 2020; Mazloumi et al., 2014). Knowledge of heat stress impacts on cognitive performance is applied in military training (Radakovic et al., 2007), sports science (Schmit et al., 2017), building engineering (Yeganeh et al., 2018), and education (Wargoeki et al., 2019). For example, recent studies show that in the absence of air-conditioning, student attention and memory decline during heatwaves (Cedeño-Laurent et al., 2018), and the number of hot school days predicts learning outcomes in over 50 countries (Park et al., 2021).

Elemental brain neurophysiology is evolutionarily conserved across invertebrates and vertebrates (Perry et al., 2013; Grillner & Robertson, 2016; Morand-Ferron, 2017; Ortega & Olivares-Bañuelos, 2020). Therefore, the main patterns found for the relationship between heat stress and human cognition may provide a useful reference for investigating heat stress effects on animal cognition. In humans, heat stress can affect attention, short-term memory, learning and decision-making (Allen & Fischer, 1978; Bell, 1985; Razmjou, 1996; Hocking et al., 2001; Sun et al., 2012; Taylor et al., 2016; Malcolm et al., 2018).³ The magnitude of heat-induced cognitive impairment depends on the complexity of the task and the duration of exposure to high temperatures (Hancock & Vasmatazidis, 2003). Tasks that require sustained attention to a stimulus, such as tracking the movements of an object, or performing two tasks simultaneously, show the greatest decline (López-Sánchez & Hancock, 2018). The general decrease in attention under heat stress translates into delayed reaction time (López-Sánchez & Hancock, 2018; Malcolm et al., 2018; Kingma et al., 2020). Cognitive impairment is greater when the increase in body temperature is faster (Hancock & Vasmatazidis, 2003). However, declines in cognitive performance have been observed even before changes in body temperature: the perception of thermal discomfort caused by variation in skin temperature alone may impact the attentional resources available for cognitive tasks (Gaoua et al., 2012).

2.5.1 | Heat stress and cognition in nonhuman animals

In animals, exposure to stressors is known to diminish attention to tasks, increasing mistakes and impairing decision-making, due to the diversion of attentional resources to the monitoring of a threat in the short-term, and fatigue in the long-term (Mendl, 1999). A thermal stressor may act on animal cognition similarly, initially reducing the focus on cognitive tasks, and directly impairing cognitive processes as the intensity and duration of exposure increases.

Even a mild cognitive impairment can make the difference between death and survival in the wild. In female African striped mice, reaction time under predator exposure positively predicts survival (Maille & Schradin, 2016), hence, a slow reaction due to heat stress may be fatal. Decreased responsiveness to predator cues caused by cognitive decline may help to explain higher predation rates found in a marine fish when temperatures increase (Allan et al., 2017). In hot environments, disruption of spatial memory (e.g., Lee et al., 2015) may hinder foraging, dispersal, territory defense, or mating (Spritzer et al., 2005; Maille & Schradin, 2016; Araya-Salas et al., 2018; Branch et al., 2019; Sonnenberg et al., 2019). Importantly, poorer decision-making under heat stress (e.g., Coomes et al., 2019), paired with a reduced ability to learn novel cues and behaviors (e.g., Rozan et al., 2007), may limit the ability to adaptively adjust to changing environmental conditions.

The timing of a heat stress event might be even more critical than its duration and intensity: heat stress during pregnancy or incubation might permanently change cognitive performance of developing young. Indeed, stressful events are known to modify cognitive development (Buchanan et al., 2013). For example, in some bird species, nutritional stress during rearing alters learning, spatial memory, inhibitory control and decision-making later in life (Pravosudov et al., 2005; Fisher et al., 2006; Bateson et al., 2015; Farrell et al., 2016). Therefore, heatwaves during breeding might impair cognitive performance of an entire cohort. These population-level changes could have amplified impacts on wildlife adaptability to climate change.

2.5.2 | Short-term effects of heat stress on animal cognition

Most studies on heat stress and animal cognition have focused on short-term effects on memory. A temperature increase within the natural range currently experienced by species can have no effect or improve memory (Abram

et al., 2015; Sunada et al., 2016; Teskey et al., 2012; Tan & Lukowiak, 2018). In these cases, evolution might have favored adaptive responses to short-term thermal stress. For example, great pond snails (*Lymnea stagnalis*) experience broad temperature fluctuations in their habitats. When exposed for 1 h to 30°C, they produced heat shock proteins preventing cellular damage and modified gene expression, improving memory formation (Sunada et al., 2016). This aligns with theory predicting that organisms in a poor state should maximize memory duration, because the fitness cost of not responding correctly to a stimulus may be substantial (Dunlap et al., 2009).

Intense or chronic heat stress disrupts memory—this is the most consistent finding across laboratory experiments on a wide range of taxa, including nematodes (*Caenorhabditis elegans*), fruit flies (*Drosophila melanogaster*), goldfish (*Carassius auratus*), mice (*Mus musculus*), and rats (*Rattus norvegicus*) (Table 1). Some experiments induced extreme heat stress, causing heat necrosis in goldfish (Cerf & Otis, 1957), or convulsions in mice (Kane & Jarvik, 1970) and rats (Mactutus et al., 1980). In other cases, the hot condition more closely mimicked natural heat stress events (Roussel et al., 1982; Rozan et al., 2007). A 2-h exposure to 40°C for example, led to intense heat stress in rats (over 3°C increase in body temperature above normal) associated with a significant decrease in spatial learning and memory in a simple navigation task (Rozan et al., 2007).

The magnitude of cognitive impairment depends on the degree of hyperthermia (Misanin et al., 1979), but also the nature of the information. For instance, rats fail to recognize previously encountered objects when body temperature increases 3°C above normal (Mickley & Cobb, 1998), but they still remember to avoid aversive stimuli with increases of 4°C (Ahlers & Riccio, 1987). Memory loss has been reported when heat stress is experienced during memory acquisition (Ahlers & Riccio, 1987; Beck & Rankin, 1995; Teskey et al., 2012) and consolidation (Cerf & Otis, 1957; Jacobs & Sorenson, 1969; Kane & Jarvik, 1970; Misanin et al., 1979; Zhao et al., 2008), but also during information retrieval (Rauch et al., 1989; Teskey et al., 2012). Negative effects on memory may occur even when heat stress events happen days before the acquisition of new information. In rats, a short heat stress event (2 h at 40°C) reduced performance on a spatial memory task undertaken 5 days later (Rozan et al., 2007).

