**Introduction**

Diving ectotherms are crucial to the functioning of aquatic ecosystems and represent a taxonomically diverse group (Butler and Jones, 1982; Costa, 2007). The evolution of air-breathing organs made terrestrial environs habitable, but many species returned to aquatic habitats, leading to the reinvasion of air-breathing species (Butler and Jones, 1982; Seymour, 1982). This transition occurred in all groups of tetrapod vertebrates across multiple points in evolutionary history, leading to a diverse array of diving ectotherms (turtles, snakes, crocodiles, iguanas, frogs and salamanders) living in freshwater and marine habitats (Butler and Jones, 1982). The ecology of these species in closely tied to the underwater environment and submergences are necessary to fulfill a range of critical tasks. For example, the viperine water snake (*Natrix maura*) dives to hunt fish by actively chasing them or by using a sit-and-wait strategy (Aubret et al., 2015). In contrast, juvenile estuarine crocodiles (*Crocodylus porosus*) dive to avoid both aerial and subsurface predators, whilst in adult crocodiles, diving is more important for social interactions, facilitating sit-and-wait hunting and avoiding rapid surface water currents (Campbell et al., 2010b; Grigg and Kirshner, 2015). Time available for these underwater tasks is, however, constrained by the need to surface to replenish oxygen stores (Butler and Jones, 1982).

The maximum amount of time an air-breathing animal can remain underwater prior to the switch to anaerobic metabolism and concomitant lactate accumulation is termed the aerobic dive limit (ADL; Butler, 2006). A diver’s ADL can be calculated by dividing its total body oxygen stores (stored in the lungs, blood and tissue) by the rate at which oxygen is consumed (i.e. metabolic rate). The ADL of ectotherms is inversely related to water temperature, due to the thermal sensitivity of metabolism (Rodgers and Franklin, 2017). As the body temperature of a diving ectotherm equilibrates with water temperature, the rate at which body oxygen stores are consumed becomes directly related to water temperature, with oxygen stores consumed more rapidly as temperatures rise. For example, ectotherm metabolic rates typically double (or even triples) with every 10°C increase in body temperature, meaning that an ectotherm diving at 30°C is predicted to dive for only half as long compared to an ectotherm diving at 20°C. For example, the ADL of a freshwater turtle (*Mauremys caspica leprosa*) fell from 221 min at 15°C to 58 min at 25°C (Fuster et al., 1997). Anthropogenically forced warming in marine and freshwater habitats therefore poses a threat to ectothermic divers, with the duration of time performing critical underwater tasks potentially being greatly reduced.

The threat of climate warming to diving ectotherms has been largely overlooked, despite many studies showing substantial decreases in dive durations as temperatures rise. Dive durations in the Arafura file snake (*Acrochordus arafurae)*, for example, decreased by 63% in response to an acute temperature increase from 20°C to 32°C (Pratt and Franklin, 2010). Similarly, during a one-hour continual predator threat juvenile *C. porosus* were able to remain submerged for 36.8 min at 28°C and only 21.3 min at 35°C (Rodgers et al., 2015). Dive durations are also influenced by seasonal temperature increases. Field studies have shown marked declines in dive durations during summer months compared to winter months in both turtles (Bentivegna et al., 2003; Bradshaw et al., 2007; Gordos et al., 2003) and crocodilians (Campbell et al., 2010a). Warmer waters, brought about by climate change, could have deleterious consequences for diving ectotherms. Elevated temperatures may cut short time available for critical underwater activities (e.g. foraging, predator-avoidance and social interactions) and force animals to spend more time at the water’s surface where predation risk is highest.

The deleterious effects of climate change on ectotherms diving behaviour may, however, be counteracted by thermal acclimatization responses (Seebacher et al., 2015). Increased oxygen demands at elevated temperatures could be offset by thermal acclimation (under experimentally controlled conditions) or acclimatization (in a natural field setting) (Johnston and Dunn, 1987; Wilson and Franklin, 2002). Thermal acclimation/acclimatization involves physiological remodelling across multiple levels of organismal organisation- from the up- or downregulation of particular genes (Podrabsky and Somero, 2004), to the alteration of enzyme reaction rates and changes to cell membrane thickness (Glanville and Seebacher, 2006), to alterations to muscle contractility (Shuman and J., 2018) and cardiovascular functioning (Keen et al., 2017). In the context of diving in a warming world, thermal acclimation/acclimatization would involve a dampening of thermodynamic effects on metabolism at elevated temperatures, so that total body oxygen stores are consumed at a slow rate.

