

REVIEW

Diving in hot water: a meta-analytic review of how diving vertebrate ectotherms will fare in a warmer world

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ABSTRACT

Diving ectothermic vertebrates are an important component of many aquatic ecosystems, but the threat of climate warming is particularly salient to this group. Dive durations typically decrease as water temperatures rise; yet, we lack an understanding of whether this trend is apparent in all diving ectotherms and how this group will fare under climate warming. We compiled data from 27 studies on 20 ectothermic vertebrate species to quantify the effect of temperature on dive durations. Using meta-analytic approaches, we show that, on average, dive durations decreased by 11% with every 1°C increase in water temperature. Larger increases in temperature (e.g. +3°C versus +8–9°C) exerted stronger effects on dive durations. Although species that respire bimodally are projected to be more resilient to the effects of temperature on dive durations than purely aerial breathers, we found no significant difference between these groups. Body mass had a weak impact on mean dive durations, with smaller divers being impacted by temperature more strongly. Few studies have examined thermal phenotypic plasticity ($N=4$) in diving ectotherms, and all report limited plasticity. Average water temperatures in marine and freshwater habitats are projected to increase between 1.5 and 4°C in the next century, and our data suggest that this magnitude of warming could translate to substantial decreases in dive durations, by approximately 16–44%. Together, these data shed light on an overlooked threat to diving ectothermic vertebrates and suggest that time available for underwater activities, such as predator avoidance and foraging, may be shortened under future warming.

KEY WORDS: Climate change, Aerobic dive limit, Diving lactate threshold, Dive durations, Bimodal breathers, Acclimation

Introduction

Diving ectothermic vertebrates play an important role in the functioning of many aquatic ecosystems and represent a taxonomically diverse group (Butler and Jones, 1982; Costa, 2007). The evolution of air-breathing organs made terrestrial environments habitable, but many species returned to aquatic habitats (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 (sea turtles, freshwater 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), and many sea turtles dive to forage in coastal seagrass meadows (Ballorain et al., 2013). Alternatively, juvenile estuarine crocodiles (*Crocodylus porosus*) dive to avoid both aerial and subsurface predators, while 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). However, the time available for these underwater tasks is 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 switching to anaerobic metabolism (with concomitant lactate accumulation) is termed the aerobic dive limit (ADL; Butler, 2006). The ADL can be calculated by dividing total body oxygen stores (stored in the lungs, blood and muscle tissue) by the rate at which oxygen is consumed (i.e. metabolic rate). In ectotherms, the ADL is inversely related to water temperature, owing 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 expected to dive for only half as long as a conspecific diving at 20°C (Fig. 1). 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 diving vertebrates, with the duration of time performing critical underwater tasks potentially being greatly reduced.

The threat of climate warming to the diving capacity of diving ectotherms has been largely overlooked, despite many studies showing substantial decreases in dive durations as temperatures rise (e.g. Rodgers and Franklin, 2019; Šamajová and Gvoždík, 2009; Udyawer et al., 2016). 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 1-h continual predator threat, juvenile *C. porosus* were able to remain submerged for 37 min at 28°C and only 21 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 with winter months in turtles (Ballorain et al., 2013; Bradshaw et al., 2007; Gordos et al., 2003; Hazel et al., 2009; Southwood et al., 2005; Storch et al., 2005) and crocodylians (Campbell et al., 2010a). For example, dive durations

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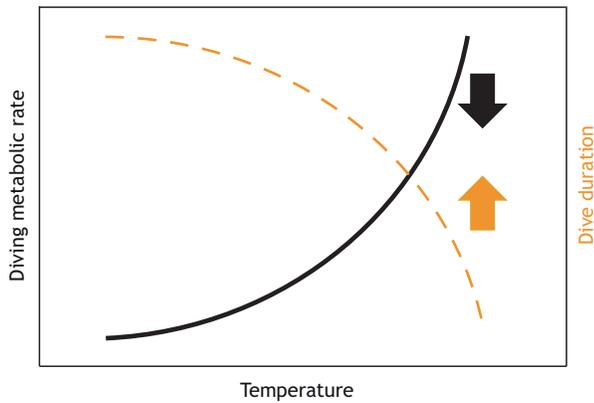


Fig. 1. Schematic showing the theoretical relationship between diving metabolic rate and dive duration versus temperature in vertebrate ectotherms. Diving metabolic rate (solid black line) typically increases exponentially with rising temperature, whereas dive duration (segmented yellow line) typically decreases exponentially with rising temperature. The arrows show how each curve is expected to change following acclimation or acclimatisation to warm temperatures; diving metabolic rates decrease and dive durations increase.

of juvenile green turtles (*Chelonia mydas*) were reduced by 50% in summer compared with winter (Southwood et al., 2003). Despite the strong influence of temperature on ectothermic dive durations, the potential deleterious consequences of warming waters have received little attention. Elevated water temperatures, brought about by climate warming, may cut critical underwater activities short and force animals to spend more time at the water's surface, where predation risk is highest (Heithaus and Dill, 2002; Heithaus and Frid, 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 diving species 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 (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). Because of these advantages, it has been proposed that bimodal breathers may be less sensitive to the effects of temperature on dive durations compared with divers solely reliant on pulmonary gas exchange. Bimodal breathers are predicted to upregulate their reliance on aquatic respiration at high temperatures to meet increased metabolic demands and defend dive durations. Bimodal breathers may be able upregulate aquatic respiration at high temperatures by increasing blood flow to the skin to maximise capillary recruitment or by increasing ventilation frequency and tidal volume of cloacal bursae (Burggren and Moalli, 1984).