Repeated exposure to high temperatures can initially buffer cognitive decline through acclimation, but leads to substantial cognitive impairment when prolonged. For example, rats exposed to high temperatures on two consecutive days showed a lower increase in body temperature and milder cognitive impairment than those exposed to high temperatures only on the first day (Mickley & Cobb, 1998). However, repeated daily exposure to extreme temperatures (42–43°C) as brief as 15 min significantly impaired spatial memory and long-term memory of object features in both mice and rats (Lee et al., 2015; Moon et al., 2017; Erfani et al., 2019). In addition, humidity can increase heat stress by constraining evaporative cooling (van Dyk et al., 2019): Inan and Aksu (2002) showed that although exposure to 40°C and 70% humidity does not impair spatial memory in mice, exposure to 28°C and 97% humidity causes a significant impairment.

Heat stress has also been found to impact other cognitive domains. It negatively affected spatial and associative learning in mice, rats, and zebrafish (Table 1). The observed heat-induced impairment has been related to changes in stress hormone levels, brain temperature and function (Mickley et al., 1994; Moon et al., 2017; Toni et al., 2019). Heat stress might also affect decision-making. For example, female zebra finches (*Teanopygia guttata*) show a spontaneous preference for conspecific calls, but when they have to choose between two perches located close to either a conspecific or a heterospecific call under heat stress, they show no preference (Coomes et al., 2019). Whether this is due to impacts on attention, auditory discrimination or decision-making mechanisms remains to be determined. An additional unexplored possibility is that heat stress generates pessimistic biases in decision-making (i.e., interpreting an ambiguous stimulus as negative), as is known to occur following exposure to other stressors (Bateson, 2016). For example, chickens (*Gallus gallus domesticus*) with increased stress hormone levels show higher latencies to approach a paper cone placed in an intermediate position between two positions previously associated with either a reward (mealworm) or a punishment (air puff), indicating they attribute a higher likelihood to the negative outcome (Iyasere et al., 2017).

2.5.3 | Long-term effects of heat stress on animal cognition

Heat stress events can occur at all life history stages. By altering brain development, thermal stressors experienced during early life can impair motor, associative, and reversal learning, as well as spatial learning and memory later in life (Table 2). *Drosophila* pupae exposed to high temperatures daily had fewer neurons as adults in brain areas involved in the processing and memory of olfactory inputs, and were less able to learn the association between an olfactory cue and an aversive stimulus (Wang et al., 2007; but no effect of a single brief exposure, Nikitina et al., 2003). Similarly,

TABLE 1 Short-term effects of heat stress on cognitive performance

Study	Study species	Measure of heat stress	Measure of cognition	Effect of heat stress on cognition
Cerf & Otis, 1957	Goldfish (<i>Carassius auratus</i>)	Body T raised at +7°C from VTM	Long-term memory	Negative
Beck & Rankin, 1995	Nematode (<i>Caenorhabditis elegans</i>)	45 min +7°C from VTM	Long-term memory	Negative
Jacobs & Sorenson, 1969	Mouse (<i>Mus musculus</i>)	<1 min +11°C from body T: 0.8°C increase in body T	Long-term memory	Negative
Kane & Jarvik, 1970	Mouse	3 min heater: 4°C increase in body T	Long-term memory	Negative
Grosser & Percy, 1971	Mouse	<1 min +11°C from body T	Long-term memory	No effect
Roussel et al., 1982	Mouse	21 days -3°C ^a from body T	Associative learning	Negative
Inan & Aksu, 2002	Mouse	7 days +2°C from body T: 2°C increase in body T	Spatial memory	No effect
Lee et al., 2015	Mouse	>7 days 15 min daily +6°C from body T	Spatial memory, long-term memory	Negative
Moon et al., 2017	Mouse	3 days 15 min daily +6°C from body T: 2°C increase in body T	Spatial memory, long-term memory	Negative
Johnson, 1970	Earthworm (<i>Lumbricus terrestris</i>)	10 min +7°C from VTM, 20 min +7°C from VTM	Long-term memory	No Effect, negative
Misanin et al., 1979	Rat (<i>Rattus norvegicus</i>)	5 min +7°C from body T: 3.5°C increase in body T	Long-term memory	Negative
Mactutus et al., 1980	Rat	<10 min +7°C from body T: 6°C increase in body T	Long-term memory	Negative
Ahlers & Riccio, 1987	Rat	+7°C from body T until 4°C increase in body T	Short-term memory, long-term memory	No effect, negative
Rauch et al., 1989	Rat	<15 min +4°C from body T: > 2°C increase in body T	Spatial memory	Negative
Mickley et al., 1994	Rat	Microwave: 1°C increase in body T	Short-term memory	Negative
Moser, 1995	Rat	Heater: 2°C increase in brain T	Spatial learning	No Effect
Mickley & Cobb, 1998	Rat	Microwave: 2°C increase in body T, 3°C increase in body T	Short-term memory	No effect, negative
Lieberman et al., 2005	Rat	+3°C from body T until 2°C increase in body T	Spatial memory	Negative
Rozan et al., 2007	Rat	2 h + 2°C from body T: > 3.5°C increase in body T	Associative learning, spatial learning and memory	Negative
Zhao et al., 2008	Rat	35 min incubator: > 1.5°C increase in body T	Spatial memory	Negative
Erfani et al., 2019	Rat	14 days 15 min daily +5°C from body T	Long-term memory, spatial learning	Negative

(Continues)

TABLE 1 (Continued)

