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

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**Running title:** Diving in hot water

**Key words:** climate change, aerobic dive limit, diving lactate threshold, dive durations, bimodal breathers, acclimation

**Summary statement:** Using meta-analytic approaches, we show that diving ectotherms are particularly vulnerable to climate warming. On average, dive durations decreased by 11% with every 1°C increase in water temperature.

**Abstract**

Diving ectotherms are a crucial component of aquatic ecosystems, but the threat of climate warming may be 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 increases 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 duration means. Although bimodal breathers are predicted to be more resilient to the effects of temperature on dive durations than 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 acclimation capacity in diving ectotherms (N = 4), but all report limited thermal phenotypic plasticity. Average water temperatures in marine and freshwater habitats are projected to increase between 1.5 – 4°C in the next century, and our data suggest that this magnitude of warming could translate to substantial cuts in dive durations, by approximately 16 – 44%. Together, these data shed light on an overlooked threat to diving ectotherms and suggest that time available for underwater activities, like predator avoidance and foraging, may be cut short under future warming.

**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 environments 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). 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). The 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 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, 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 (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 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 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 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. Bimodal breathers are predicted to upregulate their reliance on aquatic respiration at high temperatures to meet increased metabolic demands and defend dive durations. However, 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 (Hayward et al., 2016). 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 water temperature, dive durations increased as a power law with body mass. 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 (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 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 warming on ectotherm diving behaviour may be counteracted by phenotypic plasticity in the form of thermal acclimatization responses (Seebacher et al., 2015). The capacity to 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 involves 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/function, cell membrane thickness, muscle contractility and cardiovascular functioning (Glanville and Seebacher, 2006; Keen et al., 2017; Shuman and Coughlin, 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 pressures 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 variance (O'Dea et al., 2018). However, it remains unknown if 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, 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) 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 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 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 finding 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.

**Materials and 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 = 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 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 due to 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). Only one study met the above criteria for invertebrates (Calosi et al., 2012), so we chose to focus exclusively on vertebrates. 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 (assuming 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 maximum dive durations 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 recording 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 log response ratio (*ln*RR; Lajeunesse, 2011; Lajeunesse, 2015) 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 temperature 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 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 (*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) the magnitude of temperature change between treatments (i.e. ΔT), 2) species respiration mode (i.e., aerial or bimodal); 3) body mass (g) and 4) the average temperature of the two treatments (Tmean). 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 low temperatures only small 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 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 estimated 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 (Tmean), respiration mode (i.e. aerial or bimodal), logged body mass (g) and study type (lab- or field-based) 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 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, 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. 1). 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 analyzing contrast-based effect sizes, we also estimated the effect of temperature on *lnMean and lnSD* dive durations in laboratory-based studies directly using a Bayesian arm-based meta-analytic model in the *MCMCglmm* package (Hadfield, 2010). Given all data was in the same units (minutes), 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 *lnSD* as a function of *ln*Mean Tw, log body mass, respiration mode and study type. Log mean dive duration (*ln*Mean) 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.

*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:

where is the mean dive duration measured at test temperature 2 () and d1 is the mean dive duration measured at test temperature 1 (), and > . 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.

*Publication bias*

We explored the potential for publication bias by plotting funnel plots of residuals from our multilevel meta-regression 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 multilevel meta-regression model, while also accounting for all other fixed and random effects (i.e., study and species). This approach allows for sources of nonindependence 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.

**Results**

Our laboratory-based dataset includes 15 papers reporting data on 16 species spanning four orders (Testudines, Crocodilia, 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 2 – 4 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 – 35°C. The weighted average body mass of diving species was 246 ± 567 g (mean ± S.D.) 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 mean ± S.D.) and bimodal (625 ± 800 g mean ± S.D.) breathers. Figure 1 shows the spread of species across the four orders and which species respire aerially or bimodally.

Our field-based dataset includes 12 papers reporting data on four species spanning two orders (Testudines and Crocodilia). We calculated 16 effect sizes for pairwise temperature comparisons. Across species we had between 1 – 5 temperature comparisons within each species, with the weighted average temperature difference being 4.7 ± 5.6°C (weighted mean ± S.D; range = 2.7 – 13.5°C) and field water temperatures ranging from 17 – 32°C). The weighted average body mass of diving species was 63 514 ± 74 051 g (weighted mean ± S.D.) 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 were examined due to the smaller size of the field-based dataset, and we were unable to determine species effects due to the small number of species (i.e. four).