Alternatively, the rate of diffusion of respiratory gases between the water and skin may be increased by lowering blood P_{O_2} , by, for example, initiating a cardiovascular shunt, which allows blood to circumvent the lungs and recirculate to the systemic system. However, studies testing this prediction have returned mixed findings, with some 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 (Hayward et al., 2016). The influence of body mass on dive durations appears to be weaker in ectotherms compared with endotherms (Brischoux et al., 2008; Campbell et al., 2010b; Mathie and Franklin, 2006). However, Hayward et al. (2016) found that after controlling for the effect of water temperature, dive durations increased as a power law with body mass in ectotherms. 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 to 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 (Kleiber, 1932). The implications of the differential scaling of oxygen stores and oxygen usage means that larger divers not only have larger oxygen stores, but they also consume these stores more slowly. 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 warming on ectotherm diving constraints may be counteracted by phenotypic plasticity in the form of thermal acclimatisation responses (Seebacher et al., 2015). The capacity to alter the thermal sensitivity of underlying physiology in response to a changing environment is termed acclimatisation when observed in the field under natural conditions, or alternatively termed acclimation when observed under experimentally controlled conditions (Wilson and Franklin, 2002). In the context of diving at elevated temperatures, thermal acclimation/acclimatisation involves a dampening of thermodynamic effects on metabolism at high temperatures (Fig. 1), 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 projected to create or strengthen selection pressures favouring plastic or thermally insensitive phenotypes, particularly in long-lived species, such as crocodylians, 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). Changes in phenotypic variation can arise from developmental acclimation, maternal effects or genetic variation (Hoffmann and Sgrò, 2018; Sorensen et al., 2001; Tonione et al., 2020). Populations with greater phenotypic variation are projected to cope better with extreme climatic events, such as 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 variance (O’Dea et al., 2019). However, it remains unknown whether rises in water temperature increase phenotypic variance 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 and has profound effects on organismal physiology (e.g. metabolism, growth and locomotor performance), the direct effects of climate warming on diving capacity have received little attention. 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 report that dive durations tend to decrease as temperatures rise in ectothermic vertebrates (Hayward et al., 2016; Jackson, 2007), but a systematic review, with a focus on climate warming, has not yet been conducted. Here, we tested whether diving is thermally sensitive in ectotherms using meta-analytic methods. Specifically, we tested the following predictions: (i) increases in temperature decrease mean dive durations in both laboratory and natural field settings, (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 with aerial breathers, (iv) the effects of temperature on mean dive durations will be weaker in larger (in terms of body mass) divers compared with 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 affect phenotypic variability, we also explored how elevated temperatures and moderating variables (i.e. magnitude of temperature increase, breathing mode and body size) affect variability in dive durations. These findings were then used to understand how much underwater time could be lost to climate warming and how diving, ectothermic vertebrates may fare in a warmer world.

Review protocol

We searched for experimental studies that measured dive durations (i.e. minutes submerged) in diving vertebrates at two or 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*’ OR alligator OR caiman) 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*’ OR ‘alligator’ OR ‘caiman’) 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 ($N=2$). 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 vertebrate 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 excluded studies where animals were forced to dive as a result of atypical physiological alterations

induced by forced submergence (Seymour, 1982). Studies on leatherback turtles (*Dermochelys coriacea*) were excluded because they are functionally endothermic ($N=25$; Bostrom and Jones, 2007; Southwood et al., 2005). We included field studies where dive durations were measured in free-ranging animals across one or more seasons using biotelemetry tags (e.g. time–depth recorders, satellite tags). These field studies needed to couple dive duration recordings with either direct body temperature measures or water temperature measurements (and assumed animal body temperature equaled water temperature).

Following these exclusion steps, we identified 27 papers with extractable data (Fig. S1). From these papers, we extracted means, variance (standard errors, standard deviations or confidence intervals) and sample sizes. We avoided extracting maximum dive durations because they were rarely reported and likely had anaerobic contributions. Data presented in figures were extracted using metaDigitise (Pick et al., 2018). Authors were contacted to request missing summary statistics where necessary ($N=1$), and if they could not be obtained, we excluded these studies. We only included comparisons for treatment groups or field recordings when they had two 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 natural log response ratio (lnRR; Lajeunesse, 2011, 2015) and the natural log coefficient of variation ratio (lnCVR; 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 lnRR, which is the natural logarithm of the ratio between mean dive durations between treatments. Changes in the variability in dive duration across temperature treatments were quantified using lnCVR, which is the ratio between the coefficients of variation (i.e. s.d. divided by the mean) for treatments. We used lnRR and lnCVR because they are less susceptible to issues of non-independence (Noble et al., 2017) and are easy to interpret. For example, using lnRR and lnCVR allows us to interpret changes in mean and variance in dive duration as the percentage increase or decrease relative to a reference group (i.e. dive duration for animals held at cooler temperatures – see below). We also used lnCVR because we observed strong mean–variance relationships in our data; lnCVR controls for these strong mean–variance relationships such that we can interpret changes in variance independent of the mean. When dive durations were measured at multiple temperatures in laboratory-based studies, we took each pairwise temperature comparison. When dive durations were measured in the field, we took either seasonal mean dive durations (i.e. winter versus summer) or mean dive durations for the highest and lowest reported temperature (e.g. warmest/coolest month or warmest/coolest temperature reported across a habitat thermal gradient). For both effect sizes (lnRR and lnCVR), 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.

Moderator/predictor variables

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) the magnitude of temperature change

between treatments (i.e. $\Delta T = T_2 - T_1$, where T_2 is the warmer temperature and T_1 is the cooler, control temperature), (2) species respiration mode (i.e. aerial or bimodal), (3) body mass (g) and (4) the average temperature of the two temperature treatments [$T_{\text{mean}} = (T_1 + T_2) / 2$]. Including the magnitude of temperature change between treatments (i.e. ΔT) was important because we expected that the magnitude of effect sizes would be larger for experimental treatments farther apart in temperature. Additionally, the magnitude of effect sizes were expected to depend on the general temperature at which dive performance was measured (i.e. T_{mean}). If temperature treatments were at low temperatures, only small differences in dive duration were expected. Conversely, if temperature treatments were at high temperatures, large differences in dive durations were expected because of the exponential relationship between ectotherm metabolism and temperature (Fig. 1). When body mass data were not presented ($N=1$), we obtained body mass estimates for the same species and life stage from published literature (Denoël et al., 2005).

Meta-analysis

We fitted multilevel meta-analytic (MLMA) and meta-regression (MLMR) 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. Confidence intervals were constructed using the t -distribution given small study numbers in some levels of categorical moderators. We calculated overall mean estimates and between-study and phylogenetic heterogeneity using our MLMA models (according to Nakagawa and Santos, 2012). The magnitude of temperature change (i.e. ΔT), mean temperature (T_{mean}), respiration mode (i.e. aerial or bimodal), log-transformed body mass (g) and study type (laboratory- or field-based) were included as moderator variables. To visualise the impact of moderator variables, effect sizes were calculated for different magnitudes of temperature increases (i.e. $+3^\circ\text{C}$, $+5$ – 7°C , $+8$ – 9°C and $\geq 10^\circ\text{C}$) and for aerial versus bimodal breathers and plotted using orchard plots (Nakagawa et al., 2020). Our data contained several sources of non-independence, such as shared sampling covariances between effect sizes where the same group of animals was used to generate 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 estimated 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. 2). 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 (Clark et al., 2008; study 23, observation 48) in the laboratory-based dataset, 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 analysing contrast-based effect sizes (i.e. $\ln\text{RR}$ and $\ln\text{CVR}$), we also estimated the effect of temperature on $\ln\text{Mean}$ and $\ln\text{SD}$ dive duration directly using a Bayesian multi-level meta-analytic model (BMLM) in the `MCMCglmm` package (Hadfield, 2010). Given all diving data were in the same units (minutes submerged), modelling $\ln\text{Mean}$ and $\ln\text{SD}$ can provide clearer predictions of how mean and variance in dive duration will be impacted, rather than predicting the change in dive duration with temperature, which contrast-based effect sizes provide. Such a modelling approach also acts as a sensitivity analysis to evaluate assumptions inherent to using $\ln\text{CVR}$ (Nakagawa et al., 2015). Our BMLM models accounted for sampling variance for $\ln\text{Mean}$ and $\ln\text{SD}$ (see Nakagawa et al., 2015 for equations to calculate sampling variance). We also included a within-species temperature slope, which we refer to as T_w . 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 fitted separate models that included fixed effects of log body mass and respiration mode. We also included a random species slope and intercept for T_w 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 $\ln\text{SD}$ as a function of $\ln\text{Mean}$ T_w , log body mass,