Study	Study species	Measure of heat stress	Measure of cognition	Effect of heat stress on cognition
Nikitina et al., 2003	Fruit fly (<i>Drosophila melanogaster</i>)	30 min +8°C from VTM	Associative learning, short-term memory	No effect
Le Bourg et al., 2004	Fruit fly	30–120 min +8°C from VTM	Associative learning/inhibitory control	No effect <60 min, negative >60 min in males only
Zhang et al., 2008	Fruit fly	19 min at +9°C from VTM	Short-term memory	Negative
Li et al., 2009	Fruit fly	24 h at +2°C from VTM, 2 h at +7°C from VTM	Short-term memory	No effect
Teskey et al., 2012	Great pond snail (<i>Lymnea stagnalis</i>)	1 h + 5°C from VTM	Long-term memory	Positive
Sunada et al., 2016	Great pond snail	1 h + 5°C from VTM	Long-term memory	Positive
Tan & Lukowiak, 2018	Great pond snail	1 h + 5°C from VTM	Long-term memory	Positive
Abram et al., 2015	Parasitoid wasp (<i>Trissolcus basalis</i>)	1 h at 40°C, daily cycle T max 30°C ^b	Short-term memory, long-term memory	No effect, positive
Triki et al., 2018	Cleaner fish (<i>Labroides dimidiatus</i>)	El Niño: +4°C water T	Decision-making	Mixed
Toni et al., 2019	Zebrafish (<i>Danio rerio</i>)	21 days +2°C from VTM	Spatial/associative learning	Negative
Coomes et al., 2019	Zebra finch (<i>Taeniopygia guttata</i>)	> 12 h + 1°C from body T	Decision-making/auditory discrimination	Negative
Danner et al., 2021	Zebra finch	+3–4°C from body T during cognitive testing	Long-term memory, inhibitory control	No effect, negative

Notes: When the study did not explicitly state the species' voluntary thermal maximum, "VTM" (ectotherms) or normothermic body temperature, "body T" (endotherms), we used the following references: 30°C for goldfish (Reynolds et al., 1978), 25°C for nematodes (Anderson et al., 2007), 39°C for Guinea pigs (Akita et al., 2001), 37°C for mice (Mousel et al., 2001), 20°C for earthworms (Khan et al., 2012), 38°C for rats (Hainsworth, 1967), 29°C for fruit flies (Sayeed & Benzer, 1996), 25°C for great pond snails (Van der Schalie & Berry, 1973), 32°C for zebrafish (Rey et al., 2015), and 40°C for zebra finches (McNab, 1966). We abbreviated temperature to "T." We indicated the effect of heat stress on cognition as "negative" if there was a significant cognitive decline, "positive" if there was a significant improvement, "no effect" if heat stress did not affect cognitive performance, and "mixed" if heat stress affected cognition but a significant improvement/decline cannot be determined. All the studies were performed in captivity and none measured the fitness consequences of heat stress-induced changes in cognitive performance.

^aMice were housed at 34°C, which is lower than average normal body temperature of 37°C, but still above the temperature at which passive heat dissipation suffices to dissipate excess metabolic heat (30°C; Fischer et al., 2018).

^bVTM not available for this species. Heat stupor (critical thermal maximum) has been recorded at 42–43°C (Abram et al., 2015).

cognitive decline paired with lower brain weight and neuron numbers of newborns from heat stressed mothers have been reported in guinea pigs (*Cavia porcellus*) (impacts vary according to gestation stage; see Edwards et al., 1971; Edwards et al., 1976; Jonson et al., 1976; Edwards et al., 1984), mice (Shiota & Kayamura, 1989), and rats (Chang et al., 2011). Exposing rat pups to high temperatures also caused a later decline in spatial learning, memory and reversal learning, but only under high heat stress intensity and task complexity (Werboff & Havlena, 1963; Kornelsen et al., 1996; Mesquita et al., 2006). In trout (*Oncorhynchus mykiss*), maternal heat stress was related to altered expression of neurodevelopmental genes in the eggs and reduced ability of offspring to locate a food reward in a simple maze (Colson et al., 2019). Finally, a study on aphid parasitoids (*Aphidius ervi*) highlights a potential effect of developmental heat stress on decision-making: females that developed under high temperatures chose to lay eggs in low-quality host

TABLE 2 Long-term effects of heat stress on cognitive performance

Study	Study species	Measure of heat stress	Measure of cognition	Effect of heat stress on cognition
Werboff & Havlena, 1963	Rat (<i>Rattus norvegicus</i>)	Pups >1 min microwave: +4°C from body T	Spatial learning and memory	No Effect
Kornelsen et al., 1996	Rat	Pups +26°C from body T until convulsions	Spatial learning, reversal learning	Negative
Mesquita et al., 2006	Rat	Pups 30 min +5°C from body T	Spatial learning and memory, reversal learning	No Effect
Chang et al., 2011	Rat	Maternal exposure <1 h +2°C from body T	Spatial learning and memory	Negative
Lyle et al., 1973	Guinea pig (<i>Cavia porcellus</i>)	Maternal exposure 5 days 1 h daily +3°C from body T: +3°C increase in body T	Associative learning, reversal learning	No effect, negative
Jonson et al., 1976	Guinea pig	Maternal exposure 5 days 1 h daily +3°C from body T: +3°C increase in body T	Associative learning, reversal learning	Negative
Shiota & Kayamura, 1989	Mouse (<i>Mus musculus</i>)	Maternal exposure 3 days >10 min daily +6°C from body T	Associative learning, spatial learning and memory, long-term memory	Negative
Borsook et al., 1978	Common carp (<i>Cyprinus carpio</i>)	Juveniles 21 days +2°C from VTM	Motor learning	Negative
Jones et al., 2005	Honey bee (<i>Apis mellifera</i>)	50% of pupal development +1°C from normal brood nest T	Long-term memory	No Effect
Nikitina et al., 2003	Fruit fly (<i>Drosophila melanogaster</i>)	First instar or prepupal stage 30 min +5°C from VTM	Associative learning, short-term memory	No effect
Wang et al., 2007	Fruit fly	Larvae and pupae development 35 min daily +7.5°C from VTM	Associative learning, short-term memory	Negative
Amiel & Shine, 2012	Three-lined skink (<i>Bassiana duperreyi</i>)	Egg incubation +3°C compared to past decade	Spatial/associative learning and memory	Positive
Amiel et al., 2014	Three-lined skink	Egg incubation +3°C compared to past decade	Spatial/associative learning and memory	Positive
Clark et al., 2014	Three-lined skink	Egg incubation +3°C compared to past decade	Learning a novel motor task	Positive
Moiroux et al., 2015	Aphid parasitoid (<i>Aphidius ervi</i>)	Egg and immature stage at +8°C from optimal T ^a	Decision-making	Negative
Sampaio et al., 2016	Flatfish (<i>Solea senegalensis</i>)	Juveniles 28 days +4°C compared to current T	Decision-making	No effect
Domenici et al., 2017	Chilean abalone (<i>Concholepas concholepas</i>)	Juveniles 6 months +4°C compared to current T	Spatial learning	No Effect