Gas-exchange systems may also play an important role in mediating the effects of elevated temperatures on diving behaviour. Many divers rely solely on pulmonary gas exchange and have a negligible capacity for aquatic respiration (Wright, 1986). In contrast, bimodal breathers can supplement aerial respiration with aquatic respiration. Aquatic gas exchange typically occurs via diffusion across the skin (i.e. cutaneous respiration; Feder and Burggren, 1985), but some divers also have specialised organs (e.g. buccopharyngeal cavity, cloacal bursae) to facilitate the exchange of respiratory gases with the aquatic environment (Maina, 2002). For example, several freshwater turtles (e.g. *Elseya albagula, Elusor macrurus* and *Rheodytes leukops)* have cloacal bursae which are highly vascularised, sac-like evaginations of the cloaca, that are ventilated with water by the contraction of cloacal muscles (FitzGibbon and Franklin, 2010; Gordos and Franklin, 2002; Storey et al., 2008). The ability to respire aquatically allows bimodal breathers to prolong dive durations and it has been suggested that supplemental aquatic respiration may reduce the energetic cost of diving, prolong time available for underwater tasks and facilitate the exploitation of oxygen-rich riffle zones (Mathie and Franklin, 2006; Storey et al., 2008; Tucker et al., 2001). Due to these advantages, it has been hypothesised that bimodal breathers may be less sensitive to the effects of temperature on dive duration compared to divers solely reliant on pulmonary gas exchange. Moreover, bimodal breathers are predicted to upregulate their reliance on aquatic respiration at high temperatures to meet increased metabolic demands and defend dive durations. Studies testing this prediction have returned mixed findings, with some studies suggesting reliance on aquatic respiration is independent of temperature (Bruton et al., 2012; Prassack et al., 2001; Pratt and Franklin, 2010; Udyawer et al., 2016).

Although the profound effects of temperature on ectotherm metabolism, life-history and fitness are well-established, the effects of elevated temperature on diving has been overlooked. Two reviews show that dive duration tend to decrease as temperatures rise in ectotherms (Hayward et al., 2016; Jackson, 2007), but a systematic review has not yet been conducted. Here, we test whether diving is thermally sensitive in ectotherms using meta-analytic methods. Specifically, we tested the following questions: (1) Do dive durations decrease with rising water temperatures? (2) Is there evidence for thermal acclimation/acclimation responses with respect to diving? and (3) Are bimodal breathers more resilient to the effects of temperature on dive durations? These finding were used to predict how much underwater time could be lost to climate warming and how diving, ectothermic vertebrates may fare in a warmer world.

**Methods**

*Literature search and data extraction*

We conducted a literature search using Scopus and Web of Science's (WoS) core collection on 25 February 2020, to identify studies seeking to test the thermal sensitivity of diving behaviour. We used the following search strings: TOPIC: (“dive” OR “diving”) AND (“temperature” OR “thermal” OR “season\*”) AND (“ectotherm\*” OR “reptile\*” OR “\*snake\*” OR “turtle\*” OR “crocod\*” OR “newt\*”) in WoS and TITLE-ABS-KEY (“dive” OR “diving”) AND (“temperature” OR “thermal” OR “season\*”) AND (“ectotherm\*” OR “reptile\*” OR “\*snake\*” OR “turtle\*” OR “crocod\*” OR “newt\*”) in Scopus.

We identified 225 and 222 studies meeting the search criteria in Scopus and WoS, respectively. A total of 149 duplicates (115 identified in EndNote, 32 identified in Rayyan) were removed leaving us with 298 papers for title and abstract screening. We cross-referenced this search with three major reviews: Jackson (2007), Brischoux et al. (2008) and Hayward et al. (2016), and included any papers missed in our initial search (n = x). Title and abstract screening was conducted in Rayyan (Ouzzani et al., 2016) and we excluded studies that: 1) were reviews or commentaries (N = 28), 2) were not on air-breathing, diving ectotherms (N = 33) or 3) did not measure volitional dive durations across two or more experimental temperatures or across seasons in the field (N =115). Studies on leatherback turtles (*Dermochelys coriacea*) were also excluded because they are functionally endothermic (N = 24) (Bostrom and Jones, 2007; Southwood et al., 2005).

Following these exclusion steps, we identified 100 papers with extractable data (Fig.1). From these papers we extracted means, variance (standard errors, standard deviations or confidence intervals) and sample sizes. Data presented in figures were extracted using metaDigitise (Pick et al., 2018). Authors were contacted to request summary statistics where necessary. Data were excluded when means, variance and sample sizes could not be obtained. What we extracted from each paper.