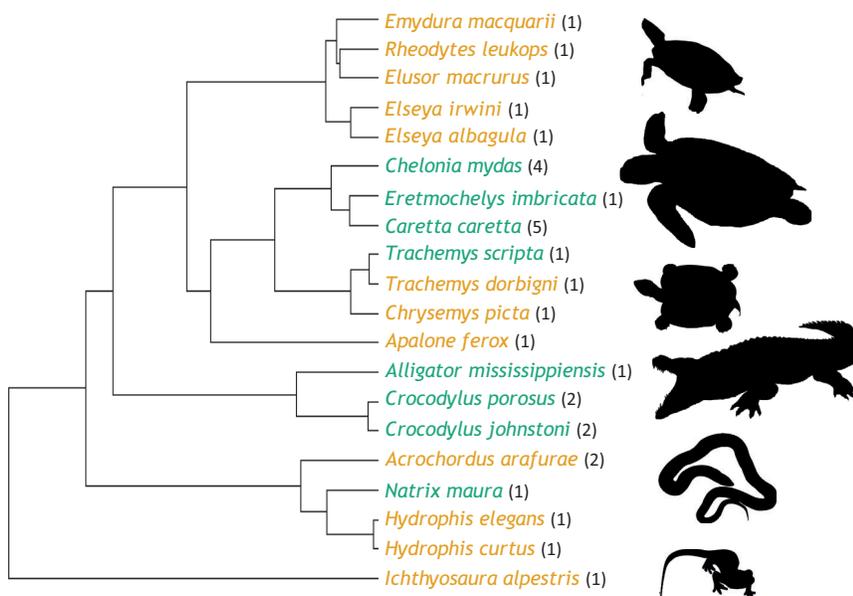


Fig. 2. Phylogeny of the diving ectotherms included in our meta-analysis. We generated the phylogenetic tree using the TimeTree database (timetree.org; Hedges et al., 2006). Bimodal breathing species names are shown in yellow and aerial breathing species are shown in green. Numbers in brackets indicate the numbers of studies conducted on each species.

respiration mode and study type. Log mean dive duration (lnMean) 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 an intercept for T_w . Markov chain Monte Carlo chains were run for 130,000 iterations, with a 30,000 burn-in and a thinning interval of 50 (effective sample size=2000). We visually checked whether chains were mixing well, and there were no problems of autocorrelation.

Temperature coefficient values

We supplemented our meta-analysis by calculating temperature coefficient (Q_{10}) values for each temperature pairwise comparison to provide a familiar measure of thermal sensitivity over a 10°C range. The following equation was used to calculate Q_{10} values:

$$Q_{10} = (d_2/d_1)^{10/(t_2-t_1)}, \quad (1)$$

where d_2 is the mean dive duration measured at test temperature 2 (t_2), d_1 is the mean dive duration measured at test temperature 1 (t_1), and $t_2 > t_1$. It is important to note that descriptive statistics of Q_{10} values are not equivalent to overall effect size estimates from our meta-analytic approaches given that our MLMA and MLMR models provide greater flexibility in controlling for sampling variance (weighting higher quality estimates more heavily) and sources of heterogeneity within the data.

Assessing for publication bias

We explored the potential for publication bias by plotting funnel plots of residuals from our MLMR models (Nakagawa and Santos, 2012), and using a modified version of Egger's regression. Our Egger's regression approach involved including effect size sampling variance in our MLMR model, while also accounting for all other fixed and random effects (i.e. study and species). This approach allows for sources of non-independence and factors affecting heterogeneity to be accounted for when statistically assessing Egger regression results. Asymmetry in funnel plots and/or a sampling variance estimate from Eggers regression suggests the possibility for publication bias.

Literature overview

The dataset from laboratory-based studies comprised 15 papers reporting data on 16 species spanning four orders (Testudines, Crocodylia, Serpentes and Urodela). We were able to disentangle study effects from species effects because three studies tested more than one species and two species were replicated across multiple studies. We calculated 55 effect sizes for pairwise temperature treatment comparisons. Across species, we had between two and four temperature treatment manipulations within a species, with the weighted average temperature difference being 10.6±11.8°C (weighted mean±s.d.; range=3–20°C) and test temperatures ranging from 9 to 35°C. The weighted mean (±s.d.) body mass of diving species was 246±567 g and ranged from 2.5 g in juvenile viperine water snakes (*Natrix maura*) to 3813 g in adult freshwater Irwin's turtles (*Elseya irwini*). Body masses were comparable between aerial (615±362 g) and bimodal (625±800 g) breathers. Fig. 2 shows the spread of species across the four orders and which species respire aerially or bimodally.

The dataset compiled from field-based studies comprised 12 papers reporting data on four species spanning two orders (Testudines and Crocodylia). We calculated 16 effect sizes for

pairwise temperature comparisons. Across species we had between one and five temperature comparisons within each species, with the weighted mean±s.d. temperature difference being 4.7±5.6°C (range=2.7–13.5°C) and field water temperatures ranging from 17 to 32°C. The weighted mean±s.d. body mass of diving species was 63,514±74,051 g and ranged from 1154 g in adult western sawshelled turtles (*Myuchelys bellii*) to 110,500 g in adult green sea turtles (*Chelonia mydas*). Only the overall effect of temperature increases on dive duration means and variability was examined because of the smaller size of the field-based dataset, and we were unable to determine species effects owing to the small number of species (i.e. four).

Did acute increases in temperature reduce overall dive duration mean and variability in the laboratory and field?

Q_{10} values clustered around 0.38 ($Q_{10}=0.38±0.26$, pooled across orders and laboratory/field studies, mean±s.d.; Fig. 3), which equates to an approximate 62% decrease in dive durations for every 10°C increase in body temperature. In laboratory-based studies, order-specific Q_{10} values were 0.36±0.35, 0.25±0.08, 0.42±0.25 and 0.32±0.08 for Testudines, Crocodylia, Serpentes and Urodela, respectively (Fig. 3). Field-based Q_{10} values were similar for Testudines ($Q_{10}=0.41±0.31$), but higher for Crocodylia ($Q_{10}=0.47±0.04$).