(Continues)

TABLE 2 (Continued)

Study	Study species	Measure of heat stress	Measure of cognition	Effect of heat stress on cognition
Dayananda & Webb, 2017	Velvet gecko (<i>Amalosa lesueurii</i>)	Egg incubation +4°C compared to current T	Spatial learning and memory	Negative
Vila Pouca et al., 2019	Port Jackson sharks	Egg incubation +3°C compared to current T	Associative learning/quantity discrimination	Positive
Colson et al., 2019	Rainbow trout (<i>Oncorhynchus mykiss</i>)	Maternal exposure 6 weeks +1°C from VTM	Spatial learning and memory	Negative
Beltrán et al., 2020	Three-toed skink (<i>Saiphos equalis</i>)	Egg/maternal incubation +3°C compared to current T	Spatial learning and memory	Positive/no effect

Notes: When the study did not explicitly state the species' voluntary thermal maximum, "VTM" (ectotherms) or normothermic body temperature, "body T" (endotherms) during the developmental stage considered, we used the temperature references listed for Table 1, and the following: 32°C for fruit fly larvae (Wang et al., 2008), 31°C for juvenile common carps (Golovanov, 2013), 36°C for rat pups (Schmidt et al., 1986), 16°C for rainbow trouts (Schurmann et al., 1991). Historical temperature reference for three-lined skinks was 19°C (Telemeco et al., 2009). We abbreviated temperature to "T." We indicated the effect of heat stress on cognition as "negative" if there was a significant cognitive decline, "positive" if there was a significant improvement, and "no effect" if heat stress did not affect cognitive performance. All studies were performed in captivity, and the only study that measured the fitness consequences of heat stress-induced changes in cognitive performance found reduced survival of hot-incubated velvet geckos after release in the wild (Dayananda & Webb, 2017). *VTM of larvae not available due to initial development inside the body of the host aphid.

aphids (Moiroux et al., 2015). These studies prove that heat stress experienced during early life can have long-term effects on cognition.

Some studies on ectotherms, however, found that increased temperatures during development did not affect cognitive performance later in life (Jones et al., 2005; Sampaio et al., 2016; Domenici et al., 2017), or had a positive effect (Amiel & Shine, 2012; Amiel et al., 2014; Clark et al., 2014; Vila Pouca et al., 2019; Beltrán et al., 2020). In these cases, the temperature treatment represented an increase relative to current or historical environmental temperatures but did not exceed the VTM for the species, so it was unlikely to cause heat stress. For example, Domenici et al. (2017) reared juvenile abalones (*Concholepas concholepas*) at 19°C (end-of-century projected temperature) instead of 15°C (current summer average), and found that spatial learning performance was unchanged. However, the fact that shell growth improved at 19°C, suggests abalones might benefit from slightly warmer water temperatures, rather than suffer heat stress. The only exception to this trend is found in Port Jackson sharks (*Heterodontus portjacksoni*) where juveniles surviving heat stress during incubation made fewer mistakes in a quantity discrimination task (Vila Pouca et al., 2019). However, only five "hot-incubated" sharks were tested, so it may be premature to conclude that developmental heat stress enhanced cognitive performance in this species.

2.5.4 | Interaction between heat stress and other impacts of climate change

Interactive effects of higher temperatures and other impacts of climate change, such as increased CO₂ levels and frequency of extreme weather events, may amplify the magnitude of climate-induced cognitive impairment in wild animals. Wildfires and hurricanes can exacerbate heat stress by temporarily reducing vegetation cover, and hence the availability of thermal refugia (Scheffers et al., 2014). This may diminish the opportunities for thermoregulation and shorten the time window in which species can be active or constrain foraging to certain areas (Engbrecht & Lannoo, 2012; Elzer et al., 2013). By reducing canopy cover and increasing direct exposure to solar radiation, wildfires can also influence the temperature of freshwater bodies. For example, Isaak et al. (2010) estimated that burnt areas across the Boise River Basin experienced a warming rate twice as high as the basin average from 1993 to 2006. The shift in thermal habitat across the river basin caused the loss of 10–20% of stream areas suitable for bull trout (*Salvelinus confluentus*) spawning, potentially affecting future population stability (Isaak et al., 2010). Droughts can further increase the severity of heat stress because reduced water availability constrains thermoregulation (Sannolo & Carretero, 2019;

Veldhuis et al., 2019; Rozen-Rechels et al., 2020), and dehydration itself causes cognitive impairment (Santollo et al., 2019). Acidification interacts with warming in affecting cognitive performance and behavioral responses of marine animals (Nagelkerken & Munday, 2016; Domenici et al., 2017; Laubenstein et al., 2019). CO₂ levels in line with end-of-century projections can impair the ability to discriminate predator cues (Dixson et al., 2010), slowing reaction times (Allan et al., 2013; Jutfelt et al., 2013), and increasing mortality in the wild (Munday et al., 2010). A recent study also found that increased airborne CO₂ levels directly impact human cognition (Karnauskas et al., 2020), and thus potentially other terrestrial animals.