*Effect size calculation*

*Moderator variables and predictions*

*Meta-analysis*

**References**

**Aubret, F., Tort, M. and Sarraude, T.** (2015). Evolution of alternative foraging tactics driven by water temperature and physiological constraints in an amphibious snake. *Biological Journal of the Linnean Society* **115**, 411-422.

**Bentivegna, F., Hochscheid, S. and Minucci, C.** (2003). Seasonal variability in voluntary dive duration of the Mediterranean loggerhead turtle, Caretta caretta. *Scientia Marina* **67**, 371-375.

**Bostrom, B. L. and Jones, D. R.** (2007). Exercise warms adult leatherback turtles. *Comparative Biochemistry & Physiology Part A: Molecular and Integrative Physiology* **147**, 323-331.

**Bradshaw, C. J. A., McMahon, C. R. and Hays, G. C.** (2007). Behavioral inference of diving metabolic rate in free-ranging leatherback turtles. *Physiological and Biochemical Zoology* **80**, 209-219.

**Brischoux, F., Bonnet, X., Cook, T. R. and Shine, R.** (2008). Allometry of diving capacities: ectothermy vs. endothermy. *Journal of Evolutionary Biology* **21**, 324-329.

**Bruton, M. J., Cramp, R. L. and Franklin, C. E.** (2012). Benefits of thermal acclimation in a tropical aquatic ectotherm, the Arafura filesnake, Acrochordus arafurae. *Journal of Comparative Physiology B-Biochemical Systems and Environmental Physiology* **182**, 541-551.

**Butler, P. J.** (2006). Aerobic dive limit. What is it and is it always used appropriately? *Comparative Biochemistry and Physiology, Part A* **145**, 1-6.

**Butler, P. J. and Jones, D. R.** (1982). The comparative physiology of diving in vertebrates. *Advances in Comparative Physiology and Biochemistry* **8**, 179-364.

**Campbell, H. A., Dwyer, R. G., Gordos, M. and Franklin, C. E.** (2010a). Diving through the thermal window: implications for a warming world. *Proceedings: Biological Sciences* **277**, 3837-3844.

**Campbell, H. A., Watts, M. E., Sullivan, S., Read, M. A., Choukroun, S., Irwin, S. R. and Franklin, C. E.** (2010b). Estuarine crocodiles ride surface currents to facilitate long-distance travel. *Journal of Animal Ecology* **79**, 955-964.

**Costa, D. P.** (2007). Diving physiology of marine vertebrates. In *Encyclopedia of Life Sciences* pp. 1-7. Chichester: John Wiley & Sons Ltd.

**Feder, M. E. and Burggren, W. W.** (1985). Cutaneous gas exchange in vertebrates: Design, patterns, control and implications. *Biological Reviews* **60**, 1-45.

**FitzGibbon, S. I. and Franklin, C. E.** (2010). The importance of the cloacal bursae as the primary site of aquatic respiration in the freshwater turtle, Elseya albagula. *Australian Zoologist* **35**, 276-282.

**Fuster, J. F., Pages, T. and Palacios, L.** (1997). Effect of temperature on oxygen stores during aerobic diving in the freshwater turtle Mauremys caspica leprosa. *Physiological Zoology* **70**, 7-18.

**Glanville, E. J. and Seebacher, F.** (2006). Compensation for environmental change by complementary shifts of thermal sensitivity and thermoregulatory behaviour in an ectotherm. *Journal of Experimental Biology* **209**, 4869-4877.

**Gordos, M. and Franklin, C. E.** (2002). Diving behaviour of two Australian bimodally respiring turtles, Rheodytes leukops and Emydura macquarii, in a natural setting. *Journal of Zoology* **258**, 335-342.

**Gordos, M. A., Franklin, C. E. and Limpus, C. J.** (2003). Seasonal changes in the diel surfacing behaviour of the bimodally respiring turtle Rheodytes leukops. *Canadian Journal of Zoology-Revue Canadienne De Zoologie* **81**, 1614-1622.

**Grigg, G. C. and Kirshner, D.** (2015). Biology and evolution of crocodylians. . Clayton South, Australia: CSIRO Publishing.

**Hayward, A., Pajuelo, M., Haase, C. G., Anderson, D. M. and Gillooly, J. F.** (2016). Common metabolic constraints on dive duration in endothermic and ectothermic vertebrates. *Peerj* **4**, 9.

**Jackson, D. C.** (2007). Temperature and hypoxia in ectothermic tetrapods. *Journal of Thermal Biology* **32**, 125-133.

**Johnston, I. A. and Dunn, J.** (1987). Temperature acclimation and metabolism in ectotherms with particular reference to teleost fish. *Symposia of the Society for Experimental Biology* **41**, 67-93.

