**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 is 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). 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 currents (Campbell et al., 2010c; 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 muscle 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 triple) 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 a conspecific 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 in summer months compared to winter months in 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 and force animals to spend more time at the water’s surface where predation risk is highest (Heithaus and Dill, 2002; Heithaus and Dill, 2003; Heithaus et al., 2002).

Gas-exchange systems may 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 and 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, gill-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 proposed that bimodal breathers may be less sensitive to the effects of temperature on dive durations 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).

Body size is also a key determinant of ectotherm dive durations. Body oxygen stores typically scale linearly (i.e. isometrically, scaling exponent of 1) with body mass. For example,

estuarine crocodiles can undergo a 20, 000-fold increase in body size throughout a lifetime (e.g. 0.05 kg hatchling - 1000 kg adult; Grigg and Kirshner, 2015) and a similar increase in lung oxygen stores (scaling exponent = 0.9; Wright and Kirshner, 1987). In contrast to body oxygen stores, metabolic rate scales allometrically with body mass with an exponent of approximately 0.75. The implications of the differential scaling of oxygen stores and oxygen usage means that larger diving animals not only have larger reservoirs of oxygen stores, but they consume these stores more efficiently. Therefore, ADLs are mass-dependent in terms of both oxygen stores and usage, such that larger animals can remain submerged far longer than smaller animals before needing to surface. Smaller divers may therefore be disproportionately affected by increases in temperature due to small body oxygen stores and high mass-specific metabolic rates, however the potential moderating effects of body size remain unexplored.

The deleterious effects of climate change on ectotherms diving behaviour may, however, be counteracted by phenotypic plasticity in the form of thermal acclimatization responses (Seebacher et al., 2015). The capacity to responsively alter the thermal sensitivity of underlying physiology in response to a changing environment is termed acclimatization when observed in the field under natural conditions, or alternatively termed acclimation, when observed under experimentally controlled conditions (Wilson and Franklin, 2002). Thermal acclimation/acclimatization can involve physiological remodelling across multiple levels of organismal organisation; from the up- or down-regulation of particular genes (Podrabsky and Somero, 2004), to alterations in enzyme reaction rates, mitochondria density and function, cell membrane thickness, muscle contractility and cardiovascular functioning (Glanville and Seebacher, 2006; Keen et al., 2017; Shuman and J., 2018). In the context of diving at elevated temperatures, thermal acclimation/acclimatization involves a dampening of thermodynamic effects on metabolism at high temperatures, so that body oxygen stores are consumed at a slower rate, and/or an increase in body oxygen stores via an upregulation of oxygen-binding proteins (e.g. haemoglobin, myoglobin). Increases in global temperatures and thermal variability are predicted to create or strengthen selection pressure favouring plastic phenotypes, particularly in long-lived species, like crocodilians, marine turtles and marine iguanas (Kawecki, 2000). A changing environment may also favour an increase in phenotypic variability, such that the probability of a beneficial phenotype arising is maximised (Hansen et al., 2006). Populations with greater phenotypic variation are predicted to cope better with extreme climatic events, like heatwaves, because they are more likely to contain individuals, who by chance, can tolerate the changed conditions (Hansen et al., 2006). Indeed, increases in developmental temperatures have been shown to increase phenotypic variability in fishes, with larger temperature changes seeing greater increases in phenotypic variability (O'Dea et al., 2018). However, it remains unknown if rises in temperature increase phenotypic variability with respect to diving, despite the adaptive potential of this response.