2.5.5 | Fitness consequences in the wild?

Although some studies used wild-caught animals (Domenici et al., 2017; Triki et al., 2018; Beltrán et al., 2020) or eggs (Amiel & Shine, 2012; Amiel et al., 2014; Dayananda & Webb, 2017), all the studies we reviewed in Tables 1 and 2 measured cognitive performance and/or heat stress in laboratory settings. Only one study related proxies of fitness with measures of heat-mediated changes in cognitive performance: Dayananda and Webb (2017) found lower survival of “hot-incubated” velvet geckos (*Amalosa lesueurii*) after release in the wild, directly predicted by reduced learning ability. The lack of studies on the impact of heat stress on cognition in the wild, combined with the absence of fitness measures of heat-induced cognitive impairment, constitutes a *major research gap*. For this reason, we propose a framework to facilitate empirical research into the relationship between heat stress and cognition in wild animals in a standardized way that will allow researchers working on different species to collaborate and compare results.

3 | A FRAMEWORK FOR FUTURE RESEARCH

3.1 | Research gaps

There is evidence for both short and long-term effects of heat stress on cognition across taxa (Tables 1 and 2). The emerging trend indicates that minor temperature increases within the natural range experienced by the species may not affect cognitive performance, while marked or repeated temperature increases can have long-lasting negative consequences on animal cognition, especially if they happen during key developmental stages. Despite this, we need to address some crucial knowledge gaps. First, there is a bias toward studies on memory of aversive stimuli or spatial memory, so we are missing information on other relevant cognitive traits. Examples of these are reversal learning and inhibitory control, which allow animals to revise learnt information and stop an unsuccessful behavior or adopt a different response (Szabo et al., 2020). Second, wild animals are exposed to a range of pathogens, predators, resource limitations, and environmental conditions (both physical and social) that captive animals do not experience, so their body condition, thermoregulatory behaviors, and learning opportunities likely differ from animals tested in a laboratory (Geiser et al., 2007; Du Toit et al., 2012; McCune et al., 2019; Jarrett et al., 2020; Vardi et al., 2020). Hence, the susceptibility of cognition to heat stress may be different in wild animals. Additionally, laboratory experiments may fail to capture synergistic effects of increased temperatures and CO₂ levels, and loss of shade and foraging opportunities on animal cognition. Third, many studies investigating heat stress effects on cognitive development limit testing to juveniles (e.g., Chang et al., 2011; Dayananda & Webb, 2017; Colson et al., 2019), hence it is essential to undertake longitudinal studies monitoring cognitive changes until and during adulthood. Most importantly, we need to link short- and long-term impacts of heat stress on cognition to measures of fitness.

3.2 | Research framework

The goal of research into the effects of heat stress on cognition is to incorporate critical temperature thresholds for cognitive decline into models of population viability to inform wildlife management priorities under different climate change scenarios. To define these temperature thresholds, we need to collect empirical datasets on: (1) the variation of individual cognitive performance under a range of temperatures, and (2) the variation in survival, dispersal, and reproductive success relative to individual cognitive performance. The first step is being able to measure cognitive performance in the wild.

3.2.1 | Measuring cognitive performance in the wild

Researchers measure cognition from *performance* in cognitive tasks (e.g., proportion of times the individual chooses the lid hiding food versus the incorrect one). This poses at least two challenges when studying wild animals: (a) the animal has to interact with the task, and (b) we need to account for noncognitive factors influencing individual performance, such as dexterity, neophobia, motivation and prior experience (Boogert et al., 2018). Some study systems allow experimenters to present tasks to wild animals directly (e.g., Ashton et al., 2018; Shaw et al., 2019), but in many cases this may not be feasible. An alternative approach may be to use automated tasks positioned in frequently visited areas. For instance, tasks that detect and respond to animal-borne radio-frequency identification (RFID) tags have been successfully used to study spatial memory (Sonnenberg et al., 2019), reversal learning (Cauchoix et al., 2017), and social learning (Aplin et al., 2015) in wild birds. All tasks should *tap into the natural behavior* of the animal to ensure ecological relevance, and require minimal training or habituation. It is possible to account for differences in motivation by recording the latency to interact with the task (e.g., Ashton et al., 2018), or the frequency of visits to an automated task (e.g., Sonnenberg et al., 2019), as well as other variables such as seasonality and body condition (Maille et al., 2015; Shaw, 2017; Ashton et al., 2018; Boogert et al., 2018). Differences in prior experience can be controlled by using stimuli that are novel for all tested individuals, for example, colors or shapes that are uncommon in the species' habitat (Rowe & Healy, 2014). Finally, increasing the cost of making mistakes, for example by adding extra weight to the lids, can ensure that the animal relies on cognitive abilities to solve the task, rather than sampling randomly (Sanford & Clayton, 2008).

3.2.2 | Measuring cognitive performance under heat stress

To assess the effect of heat stress on cognitive performance, the same individual has to be tested under environmental temperatures representing either “heat stress” or “non-heat stress” conditions. Researchers can ensure that the cognitive tests performed in the two conditions measure the same cognitive ability while minimizing the confounding effect of memory by using causally identical but visually different variants of a cognitive task (e.g., different lid colors in an associative learning task; Ashton et al., 2018). Ideally, “heat stress” and “non-heat stress” cognitive tests should be paired close in time to reduce potential confounding effects of seasonality on cognitive performance, such as changes in food availability or hormone levels (Maille & Schradin, 2017; Carbia & Brown, 2020). Finally, testing the repeatability of cognitive performance within versus between conditions allows researchers to determine whether cognitive performance under heat stress deviates beyond natural variation in task performance (Cauchoix et al., 2020).