**Keen, A. N., Jordan, M. K., Holly, S. A. and Gillis, T. E.** (2017). Temperature-induced cardiac remodelling in fish. *Journal of Experimental Biology* **220**, 147-160.

**Maina, J. N.** (2002). Structure, function and evolution of the gas exchangers: comparative perspectives. *Journal of Anatomy* **201**, 281-304.

**Mathie, N. J. and Franklin, C. E.** (2006). The influence of body size on the diving behaviour and physiology of the bimodally respiring turtle, Elseya albagula. *Journal of Comparative Physiology B-Biochemical Systemic and Environmental Physiology* **176**, 739-747.

**Ouzzani, M., Hammady, H., Fedorowicz, Z. and Elmagarmid, A.** (2016). Rayyan — a web and mobile app for systematic reviews. *Systematic Reviews* **5**, 210.

**Pick, J. L., Nakagawa, S. and Noble, D. W. A.** (2018). Reproducible, flexible and high-throughput data extraction from primary literature: The metaDigitise R package. *Methods in Ecology and Evolution* **10**, 426-431.

**Podrabsky, J. E. and Somero, G. N.** (2004). Changes in gene expression associated with acclimation to constant temperatures and fluctuating daily temperatures in an annual killifish Austrofundulus limnaeus. *Journal of Experimental Biology* **207**, 2237-2254.

**Prassack, S. L., Bagatto, B. and Henry, R. P.** (2001). Effects of temperature and aquatic Po-2 on the physiology and behaviour of Apalone ferox and Chrysemys picta. *Journal of Experimental Biology* **204**, 2185-2195.

**Pratt, K. L. and Franklin, C. E.** (2010). Temperature independence of aquatic oxygen uptake in an air-breathing ectotherm and the implications for dive duration. *Comparative Biochemistry and Physiology a-Molecular & Integrative Physiology* **156**, 42-45.

**Rodgers, E. M. and Franklin, C. E.** (2017). Physiological mechanisms constraining ectotherm fright-dive performance at elevated temperatures. *Journal of Experimental Biology* **220**, 3556-3564.

**Rodgers, E. M., Schwartz, J. J. and Franklin, C. E.** (2015). Diving in a warming world: the thermal sensitivity and plasticity of diving performance in juvenile estuarine crocodiles (Crocodylus porosus). *Conservation Physiology* **3**, 9.

**Seebacher, F., White, C. R. and Franklin, C. E.** (2015). Physiological plasticity increases resilience of ectothermic animals to climate change. *Nature Climate Change* **5**, 61-66.

**Seymour, R. S.** (1982). Physiological adaptations to aquatic life. In *Biology of the Reptilia, Physiological Ecology*, vol. 13 eds. C. Gans and F. H. Pough), pp. 1-51: Academic Press.

**Shuman, J. L. and J., C. D.** (2018). Red muscle function and thermal acclimation to cold in rainbow smelt, Osmerus mordax, and rainbow trout, Oncorhynchus mykiss. *Journal of Experimenta Zoology Part A* **329**, 547-556.

**Southwood, A. L., Andrews, R. D., Paladino, F. V. and Jones, D. R.** (2005). Effects of diving and swimming behavior on body temperatures of Pacific leatherback turtles in tropical seas. *Physiological and Biochemical Zoology* **78**, 285-297.

**Storey, E. M., Kayes, S. M., De Vries, I. and Franklin, C. E.** (2008). Effect of water depth, velocity and temperature on the surfacing frequency of the bimodally respiring turtle Elseya albagula. *Functional Ecology* **22**, 840-846.

**Tucker, A. D., Limpus, C. J., Priest, T. E., Cay, J., Glen, C. and Guarino, E.** (2001). Home ranges of Fitzroy River turtles (Rheodytes leukops) overlap riffle zones: potential concerns related to river regulation. *Biological Conservation* **102**, 171-181.

**Udyawer, V., Simpfendorfer, C. A., Heupel, M. R. and Clark, T. D.** (2016). Coming up for air: thermal dependence of dive behaviours and metabolism in sea snakes. *Journal of Experimental Biology* **219**, 3447-3454.

**Wilson, R. S. and Franklin, C. E.** (2002). Testing the beneficial acclimation hypothesis. *Trends in Ecology & Evolution* **17**, 66-70.

**Wright, J. C.** (1986). Low to negligible cutaneous oxygen uptake in juvenile Crocodylus porosus. *Comparative Biochemistry and Physiology a-Molecular & Integrative Physiology* **84**, 479-481.