Although it is recognised that climate warming presents a major threat to the persistence of many ectothermic species, the effects of elevated temperature on diving has been largely overlooked. Diving species depend on their capacity to remain submerged to perform a myriad of fitness-related activities, such as foraging, prey-pursuit, predator-avoidance and key social interactions. Two reviews show that dive durations tend to decrease as temperatures rise in ectotherms (Hayward et al., 2016; Jackson, 2007), but a systematic review, with a focus on climate warming, has not yet been conducted. Here, we test whether diving is thermally sensitive in ectotherms using meta-analytic methods. Specifically, we tested the following predictions: (i) acute increases in temperature decrease mean dive durations, (ii) larger increases in temperature will exert a stronger effect on mean dive durations, (iii) the effects of temperature on mean dive durations will be weaker in bimodal breathers compared to aerial breathers, (iv) the effects of temperature on mean dive durations will be weaker in larger (in terms of body mass) divers compared to smaller divers, and (v) chronic exposure to elevated temperature will blunt (i.e. lessen) the effects of temperature on mean dive durations. Because changing environments can also impact phenotypic variability, we explored how elevated temperatures and moderating variables (i.e. magnitude of temperature increase, breathing mode and body size) affect variability in dive durations. These finding were then 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 searched for experimental studies that measured dive durations (i.e. minutes submerged) in diving vertebrates at two more water temperatures. Searches were conducted using Scopus and Web of Science's (WoS) core collection on 25 February 2020. 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 voluntary dive durations across two or more experimental temperatures or field seasons under laboratory or field conditions (N =115). We included field studies where dive durations were measured in free-ranging animals across one or more seasons using biotelemetry tags (e.g. **list examples**). These field studies needed to couple dive duration recordings with either direct body temperature measures or water temperature measurements (assuming animal body temperature equaled water temperature). Only one study met the above criteria for invertebrates (Calosi et al., 2012), so we chose to focus exclusively on vertebrates. We also excluded studies where animals were forced to dive due to atypical physiological alterations induced by forced submergence (**ref**). Studies on leatherback turtles (*Dermochelys coriacea*) were 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. 2). From these papers we extracted means, variance (standard errors, standard deviations or confidence intervals) and sample sizes. We avoided extracting maximum dive durations because maximum dive durations were rarely reported and likely have anaerobic contributions. Data presented in figures were extracted using *metaDigitise* (Pick et al., 2018). Authors were contacted to request missing summary statistics where necessary and if they could not be obtained, we excluded these studies (N=x). We only included comparisons for treatment groups or field recording when they had three or more animals.

*Effect size calculation*

To test the effect of temperature on the mean and variability in dive duration, we calculated two effect sizes, the log response ratio (*ln*RR; Hedges, ref) and the log coefficient of variation ratio (*ln*CVR; Nakagawa et al., 2015) using the *escalc* function in the *metafor* package (Viechtbauer, 2010) in *R*. To assess differences in mean dive duration we used *ln*RR, which is the natural logarithm of the ratio between mean dive durations between treatments. Changes in the variability in dive duration across treatments was quantified using *ln*CVR, which is the ratio between the coefficients of variation (i.e., SD divided by the mean) for treatments. We used *ln*CVR because we observed strong mean-variance relationships in our data. When dive durations were measured at multiple temperatures, we took each pairwise temperature comparison. For both logged ratios (*ln*RR and *ln*CVR), we specified the control temperature (i.e. cooler temperature) as the denominator and the treatment temperature (i.e. warmer temperature) as the numerator, so that negative effect sizes indicate a decrease in dive duration means or variance at the warmer (treatment) temperature, whereas positive effect sizes indicate an increase in dive duration means or variance at the warmer (treatment) temperature.

*Moderators*

We extracted a series of moderator variables from each study that we predicted would affect both the magnitude and direction of effect sizes. These included: 1) respiration mode (i.e. aerial or bimodal); 2) body mass (g) and 3) the magnitude of temperature change between treatments (i.e. ΔT) and 4) the average temperature of the two treatments (T\_mean). Including the temperature difference between treatments, as well as the mean temperature of treatments, was important because we expected that the magnitude of effects would be larger for experimental treatments farther apart in temperature. Additionally, effect size and magnitude are expected to depend on the general temperature at which dive performance was measured; if treatments were conducted at high temperatures only smaller differences in dive duration are expected. When body mass data were not presented (N =1), we obtained body mass estimates for the same species and life-stage from published literature (Denoel et al., 2005).

*Meta-analysis*

We fit meta-analytic and meta-regression multilevel mixed-effects models using the *rma.mv* function in the *metafor* package in *R.* When the 95% confidence intervals of model estimates did not cross zero, they were considered statistically significant. Respiration mode (i.e. aerial or bimodal), logged body mass (g) and magnitude of temperature change (i.e. ΔT) were included as moderator variables. To visualize the impact of moderator variables, effect sizes were calculated for different magnitudes of temperature increases (i.e. + 3°C, + 5-7°C, + 8-9°C and + ≥ 10°C) and for aerial versus bimodal breathers. Our data contained several sources of non-independence, such as shared sampling covariances between effect sizes, phylogenetic relationships among taxa and study-level non-independence (Noble et al. 2017). We accounted for these sources of non-independence by including random-effects that estimate study and phylogenetic variance as well as a modified sampling (co)variance matrix that explicitly accounted for the covariance between effect sizes sharing treatment groups in their calculation. To obtain a phylogenetic correlation matrix, we first generated a phylogeny by searching for species names in the TimeTree database (timetree.org; Hedges et al., 2006), which uses published molecular data to build a phylogenetic tree with branch lengths (Fig. x). We also estimated a residual variance by including an observation-level random effect as this is not estimated by default in *metafor*. There was one outlier (XX) and we conducted sensitivity analyses to ensure that our results did not change when excluding it from our models. They did not, as such we only report models including the full dataset.