In the wild, distinguishing whether an individual is in a condition of heat stress or not is not trivial. Most approaches to measure body temperature changes (e.g., thermometry, surgically implanted loggers) require trapping and handling of individuals (McCafferty et al., 2015). These procedures may confound the effect of heat stress on cognitive performance because (a) they may cause additional stress, or (b) they may entail a time lag between the measure of heat stress and the measure of cognitive performance. An alternative is to implant temperature-sensitive subcutaneous passive integrated transponder (PIT) tags *before* the beginning of the experiment. These simultaneously provide identification and temperature measurements (McCafferty et al., 2015).⁴ A PIT tag reader could then be placed next to the cognitive task to automatically record body temperature during cognitive testing. Thermal cameras represent another approach (McCafferty, 2013; Tattersall, 2016): studies in invertebrates (Gallego et al., 2016), and vertebrates including both endotherms (Thompson et al., 2017) and ectotherms (Valle et al., 2019; Barroso et al., 2020), show that infrared thermography can provide reliable measurements of body temperature. Additionally, eye temperature has been identified as a predictor of circulating stress hormone levels in wild birds (Jerem et al., 2018; Jerem et al., 2019). Importantly though, temperature measurements from thermal images are reliable only if a minimum spatial resolution (number of pixels in the surface of interest) is achieved, so thermal cameras need to be positioned at a short distance from the animal, and necessarily in the shade, as solar radiation alters measurements. A temperature logger connected to an object of known emissivity should be included in the shot for calibration (Jerem et al., 2015).⁵ A final option is quantifying behavioral indicators of heat stress, such as panting in birds (e.g., Pattinson et al., 2020), mammals (e.g., Lees et al., 2019) and reptiles (e.g., Camacho et al., 2018), superoptimal locomotor activity in insects (e.g., Gallego et al., 2016) and posture changes in amphibians (for a complete ethogram across a temperature gradient see Meza-Parral et al., 2020). It is important that the choice of heat stress measure is informed by physiological studies assessing species-specific responses to a temperature range representative of current and predicted climatic conditions.

Other environmental factors that influence the degree of heat stress such as humidity, wind speed and cloud cover (Mitchell et al., 2018; van Dyk et al., 2019), should also be measured. Recording these microclimate variables simultaneously can be logistically challenging. Measuring the temperature of animal models with the same size, shape and absorptance of live animals (e.g., painted copper hollow models, taxidermic mounts, or 3D prints) allows experimenters to integrate the effects of wind speed, radiation, air and ground temperature in a single measurement of *operative temperature* (Bakken, 1992; Bakken & Angilletta Jr, 2014). In ectotherms, the level of heat stress will be directly dependent on operative temperature, body mass and exposure duration (Christian et al., 2006). For some species, the animal model can be safely simplified to a black copper globe (black bulb thermometer; e.g., Van de Ven et al., 2019). By replicating these models within the habitat, experimenters can assess the spatial structure of the thermal environment (Hertz, 1992), which can then be integrated into climate change models to predict temperature variations under climate change at a spatial scale relevant for the study species (Logan et al., 2013).

Finally, dehydration alone impacts cognitive performance (e.g., Santollo et al., 2019). Techniques such as doubly labeled water and urinary specific gravity can be employed to measure hydration levels noninvasively (Wauters et al., 2018; Bourne et al., 2019). Alternatively, to control for different hydration levels across individuals, ambient-temperature water can be made available to animals prior to cognitive testing under both heat stress and non-heat stress conditions. Researchers should be aware that this might underestimate the overall effect of hot temperatures on cognitive performance in the wild. Indeed, limited access to water in the wild may constrain evaporative cooling, advance the onset of heat stress, and cause simultaneous dehydration and heat stress.

Carrying out cognitive testing under heat stress can be challenging because wild animals may retreat to thermal refugia and alter their activity levels. For effective testing, the task should be easily accessible and positioned in order to minimize the thermoregulatory cost of interacting with it, for example, in the shade or in proximity to a burrow. Even with this expedient, due to the engagement in thermoregulatory behaviors, the interval between trials might increase: the animal might spend some time resting and heat dissipating or might retreat in a burrow before approaching the task a second time after an unsuccessful attempt. Recording intertrial intervals allows researchers to account statistically for this effect when comparing cognitive performance between non-heat stress and heat stress conditions. However, since high temperatures often reduce the time window available for foraging (e.g., Funghi et al., 2019), some animals may be even more motivated to access a food reward when heat stressed. Figure 3 shows the example of a wild pied babbler heat dissipating while interacting with a learning task. Alternatively, tasks based on species' antipredator responses, such as reaction time during a simulated predator attack (e.g., Maille & Schradin, 2016) might be effective when the animal is not motivated to forage, as the need to react to a predator likely overrides immediate thermoregulatory needs (Angilletta et al., 2019).

3.2.3 | Population viability models and application to conservation

Testing for relationships between cognitive performance and measures of fitness allows researchers to estimate how changes in individual cognitive performance under heat stress may translate into changes in survival and recruitment rates at the population level. The indirect effect of heat-mediated cognitive impairment can be distinguished from direct lethal effects of heat stress by testing for an interaction between temperature and individual cognitive performance on survival rates, that is, differential survival during heatwaves of individuals differing in cognitive performance.

Collecting long-term life-history data requires substantial time investments to locate and identify wild animals over multiple years. However, such studies are essential to increase the accuracy of model predictions, and are the most represented and valued in environmental policy reports (Hughes et al., 2017). Note also that several animal populations worldwide already have large life-history datasets available due to ongoing long-term monitoring (Culina et al., 2020).⁶ To locate individuals, researchers can rely on animal-borne tracking technology, such as GPS tracking devices (Kays et al., 2015; Rasolofoniaina et al., 2021), or knowledge of the position of key foraging patches (Aplin et al., 2015) or territories (Shaw et al., 2015; McCune et al., 2019). In addition, recent advances in deep learning technology make it possible to automatically identify specific individuals from images and videos (Ferreira et al., 2020; Guo et al., 2020; Hou et al., 2020). For species with limited home ranges, outdoor enclosures could be built on-site allowing not only easier identification and localization but also manipulation of habitat structure and thus thermal environment (Sears et al., 2016; Li et al., 2017).