For the laboratory-based dataset, our MLMA models suggested a large overall decrease in mean dive duration as temperatures rise [lnRR –1.003, 95% confidence interval (CI): –1.444 to –0.563, a 63% reduction over approximately 10°C; Fig. 4A], but unsurprisingly, there was high between-study heterogeneity ($I^2_{study}=0.728$, 95% CI: 0.550–0.860). In contrast, acute increases in temperature had a weak effect on the variability in overall dive duration between temperature treatments (lnCVR: 0.021 95% CI: –0.309–0.351; Fig. 4C), with moderate between-study heterogeneity ($I^2_{study}=0.314$ 95% CI: 0.158–0.488). For field-based studies, the contrast-based model also suggested that as temperatures increased there was a large decrease in mean dive duration, reflecting an approximate 41% reduction in dive duration for an ~5°C increase in temperature (lnRR –0.530, 95% CI: –0.818 to –0.242; Fig. 4B). In contrast, overall variability in dive duration was weakly affected by increases in temperature in the field (lnCVR 0.03, 95% CI: –0.329 to 0.393; Fig. 4D).

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

As predicted, the magnitude of temperature increase had a significant moderating effect on dive duration means, with a larger increase in temperature exerting stronger effects (lnRR: –0.111 95% CI: –0.141 to –0.081). The BMLM models also supported this finding, suggesting that temperature, on average, decreased log mean dive duration within species ($T_w=-0.111$, 95% CI: –0.539 to 0.369), with an approximately 11% decrease in dive duration for every 1°C increase in test temperature. Within-species slopes and intercepts were also highly variable, suggesting the impact of temperature depends on species-specific responses ($\sigma^2_{slope}=0.183$, 95% CI: 0.076–0.334; $\sigma^2_{intercept}=2.46$, 95% CI=0.499–5.289). Effect size estimates for temperature increases of different magnitudes showed that increases of +3°C, +5–7°C, +8–9°C and +≥10°C reduced mean dive durations by 23%, 51%, 67% and 75%, respectively (Fig. 5A). In contrast, the magnitude of temperature increase did not have a significant moderating effect on dive duration variability (lnCVR: 0.012, 95% CI: –0.030–0.054; Fig. 5B). BMLM models also supported this finding, suggesting a weak effect on variance (lnSD), when controlling for the mean, with changes in temperature ($T_w=0.062$, 95% CI: –0.643–0.553).

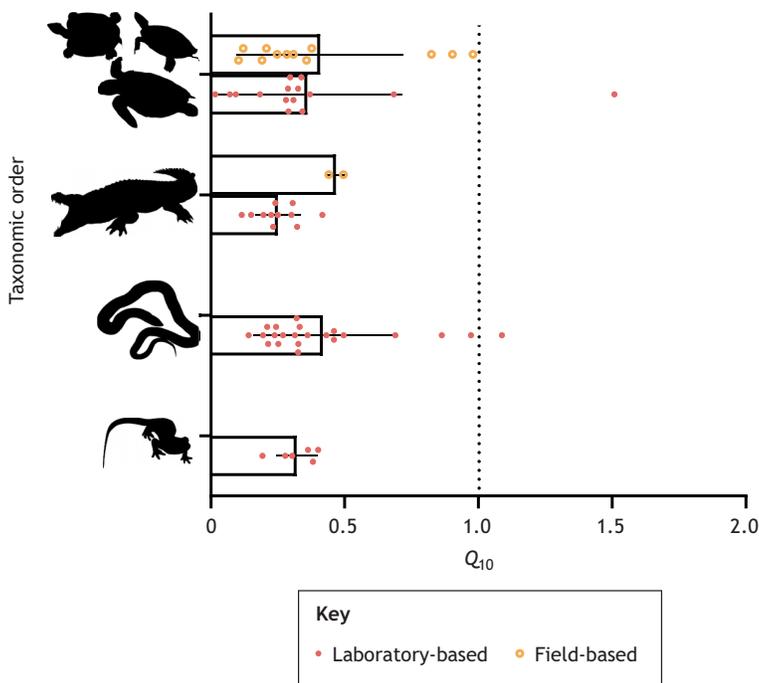


Fig. 3. Temperature coefficient (Q_{10}) values for dive durations across four orders (from top to bottom: Testudines, Crocodylia, Serpentes and Urodela) of diving ectotherms, derived from laboratory- (closed circles) and field-based (open circles) studies. Q_{10} values reflect the rate at which dive durations changed over a 10°C increase in temperature. Q_{10} values of 1, 0.5 and 2 reflect no change in dive duration (marked by the vertical dotted line), a halving of dive duration and a doubling of dive duration, respectively. Most Q_{10} values clustered around 0.38 ($Q_{10}=0.38\pm 0.26$, pooled across orders, mean \pm s.d.), which equates to an approximate 62% decrease in dive duration for every 10°C increase in body temperature. Values are shown as means \pm s.d. with raw values overlaid.

Are the effects of temperature on dive duration means and variability weaker in bimodal breathers compared with aerial breathers?

The effects of temperature on dive duration means were comparable between bimodal (lnRR -0.825 , 95% CI: -2.071 – 0.422) and aerial breathers (lnRR -0.579 , 95% CI: -1.852 – 0.695 ; Fig. 6A) when controlling for temperature differences, average temperature between groups, and body mass differences. No significant difference between these groups was detectable (contrast-based models: -0.246 , 95% CI: -1.066 – 0.574 ; BMLM models: -0.708 , 95% CI: -2.069 – 0.842). Acute increases in temperature had a tendency (although not significantly so) to increase dive duration variability by similar magnitudes in both bimodal breathers (lnCVR 0.423 , 95% CI: -0.703 – 1.550) and aerial breathers (lnCVR 0.797 , 95% CI: -0.323 – 1.917 ; Fig. 6B). However, there were no significant differences in variability between these groups (contrast-based model: -0.374 , 95% CI: -0.875 – 0.127 ; BMLM models: 1.331 , 95% CI -0.383 – 3.036).

Are the effects of temperature on dive duration means and variability weaker in larger compared with smaller divers?

Body mass (weighted mean \pm s.d.= 246 ± 567 g) had a moderating effect on the magnitude of differences observed in dive duration means (lnRR 0.114 , 95% CI: -0.020 – 0.247), when controlling for the temperature difference, mean temperature and respiration mode (i.e. aerial versus aquatic). However, this effect was marginally non-significant ($P=0.09$). In contrast, body mass had no effect on the magnitude of differences observed in dive duration variability (lnCVR -0.076 , 95% CI: -0.875 – 0.032), when controlling for the temperature difference, mean temperature and respiration mode. The effect of body mass on dive duration means was in the same direction, but was weaker in the BMLMs (lnMean: 0.046 , 95% CI: -0.195 – 0.275), and there was no effect on dive duration variability (lnSD: 0.081 , 95% CI: -0.258 – 0.460).