In addition to analyzing contrast-based effect sizes, we also estimated the effect of temperature on *lnMean and lnSD* dive durations directly using a Bayesian arm-based meta-analytic model in the *MCMCglmm* package (Hadfield, 2010). Given all data was in the same units, arm-based models have fewer issues with respect to complex patterns of non-independence and allow for greater flexibility in estimating overall within species and across species temperature effects. Our models accounted for sampling variance for *lnMean* and *lnSD* (see Nakagawa et al 2015 for equations to calculate sampling variance). They also included a within species temperature slope, which we refer to as Tw. This was calculated by centering temperature treatments around the mean for each species (i.e. by subtracting the mean test temperature for each species from each value of the input variable) (van de Pol and Wright, 2009). In addition to these variables, we fit separate models that included fixed effects of log body mass and respiration mode. We also included a random species slope and intercept for Tw to estimate how much variation in slope and intercept exists across species. To evaluate the effect of temperature on variability in dive duration, we modelled the logged standard deviation (*lnSD*) of each observation as a function of logged mean dive duration, Tw, logged body mass and respiration mode as fixed effects. Log mean dive duration was included as a fixed effect to account for mean-variance relationships. We included study- and species-specific random effects. For our species-level random effects we used the phylogenetic covariance matrix and estimated both a random slope and intercept for Tw. MCMC chains were run for 130,000 iterations, with a 30,000 burnin and a thinning interval of 50 (effective sample size = 2000). We visually checked if chains were mixing well and there were no problems of autocorrelation.

*Publication bias*

*Availability of data and code*

Raw data and code used in the meta-analysis is all located on the Open Science Framework (OSF) webpage (doi).

**Results**

Our laboratory-based dataset includes 15 papers reporting data on 16 species spanning four orders (serpentes, testudines, crocodilians and urodela). Figure x shows the spread of data across these orders and the number of aerial and bimodal breathing species. We calculated 55 effect sizes pairwise temperature treatment comparisons. Across species we had between 2–4 temperature treatment manipulations within a species with the average temperature difference being 7.4 ± 3.6°C (mean ± S.D.; range = 6 – 20°C) and test temperatures ranging from 9 – 35°C. The average body mass of the diving species was 742.8 ± 694 g (mean ± S.D.) and ranged from 29.9 g in juvenile *Elusor macrurus* to 3813 g in adult *Elseya irwini*.

Our field-based dataset includes….

*(i) Did acute increases in temperature reduce overall dive duration mean and variability?*

Acute increases in temperature decreased mean dive duration overall by 63% (*ln*RR: -1.003, 95% confidence interval, CI: -1.444 – - 0.563; Figure 1A), but there was high between study heterogeneity (I2study = 73%, 95% CI: 0.533–0.860). In contrast, acute increases in temperature had a weak effect on the variability in overall dive duration between temperature treatments (*ln*CVR: 0.021 CI: -0.309 – 0.351; an approximately 2% increase in variance, Fig. 1B).

*(ii) Do larger increases in temperature exert a strong effect on dive duration means and variability?*

The magnitude of temperature increase had a significant moderating effect on dive duration means, with a larger increase exerting stronger effects (*lnRR*: -0.111, CI: -0.141 – -0.081). Our arm-based meta-analysis also supported this finding, suggested that temperature, on average, decreased log mean dive duration within species (Tw = -0.114, 95% CI: -0.602 to 0.302), with an 11% decrease in dive duration for every 1°C increase in test temperature. Within-species slopes and intercepts where also highly variable suggesting the impact of temperature depends heavily on species-specific responses (σ2slope = 0.18, 95% CI: 0.07–0.311; σ2Intercept = 2.49, 95% CI = 0.369–5.74). Effect size estimates for temperature increases of different magnitudes showed that a + 3°C, + 5-7°C, + 8-9°C and + ≥10°C reduced mean dive durations by 30%, 54.4%, 68.4% and 76.5%, respectively (Fig. 1C; Table S1).