In Figure 4, we outline a comprehensive research framework that advises how robust testing of heat stress and cognition in wild animals can be achieved to produce temperature thresholds for cognitive decline. We show how these can be integrated into population viability models to predict population-level cognitive decline and its demographic



FIGURE 3 Southern pied babbler (*Turdoides bicolor*) interacting with an associative color discrimination learning task under a condition of heat stress. This cognitive task measures the ability to learn the association between a color cue (lid) and a food reward (mealworm inside the well). The sequence of photos shows from top to bottom: Individual panting and wingspreading to dissipate heat while perching, individual approaching the task on the ground while panting, individual searching a well and thus completing a trial. The photos were taken at the Kuruman River Reserve (Northern Cape, South Africa) during cognitive testing on a wild ringed individual as part of an ongoing research project (Ridley, 2020)

Source: Photo credit: Nicholas B. Pattinson

consequences under future increases in both the severity (magnitude of temperature increase above normal) and frequency of heat stress events. Finally, we identify two main areas of consideration for conservation (translocations, breeding programs) and management (urban biodiversity, social species) that can be applied to many wildlife populations. Temperature thresholds for the onset of heat stress at different life stages, and for maturation and spawning have already been integrated with projections of localized temperatures and behavioral considerations to predict the demographic consequences of climate change for the endangered delta smelt (*Hypomesus transpacificus*) (Brown et al., 2016). Similarly, critical temperature thresholds for embryonic development and adult foraging activity have been employed in spatial models to identify the most suitable release sites in the assisted colonization of threatened species (Mitchell et al., 2013; Jarvie et al., 2014; Mitchell et al., 2016). Cognition can affect translocation success (Krochmal et al., 2018; Roth & Krochmal, 2018), therefore the inclusion of temperature thresholds for cognitive decline in these models is important. Another potential application is in the design of nest-boxes, a conservation tool used in

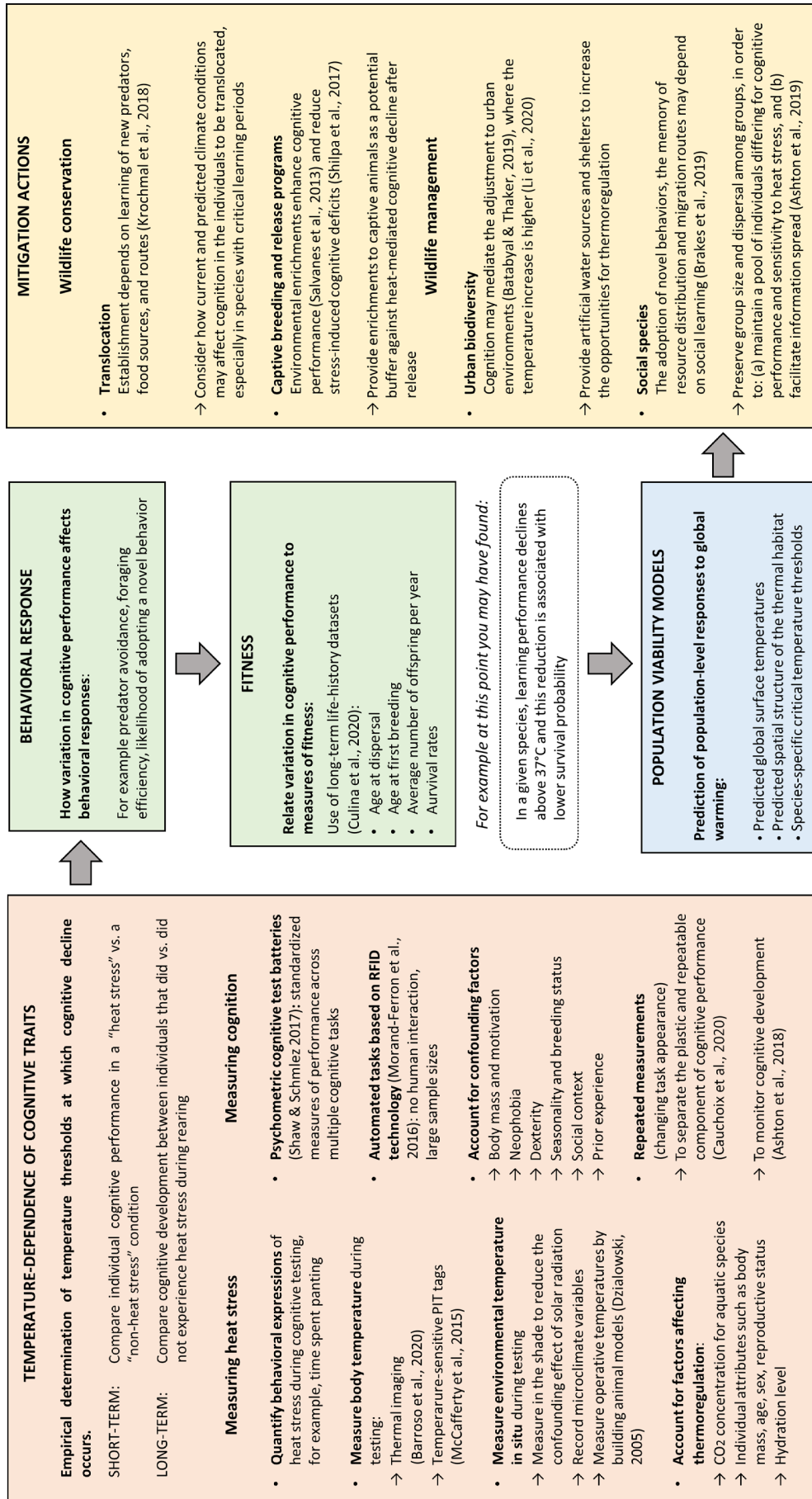


FIGURE 4 Framework for future research. We propose three steps: (1) determine the temperature-dependence of cognitive traits in the wild, (2) link variation in cognitive performance to behavioral responses and fitness measures, (3) integrate critical temperature thresholds for cognitive decline into models of population viability under future climate scenarios. Finally, we suggest potential applications to wildlife management and conservation (Ashton et al., 2018, 2019; Barroso et al., 2020; Batabyal & Thaker, 2019; Brakes et al., 2019; Cauchoix et al., 2020; Culina et al., 2020; Dzialowski, 2005; Krochmal et al., 2018; Li et al., 2020; McCafferty et al., 2015; Morand-Ferron et al., 2016; Salvanes et al., 2013; Shaw & Schmelz, 2017; Shilpa et al., 2017)