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

There were insufficient data to assess the effects of chronic exposure to elevated temperatures on dive durations. Only four studies

(Bruton et al., 2012; Clark et al., 2008; Rodgers and Franklin, 2017; Rodgers et al., 2015) on three species (*Acrochordus arafuriae*, *Elusor macrurus* and *Crocodylus porosus*) assessed the thermal plasticity of dive durations, yielding 10 effect sizes. Because a quantitative analysis was not possible, a qualitative assessment of these data is provided in the Discussion.

Publication bias

Visual inspection of funnel plots showed some asymmetry of effect sizes around the meta-analytic mean (lnRR) in the laboratory-based dataset, but showed symmetry around the meta-analytic mean (lnRR) in the field-based data set. Symmetry was also observed in funnel plots for the meta-analytic variance (lnCVR) in both the laboratory- and field-based datasets (Fig. S2A,B). However, asymmetry for lnRR may be the result of high heterogeneity among effect sizes given that Egger's regression results indicated that there was no significant publication bias in the dataset in dive durations means (laboratory-based lnRR -0.570 , 95% CI: -4.544 – 3.404 ; field-based -0.609 , 95% CI: -2.682 – 1.463) or variability (lnCVR: -0.684 , 95% CI: -4.037 – 2.668 ; field-based lnCVR 0.755 , 95% CI: -0.531 – 2.040).

Discussion

The magnitude of temperature increase matters

Underwater excursions are crucial to the survival and ecological success of many diving species, yet we report here that there is a consistent pattern across multiple studies that dive durations are cut short by temperature increases. The BMLM models showed that for every 1°C increase in water temperature, diving ectothermic vertebrates experience an 11% decrease in dive duration, on average. Average water temperatures in marine and freshwater habitats are projected to increase between 1.5 and 4°C in the next century, and marine heatwaves are already increasing in intensity, duration and frequency worldwide (Cheng et al., 2019; Hobday and Lough, 2011; Hughes et al., 2017; Pörtner et al., 2019; Stillman, 2019). Our data suggest that this

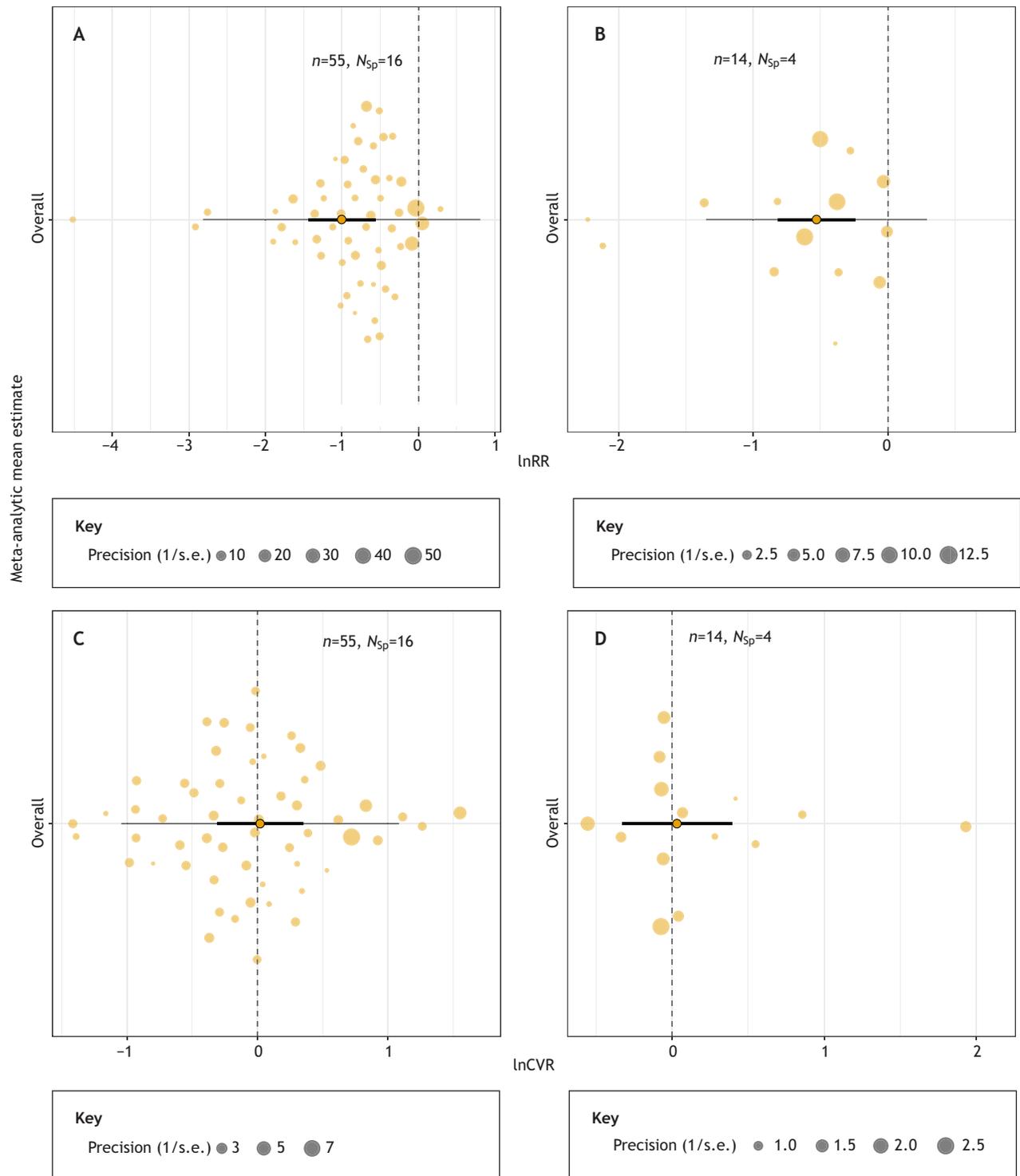


Fig. 4. Overall meta-analytic results for the effect of an increase in temperature on dive duration means and variability under laboratory and field conditions in diving ectothermic vertebrates. Increases in temperature decreased dive duration means [natural log response ratio (lnRR)] under both laboratory- (A; weighted mean \pm s.d. = $10.6 \pm 11.8^\circ\text{C}$) and field-based (B; weighted mean \pm s.d. = $4.79 \pm 5.60^\circ\text{C}$) conditions. There was no effect of increased temperature on dive duration variability [natural log coefficient of variation (lnCVR)] under both laboratory- (C) and field-based (D) conditions. Data are presented as effect sizes (lnRR or lnCVR) with 95% confidence intervals. The vertical, dashed 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 (n) and number of species (N_{sp}) are provided.

magnitude of warming could translate to substantial cuts in dive durations, by approximately 16–44%. Climate warming may therefore reduce time for obligate underwater activities (e.g. predator avoidance, foraging, social interactions) and diving

species may be required to surface more frequently if dives are to be aerobically supported.