In contrast, the magnitude of temperature increase did not have a significant moderating effect on dive duration variability (*ln*CVR: 0.012, CI: -0.031 – 0.054; Figure 1C). Arm-based meta-analytic models also supported this finding suggesting a weak effect on variance (*lnSD*, when controlling for the mean) with changes in temperature (Tw = -0.065, 95% CI: -0.637 to 0.587).

*(iii) Are the effects of temperature on dive duration means and variability weaker in bimodal breathers compared to aerial breathers?*

The effects of temperature on dive duration means were comparable between bimodal breathers (*ln*RR -0.372, CI: -1.473 – 0.73) and aerial breathers (*ln*RR -0.144, CI: - 1.205 – 0.92; Fig. 2A) when controlling for temperature differences and average temperature between groups. No significant difference between these groups was detectable (Contrast-based models: -0.23, 95% CI: -1.053–0.597; Arm-based models: -0.45, 95% CI: -2.05–1.11). Both groups experienced a 15 – 45% reduction in mean dive durations as temperatures increased. Acute increases in temperature had a tendency (although not significantly so) to increase dive duration variability by similar magnitudes in both bimodal breathers (*ln*CVR 0.451, CI: -0.911 – 1.813) and aerial breathers (*ln*CVR 0.633, CI: -0.541 – 1.808; Fig. 2B). However, there were no significant differences in variability between these groups (Contrast-based models: -0.182, 95% CI: -0.776 – 0.411; Arm-based models: 1.31, 95% CI -0.428 – 2.956).

*(iv) Are the effects of temperature on dive duration means and variability weaker in larger compared to smaller divers?*

Body mass (mean ± S.D.= 742.8 ± 694 g) had no effect on the magnitude of differences observed with increased temperature when controlling for the temperature difference, mean temperature and respiration mode in either the mean (*ln*RR; 0.126, 95% CI: -1.83 – 0.544Table S2) or variability (*ln*CVR -0.077, CI: -0.200 – 0.0468; Table S2). This was also backed up by results from the arm-based models (lnMean: 0.0513, 95%CI: -0.191 – 0.266; lnSD: 0.01, 95%CI: -0.362 – 0.361).

*(v) Does chronic exposure to elevated temperature blunt (i.e. lessen) the effects of temperature on dive duration means and variability?*

*I* ***still need to set-up the data for this analysis, because it’s very different.***

*(vi) Are effects of temperature on dive duration means and variability more pronounced under laboratory compared to field conditions?*

**Figures**

**A close up of a map

Description automatically generated**

**Figure 1:** Overall meta-analytic results for the effect of an increase in temperature (mean ± S.D. = 7.4 ± 3.6°C) on dive duration means (*ln*RR, **A**) and variability (*ln*CVR, **B**) in diving ectothermic vertebrates. Temperature increases decreased dive mean duration when controlling for the average temperature of the temperature treatment pair and body mass of the species (*lnRR* **C)**. While there was a tendency for the variability in ive duration to increase these effects were not statistically distinguishable form no effect (0) (*ln*CVR, **D**). Data are presented as effect sizes (*ln*RR or *ln*CVR) with 95% confidence intervals. The vertical, dotted zero line indicates no effect and effect sizes are considered significant when 95% confidence intervals do not cross with the zero line. Sample sizes for each group (k) and number of species (Sp) are provided. Abbreviations: ‘NS’ = not statistically significant; ‘\*’ statistically significant deviation from effect size of 0. Between study (I2study) and phylogenetic heterogeneity (I2phylogeny) provided for MLMA models.

**A close up of a map

Description automatically generated**

**Figure 2:** Effects of temperature increase (mean ± S.D. = 7.4 ± 3.6°C) on dive duration means (*ln*RR, **A**)and variability (*ln*CVR, **B**) in all diving ectothermic vertebrates (i.e. overall), aerial breathers and bimodal breathers. The effects of temperature increases on dive duration means and variability were comparable between aerial and bimodal breathers, with dive duration means decreasing and dive duration variability increasing. Data are presented as effect sizes (*ln*RR or *ln*CVR) with 95% confidence intervals. The vertical, dotted zero line indicates no effect and effect sizes are considered significant when 95% confidence intervals do not cross with the zero line. Sample sizes for each group are included in parentheses. Different lowercase letters indicate where groups are statistically different from each other.

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The influence of body mass on dive durations was originally questioned in ectotherms (Brischoux et al., 2008; Campbell et al., 2010b), however Hayward et al. (2016) found that after controlling for the effect of temperature, dive durations increase as a power law with body mass.