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

Temperature coefficient (*Q*10)values clustered around 0.38 (Fig. 2, *Q*10 = 0.38 ± 0.26, pooled across orders and lab/field studies, mean ± S.D.) 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 (mean ± S.D.) for Testudines, Crocodilia, Serpentes and Urodela, respectively (Fig. 2). Field- based *Q*10 values were similar for Testudines (*Q*10 = 0.41 ± 0.31, mean ± S.D.), but higher for Crocodilia (*Q*10 = 0.47 ± 0.04, mean ± S.D.).

In our laboratory-based dataset our multi-level meta-analysis models suggested a large overall decrease in mean dive duration as temperatures rise (*ln*RR -1.003, 95% confidence interval, 95% CI: -1.444 – -0.563, a 63% reduction over approximately 10°C; Fig. 3A), but unsurprisingly, there was high between study heterogeneity (I2study = 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 (*ln*CVR: 0.021 95% CI: -0.309 – 0.351; Fig. 3C), with moderate between-study heterogeneity (I2study = 0.314 95% CI: 0.158– 0.488). In our field-based dataset, our multi-level meta-analysis models also suggested a large overall decrease in mean dive duration as temperatures rise (*ln*RR -0.530, 95% CI: -0.818 - - 0.242, a 41% reduction over approximately 4.7°C; Fig. 3B). In contrast, increases in temperature, in the field, had a weak effect on the variability in overall dive duration (*ln*CVR 0.03, 95% CI: -0.329 – 0.393; Fig. 3D).

*(ii) 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 – -0.081). Our arm-based meta-analysis also supported this finding, suggesting that temperature, on average, decreased log mean dive duration within species (Tw = -0.111, 95% CI: -0.539 – 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 (σ2slope = 0.183, 95% CI: 0.076 – 0.334; σ2Intercept = 2.46, 95% CI = 0.499 – 5.289). 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 23%, 51%, 67% and 75%, respectively (Fig. 4A). In contrast, the magnitude of temperature increase did not have a significant moderating effect on dive duration variability (*ln*CVR: 0.012, 95% CI: -0.030 – 0.054; Fig. 4B). Arm-based meta-analytic models also supported this finding suggesting a weak effect on variance (*ln*SD), when controlling for the mean) with changes in temperature (Tw = 0.062, 95% CI: -0.643 – 0.553).

*(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 -0.825, 95% CI: -2.071 – 0.422) and aerial breathers (*ln*RR -0.579, 95%CI: -1.852 – 0.695; Fig. 5A) 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; Arm-based 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 (*ln*CVR 0.423, 95% CI: -0.703 – 1.550) and aerial breathers (*ln*CVR 0.797, 95% CI: -0.323 – 1.917; Fig. 5B). However, there were no significant differences in variability between these groups (Contrast-based model: -0.374, 95% CI: -0.875 – 0.127; Arm-based model: 1.331, 95% CI -0.383 – 3.036).

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

Body mass (weighted mean ± S.D.= 246 ± 567 g) had a moderating effect on the magnitude of differences observed in dive duration means (*ln*RR 0.114, 95% CI: - 0.020 – 0.247), when controlling for the temperature difference, mean temperature and respiration mode. 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 (*ln*CVR -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 arm-based models (*ln*Mean: 0.046, 95% CI: -0.195 – 0.275), and there was no effect on dive duration variability (*ln*SD: 0.081, 95% CI: -0.258 – 0.460).

*(v) 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 arafurae, Elusor macrurus* and *Crocodylus porosus*) assessed the thermal plasticity of dive durations, yielding 10 effect sizes. Since a quantitative analysis was not possible, a qualitative assessment of these data is provided in the discussion.