As predicted, larger increases in temperature exerted stronger effects on dive duration means, but not variability. Our contrast-

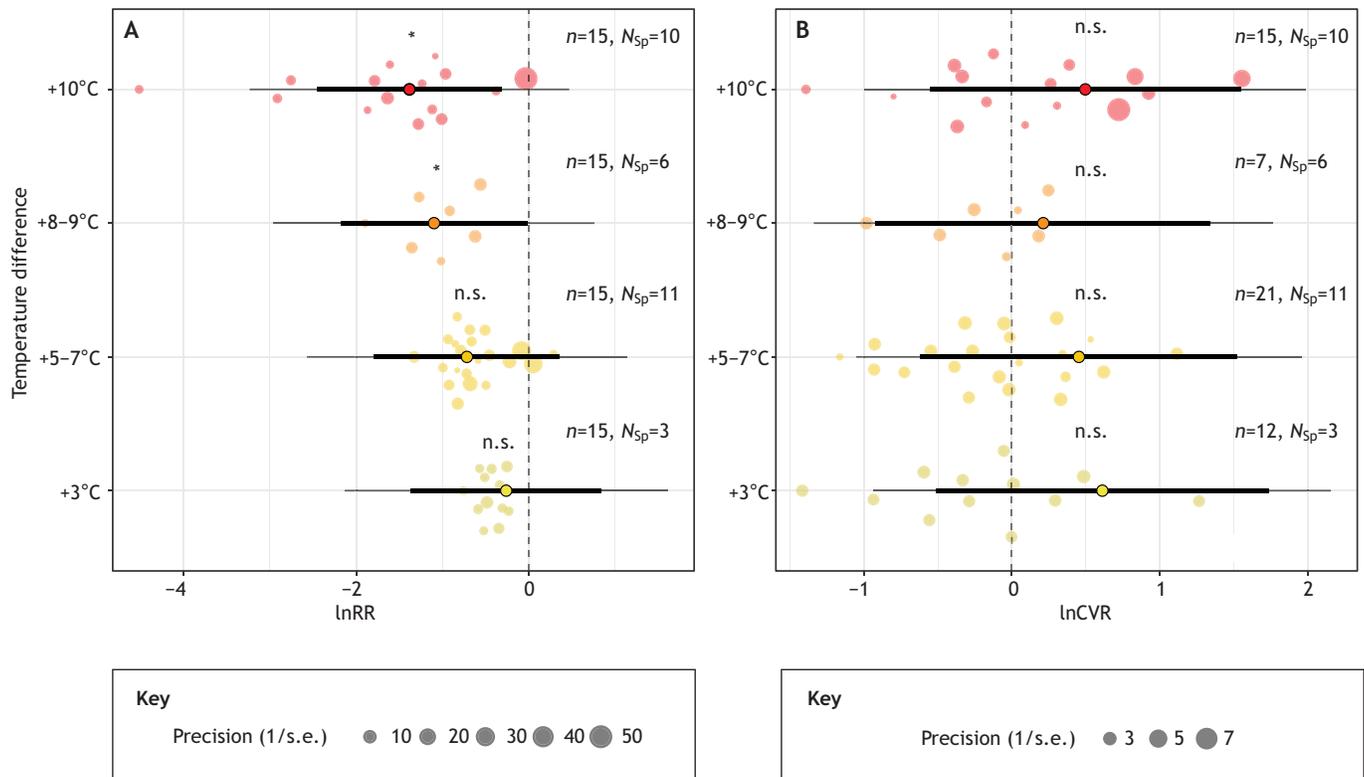


Fig. 5. Effect of the magnitude of temperature increase on dive duration means (lnRR) and dive duration variability (lnCVR). Temperature increases decreased mean dive duration, when controlling for the average temperature of the temperature treatment pair and body mass (lnRR, A). While there was a tendency for the variability in dive duration to increase, these effects were not statistically distinguishable from no effect (0) (lnCVR, B). Data are presented as effect sizes (lnRR or lnCVR) with 95% confidence intervals. The vertical, dashed 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 (n) and number of species (N_{sp}) are provided. n.s., not significant; *statistically significant deviation from effect size of 0.

based model estimated that increases of +3°C, +5–7°C, +8–9°C and +≥10°C reduced dive durations by approximately 23%, 51%, 67% and 75%, respectively. This finding is in line with current understanding, because larger increases in temperature generally correspond with greater increases in ectothermic oxygen demands, consequently reducing aerobic dive limits by a larger magnitude. Estimates from our contrast-based model (i.e. a 63% reduction over approximately 10°C) align well for with our Q_{10} values for dive durations. Q_{10} values clustered around 0.38 ($Q_{10}=0.38\pm 0.26$, mean±s.d.), which equates to an approximate 62% decrease in dive duration for every 10°C increase in body temperature. Moreover, our estimates are similar to projections generated from the temperature sensitivity of ectotherm metabolism. Ectotherm metabolic rates typically double or triple with every 10°C increase in body temperature, with Q_{10} values ranging between two and three (Seebacher et al., 2015). Thus, dive durations are expected to reduce by 50–67% for every 10°C increase. Our estimates were slightly above this range (75–77% reductions), but this may be due to diving metabolic rates (i.e. hypometabolism associated with the dive response) sometimes being more temperature sensitive than resting (at surface) metabolic rates (Rodgers and Franklin, 2017).

The magnitude of warming that aquatic habitats experience moving into the future may therefore affect how strongly diving ectotherms are impacted. Species or populations inhabiting shallow, exposed (little shade) habitats, such as small lakes and ponds, may suffer from greater declines in dive durations owing to their greater heating potential compared with more thermally stable marine habitats. Human demands placed on freshwater ecosystems, such as

water extraction and flow regulation, may exacerbate warming in these habitats, as natural flows and depths are often greatly reduced. For example, several freshwater turtles (e.g. *Emydura macquarii*, *Chelodina longicollis*, *Myuchelys bellii* and *Chelodina expansa*) inhabit Australia's Murray-Darling Basin, which is subject to intense water extraction for irrigation purposes and flow regulation (e.g. damming) (Chessman, 2011; Leblanc et al., 2012). Consequently, this habitat experiences reduced flows, which increase daily maximum temperatures and exacerbate the impacts of heatwaves (Chessman, 2011; Leblanc et al., 2012). Alternatively, species inhabiting deep, aquatic habitats may be somewhat buffered from the effects of warming if they can dive to cooler, thermally stratified regions of the water column.