many species to compensate for the loss of natural cavities for breeding. The thermal profile of nest-boxes impacts heat stress levels, growth, and mortality of offspring (Catry et al., 2011; Griffiths et al., 2017). Knowledge of how temperature affects cognitive development in the target species can be implemented in the building and positioning of nest-boxes to prevent the emergence of cognitive deficits. More generally, providing additional thermal refugia, for example, shelters, burrows, or water sources, within the breeding habitat may mitigate the effect of heat stress on cognitive development (Pike & Mitchell, 2013; Abdu et al., 2018; Falcón & Hansen, 2018; Rich et al., 2019). This will be particularly important for the management of social species, in which the ability to learn from others can be essential for ensuring population viability (Brakes et al., 2019).

4 | CONCLUSION

Here we argue that climate change could directly impact cognition and hence animals' ability to flexibly adjust their behavioral responses to a rapidly changing environment. Under optimistic global warming predictions of 1.5°C, most land regions will warm more than 1.5°C (less for ocean regions), and hot extremes will increase by 3–4°C and become more frequent, especially in tropical regions (IPCC, 2018). Our review indicates that both cognitive development and adult cognition can be impaired by heat stress at temperature increases comparable to end-of-century projections (Jonson et al., 1976; Borsook et al., 1978; Roussel et al., 1982; Chang et al., 2011; Coomes et al., 2019; Danner et al., 2021) with potential fitness consequences (Dayananda & Webb, 2017). However, thus far the majority of studies have been laboratory-based and field data on changes in animal cognition in relation to heat stress are urgently needed. The impact that hot temperatures might have on cognition in the wild is worrying because: (a) animal survival and reproductive success can depend on cognitive performance, (b) heat stress events simultaneously affect the entire population, and (c) the effect of heat stress adds to other impacts of climate change (e.g., increasing CO₂ levels) on cognition and fitness. Species already living close to their upper thermal tolerance limits, or in environments with limited water availability may face the most immediate danger (Cruz-McDonnell & Wolf, 2016; Iknayan & Beissinger, 2018). In addition, species with long developmental periods and lifespans, a generalist foraging niche, and larger brains are expected to rely more on cognitive strategies to solve ecological problems (Sol et al., 2016; Yu et al., 2018) and hence suffer higher fitness declines under heat-induced cognitive impairment. If we are to identify achievable, effective, and timely measures to prevent and mitigate the negative impacts of rapid warming on wildlife, collaboration between physiologists, cognitive scientists, climatologists, and conservation scientists is essential.

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CONFLICT OF INTEREST

The authors have declared no conflicts of interest for this article.

AUTHOR CONTRIBUTIONS

Camilla Soravia: Conceptualization; writing-original draft; writing-review & editing. **Benjamin Ashton:** Conceptualization; supervision; writing-original draft; writing-review & editing. **Alex Thornton:** Conceptualization; writing-original draft; writing-review & editing. **Amanda Ridley:** Conceptualization; supervision; writing-original draft; writing-review & editing.

DATA AVAILABILITY STATEMENT

Data sharing not applicable to this article as no datasets were generated or analysed during the current study.

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ENDNOTES

- ¹ Thermal indexes developed by Hertz et al. (1993) can be used to determine the degree to which field-active ectotherms experience body temperatures outside their preferred body temperature range and to estimate the thermal habitat quality. Christian et al. (2006) further developed these indexes to account for thermal inertia due to the animal's body mass and for movements across a thermally heterogeneous environment. See also Taylor et al. (2021) for a complete review of the methodologies to study thermal tolerance in amphibians and lizards in the field.
- ² For a discussion of the potential effects of climate change on animals' sensory ecology and its link with behavioral and cognitive responses to climate change see O'Donnell (2018).
- ³ Results vary according to gender, previous experience, and type of heat exposure (passive versus active), for a discussion of these factors see Gaoua (2010).
- ⁴ Temperature-sensitive PIT tags are lightweight (<0.1 g) and can be implanted in animals with a small body size (>15 g) with minimal risk of injury (Oswald et al., 2018).
- ⁵ This can be achieved by connecting the temperature logger to a thermocouple that is either coated in black insulation tape (see Jerem et al., 2018; Jerem et al., 2019) or embedded in an aluminum or copper plate painted with a flat black paint (see Giloh et al., 2012; McFarland et al., 2020). See also the review by Tattersall (2016) for a discussion of calibration methods and practical considerations to ensure the quality of the temperature measurements obtained from thermal images.
- ⁶ There are a number of animal populations with available long-term life-history datasets worldwide. Examples of these are a meerkat (*Suricata suricatta*) population that has been monitored in South Africa since 1993 (Kranstauber et al., 2020; The Kalahari Meerkat Project, 2021), booted eagles (*Hieraaetus pennatus*) in Spain since 1998 (Jiménez-Franco et al., 2020), great tits (*Parus major*) (The Wytham Tit Project, 2016) and red deers (*Cervus elaphus*) (Isle of Rum red deer Project, 2021) in Great Britain since 1947 and 1972, respectively, chimpanzees (*Pan troglodytes schweinfurthii*) in Tanzania since 1960 (Bray & Gilby, 2020), banded mongooses (*Mungos mungo*) in Uganda since 1995 (Banded Mongoose Research Project, 2016; Vitikainen et al., 2019), and mountain goats and bighorn sheep in Canada since the early 1980s (Festa-Bianchet et al., 2019).

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