*(vi) Publication bias*

Visual inspection of funnel plots showed some asymmetry of effect sizes around the meta-analytic mean (*ln*RR) in the laboratory-based dataset but showed symmetry around the meta-analytic mean (*ln*RR) in the field-based data set. Symmetry was also observed in funnel plots for the meta-analytic variance (*ln*CVR) in both the laboratory- and field-based datasets (Fig. S2 A-B). Asymmetry for *lnRR,* however, 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 *ln*RR -0.570, 95% CI: -4.544 – 3.404; field-based -0.609, 95% CI: -2.682 – 1.463) or variability (*ln*CVR: -0.684, 95% CI: -4.037 – 2.668; field-based *ln*CVR 0.755, 95% CI: -0.531 – 2.040).

**Discussion**

Underwater excursions are crucial to the survival and ecological success of many diving species, but we show here that dive durations can be cut short by temperature increases. Our arm-based model showed that for every 1°C increase in water temperature, diving ectotherms experience an 11% decrease in dive duration, on average. Average water temperatures in marine and freshwater habitats are projected to increase between 1.5 – 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; Stillman, 2019). Our data suggest that this 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 forced to spend more time at the water’s surface.

*The magnitude of temperature increase matters*

As predicted, larger increases in temperature exerted stronger effects on dive duration means, but not variability. Our contrast-based model estimated that + 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 intuitive because larger increases in temperature generally correspond with greater increases in ectothermic oxygen demands, consequently reducing aerobic dive limits by a larger magnitude. Our contrast-based model estimates (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 ± 0.26, mean ± S.D.) which equates to an approximate 62% decrease in dive durations for every 10°C increase in body temperature. Moreover, our estimates are similar to predictions 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 slightly above this range (75 –77% reductions) but this may due to diving metabolic rates sometimes being more temperature sensitive than resting 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 due to their greater heating potential, compared to more thermally stable marine habitats. Human demands placed on freshwater ecosystems, like 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 predicted 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 durations (weighted mean temperature increase ± S.D.: 10.6 ± 11.8°C). 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). Bimodal breathers may be able upregulate aquatic respiration by increasing blood flow to the skin to maximise capillary recruitment (Burggren and Moalli, 1984). Alternatively, the rate of diffusion of respiratory gases between the water and skin may be increased by lowering blood PO2 by, for example, initiating a cardiovascular shunt which allows blood to circumvent the lungs and recirculate to the systemic system (Lillywhite and Donald, 1989). However, several studies have shown that bimodal breathers do not upregulate aquatic respiration at high temperatures (Prassack et al., 2001; Pratt and 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 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 aquatic respiration can meet resting or routine metabolic demands, allowing some species to remain submerged for days, weeks and even months as an overwintering strategy (Penney, 1987). The benefits of aquatic respiration in prolonging dive durations therefore only appear to be realized at cooler temperatures (Clark et al., 2008; Prassack et al., 2001). Our findings show that bimodal and aerial breathers are equally sensitive to the negative effects of rising temperatures on dive durations, and we can predict that the diving behaviour of both groups will be disrupted as the climate continues to warm.

*Body mass had a weak effect on changes in dive duration*

As predicted, 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 due 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 durations 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: Mb0.77), allowing them to extract more oxygen from the water (Mathie and Franklin, 2006). Nonetheless, our findings suggest that large divers may be slightly buffered to the effects of warming on diving durations, but this effect can be highly variable across species.

*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 ectotherms. Nonetheless, the findings from these studies are similar and suggest 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 three 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°C or 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 eight 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 at elevated temperatures (Rodgers and Franklin, 2017). 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, like heatwaves, because they are more likely to contain individuals who can tolerate the 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 individuals responses does not increase under acute warming, further elevating the vulnerability of diving ectotherms to warming. A previous meta-analysis revealed that warmer than average developmental temperatures increased phenotypic variability in fishes. Changes in phenotypic variability may therefore be more likely to occur if animals are exposed during critical, early-life stages because developmental environments often have long-lasting effects on adult phenotypes (Noble et al., 2018). No studies to date have examined developmental plasticity in diving ectotherms and experiments manipulating early life thermal regimes would offer valuable insight.