Bimodal breathers are just as vulnerable as aerial breathers

Although bimodal breathers are projected to be more resilient to the effects of temperature on dive durations than aerial breathers, we found no significant difference between these groups. Both groups were similarly affected by temperature increases and experienced an 18–53% reduction in mean dive duration (weighted mean±s.d. temperature increase: $10.6\pm 11.8^\circ\text{C}$); however, the negative effects of temperature on dive duration were slightly stronger in bimodal compared with aerial breathers. Bimodal breathers have been predicted to defend dive durations at elevated temperatures by increasing their reliance on aquatic respiration to meet increased metabolic demands (Pratt and Franklin, 2010). But, several studies have shown that bimodal breathers are not able to upregulate aquatic respiration at high temperatures (Prassack et al., 2001; Pratt and

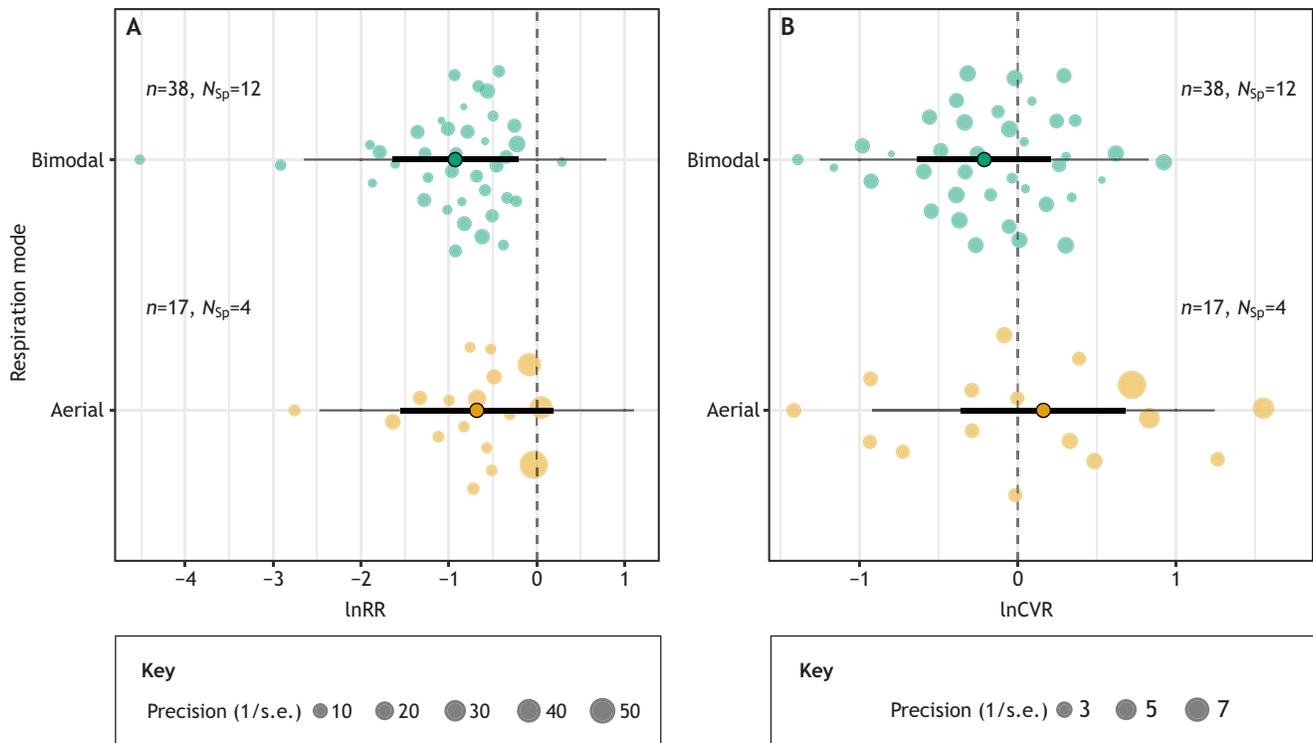


Fig. 6. Effects of temperature increase (weighted mean \pm s.d. = $10.6 \pm 11.8^\circ\text{C}$) on dive duration means (lnRR) and variability (lnCVR) in aerial breathers and bimodal breathers. The effect of temperature increases on dive duration means (A) and variability (B) were comparable between aerial and bimodal breathers, when controlling for the average temperature of the temperature treatment pair and body mass. Data are presented as effect sizes (lnRR or lnCVR) 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 (n) and number of species (N_{Sp}) are provided.

Franklin, 2010; Udyawer et al., 2016). Moreover, there is a marked difference in the temperature sensitivity of tissue gas diffusion and ectotherm metabolic rate (Jackson, 2007). Tissue gas diffusion increases by only 10% with every 10°C increase in body temperature ($Q_{10}=1.1$; Dejours, 1981), whereas ectotherm metabolic rate typically doubles or triples for the same 10°C increase in body temperature ($Q_{10}=2-3$; Seebacher et al., 2015). Consequently, aquatic respiration rates cannot keep pace with this exponential rise in oxygen demands and the relative contribution of aquatic respiration to total respiration decreases as temperatures increase (Jackson, 2007). Additionally, the solubility and partial pressure of oxygen in water declines as temperature increases, further reducing the efficiency of aquatic respiration. Several studies have shown that the relative contribution of aquatic respiration to total respiration either decreases with rising temperature or remains temperature-independent (Prassack et al., 2001; Pratt and Franklin, 2010; Udyawer et al., 2016). Rather, bimodal respiration becomes advantageous at cold temperatures, when resting or routine metabolic demands are lowered, or even depressed. The benefits of aquatic respiration in prolonging dive durations therefore only appear to be realised at cooler temperatures (Clark et al., 2008; Prassack et al., 2001). Based on the available estimates, we found no support that dive durations of bimodal and aerial breathers are affected differently, but current sample sizes may be too limited to draw strong conclusions.

Body mass has a weak effect on changes in dive duration

As expected, temperature effects on the change in mean dive duration were smaller for larger divers; however, body size effects were generally weaker than expected. Smaller divers are expected to

be disproportionately affected by temperature increases owing to their relatively small body oxygen stores and high mass-specific metabolic rates. Despite some support for this prediction, weaker than expected effects may be due to the high variability among species in how dive performance is affected by temperature. This may be partly driven by the unusual scaling relationships between body mass and dive duration in some species, such as bimodal breathers (Mathie and Franklin, 2006; Stone et al., 1992). For example, the freshwater white-throated snapping turtle (*Elseya albagula*) uses cloacal bursae to respire aquatically, and small turtles are able to dive for just as long as large turtles (size range: 19–6725 g; Mathie and Franklin, 2006). Their capacity to defend dive durations is attributable to smaller turtles having higher mass-specific cloacal bursae surface areas (scaling exponent: $M_b^{0.77}$), allowing them to extract more oxygen from the water (Mathie and Franklin, 2006). Surface area of breathing organs (e.g. integument, cloacal bursae, buccopharyngeal cavity) may therefore be a better predictor of dive duration in bimodal breathers. However, our contrast-based model showed that there was no significant interaction between respiration mode and body mass and suggests that large divers may be slightly buffered against the effects of warming on dive durations.

Limited thermal plasticity in dive duration

Thermal acclimation capacity remains unassessed in most ectothermic divers and represents a pressing knowledge gap. Only four studies (Bruton et al., 2012; Clark et al., 2008; Rodgers and Franklin, 2017; Rodgers et al., 2015) have assessed thermal acclimation capacity in diving ectothermic vertebrates. Nonetheless, the findings from these studies are similar and suggest that diving

ectotherms have a limited capacity for thermal plasticity in dive durations. For example, Bruton et al. (2012) examined the thermal acclimation capacity of the Arafura filesnake (*Acrochordus arafurae*) by holding two groups of snakes at 24°C or 32°C for 3 months before assessing diving performance at both temperatures. Partial thermal acclimation was observed in maximum dive durations, and warm-acclimated snakes dived for longer at both test temperatures. However, this acclimation response was very weak and warm-acclimated snakes still experienced a halving in dive durations between 24 and 32°C (cool-acclimated Q_{10} : 0.39; warm-acclimated Q_{10} : 0.41). Moreover, no acclimation response was observed in mean dive durations (Bruton et al., 2012). In a similar study, Clark et al. (2008) exposed hatchling Mary River turtles (*Elusor macrurus*) to either 17°C or 28°C for 8 weeks, finding that turtles had the capacity to partially acclimate mean and maximum dive durations to the cool temperature (512% increase in dive duration), but acclimation to the warm temperature was entirely absent. Acclimation of diving performance to temperatures mimicking climate warming scenarios has also been investigated (Rodgers and Franklin, 2017; Rodgers et al., 2015). Rodgers et al. (2015) acclimated juvenile estuarine crocodiles (*Crocodylus porosus*) to three climate warming scenarios (current summer, 28°C; moderate climate warming, 31.5°C; high climate warming, 35°C) for 30 days and found no evidence of thermal acclimation. A follow-up study showed that this absence of plasticity in dive durations was underscored by an inability to adjust diving metabolic rate at elevated temperatures (Rodgers and Franklin, 2017). Moreover, we report strong effects of temperature on dive durations across seasons in field studies (e.g. Campbell et al., 2010c), suggesting that seasonal acclimatisation of diving metabolic rate is insufficient to defend dive durations. The strong effect of temperature increases on mean dive duration was similar between field- and laboratory-based studies. However, direct comparisons between these datasets are difficult owing to little overlap in species composition and differences in the average magnitude of temperature increases (field-based: $+4.7 \pm 5.6^\circ\text{C}$; laboratory-based: $+10.6 \pm 11.8^\circ\text{C}$, weighted mean \pm s.d.). Nonetheless, limited thermal acclimation capacity appears to be a shared trait among diving ectotherms, but more research is urgently needed to test the universality of this trend.

Acute increases in temperatures do not increase dive duration variability

Populations with greater phenotypic variation may be more resilient to extreme climatic perturbations, such as heatwaves, because they are more likely to contain individuals who can tolerate novel conditions (Hansen et al., 2006). Despite the potential for greater phenotypic variation to have evolutionary consequences, acute temperature increases had no effect on dive duration variability. Accurate estimates of how a population will fare under climate warming are dependent on both the average response of the population, together with, the breadth of individual responses. Our results suggest that the breadth of individual responses does not increase under acute warming, further elevating the vulnerability of diving ectotherms to warming.

Implications of climate warming for diving ectotherms and future directions

Our meta-analysis identifies some key knowledge gaps and highlights a previously overlooked threat to ectothermic divers – climate warming. As marine and freshwater ecosystems continue to warm, we project that dive durations will decrease by approximately 11% with every 1°C rise in temperature. Shortened dive durations will force diving ectotherms to surface and replenish oxygen stores

more frequently. The consequences of increased surfacing frequency are threefold: predation risk is highest at the surface of the water (Heithaus and Dill, 2002; Heithaus and Frid, 2003; Heithaus et al., 2002), diving becomes more energetically costly with frequent ascent and descent movements, and time for underwater foraging, rest and social interactions is reduced. It is difficult to predict precisely how much cumulative underwater time will be lost for dive-dependent activities because many studies have focused exclusively on how elevated temperatures affect individual dive durations, rather than continuous diving behaviour. Losses of cumulative underwater time (e.g. total time spent submerged per day) may be partially offset by increasing dive frequency or by making behavioural adjustments to the dive cycle (e.g. altering dive angles or swim speeds). For example, at high temperatures, the alpine newt (*Triturus alpestris*) increased its dive frequency and altered its swimming behaviour so that the descent phases of their dives were more efficient (Šamajová and Gvoždík, 2009). However, this beneficial change in behaviour is not apparent in all species. Cumulative submergence time of juvenile estuarine crocodiles (*C. porosus*), during a 1 h continual predator threat trial, was reduced by 15 min at high temperatures (35°C) compared with cooler control temperatures (28°C), and no significant changes in dive frequency were observed (Rodgers et al., 2015). Understanding how elevated temperatures alter predation rates, foraging success and total time spent submerged is a pressing knowledge gap, and well-designed ecological field studies may offer valuable insight.

The few tests of thermal acclimation capacity in diving ectotherms suggest that physiological compensation in dive duration is limited (Bruton et al., 2012; Clark et al., 2008; Rodgers and Franklin, 2017; Rodgers et al., 2015). Long-term field monitoring of diving behaviour will provide a greater understanding of how warming and heat wave events are affecting diving vertebrates. Many of these species are late to mature and long-lived, suggesting that transgenerational acclimation will be an ineffective buffer if warming is rapid. Behavioural compensation, in the form of poleward migrations or seeking cool waters at a depth, may be the only safeguard if these species are subject to intense heatwaves. In summary, our results suggest that the dive durations of ectothermic vertebrates will be cut short under climate warming, bringing to light a previously overlooked threat.

Competing interests

The authors declare no competing or financial interests.

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Data availability

Raw data and code used in the meta-analysis are available from the Open Science Framework: <https://doi.org/10.17605/OSF.IO/3YKG5>.

Supplementary information

Supplementary information available online at <https://jeb.biologists.org/lookup/doi/10.1242/jeb.228213.supplemental>

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