*Limitations*

### Our data only included ectothermic vertebrates despite there being many invertebrates which dive. For example, there are over 4000 species of diving beetles (Dytiscidae) which dive to pursue prey (larval fish and aquatic insects) (White, 2009). Our literature search only identified a single study which had examined the effects of temperature on diving invertebrates. Calosi et al. (2012) found that in order to meet higher oxygen demands at elevated temperatures, *Ilybius* species decreased dive durations and *Deronectes* species increased their surfacing frequency. These findings suggest that diving beetles may be similarly affected by climate warming, but further research is warranted, particularly when the substantial biodiversity of diving invertebrates is considered. Another issue with studying diving vertebrates is small samples sizes, often due to large space requirements and ethical limits. Many studies were low-powered (N = 11 ± 4; median ± interquartile range). If a statistical difference is detected in low-powered studies, the magnitude of this effect is necessarily large. This phenomenon is known as the ‘*winner’s curse*’ because the experimenter fortunate enough to detect an effect with a small sample size is also ‘cursed’ because they likely overestimated the strength of that effect (Ioannidis, 2008). However, it is important to note that strong temperature effects were observed in a very high-powered study in our dataset (N = 231; Aubret et al., 2015).

*Implications of climate warming for diving ectotherms*

Our meta-analysis highlights a previously overlooked threat to ectothermic divers – climate warming. As marine and freshwater ecosystems continue to warm, we predict that dive durations will decrease by approximately 11% with every 1°C rise in temperature. The few tests of thermal acclimation capacity in this group suggest that physiological compensation is limited (Bruton et al., 2012; Clark et al., 2008; Rodgers and Franklin, 2017; Rodgers et al., 2015). Many of these species are late to mature and long-lived, suggesting transgenerational acclimation will be an ineffective buffer if warming is rapid. Shortened dive durations will see cumulated time available for underwater activities cut short, forcing animals to spend a greater amount of time at the water’s surface. The consequence of spending more time at the water’s surface are twofold; predation risk is greater (Heithaus and Dill, 2002; Heithaus and Dill, 2003; Heithaus et al., 2002) and time for underwater foraging, rest and social interactions is reduced. More frequent trips to the water’s surface, coupled with less time available for foraging, may compromise performance and fitness in many diving ectotherms. 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 diving behaviour of ectothermic vertebrates will be seriously disrupted under climate warming, bringing to light the severity of a previously overlooked threat.

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**Competing interests**

No competing interests declared.

**Data availability**

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

**References**

No asterisk indicates papers included in the main text only

\* denotes papers included in the meta-analysis only

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**Figures**



**Fig. 1: 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.



**Fig. 2: Temperature coefficient (*Q*10) values for dive durations across four orders (from top to bottom: Testudines, Crocodilia, Serpentes and Urodela) of diving ectotherms, derived from laboratory- (closed circles) and field-based (open circles) studies.** Temperaturecoefficient 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 ± 0.26, pooled across orders, mean ± S.D.) which equates to an approximate 62% decrease in dive durations for every 10°C increase in body temperature. Values are shown as mean ± S.D. with raw values overlaid.

**A close up of a map

Description automatically generated**

**Fig. 3: Overall meta-analytic results for the effect of an increase in temperature (lab: weighted mean ± S.D. = 10.6 ± 11.8°C; field: weighted mean ± S.D. = 4.79 ± 5.60°C) on dive duration means (*****ln*RR, A, B) and variability (*ln*CVR, C,D) in diving ectothermic vertebrates for laboratory based (A,C) and field-based (B,D) studies.** 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.

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**Fig. 4:** Temperature increases decrease dive mean duration when controlling for the average temperature of the temperature treatment pair and body mass (*ln*RR, **A**). While there was a tendency for the variability in dive duration to increase these effects were not statistically distinguishable from no effect (0) (*ln*CVR, **B**). 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.

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**Fig. 5: Effects of temperature increase (weighted mean ± S.D. = 10.6 ± 11.8°C)** **on dive duration means (*ln*RR, A) and variability (*ln*CVR, B) in aerial breathers and bimodal breathers.** The effect of temperature increases on dive duration means and variability 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 (*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.

**Supplementary material**

Search: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.

Web of Science

(n = 222)

Scopus

(n = 225)

Additional papers from bibliographies

(n = 2)

## **Screening**

Records after duplicates removed  
(n = 303)

Records excluded

(n = 204)

Records screened based on abstract

(n = 303)

Full texts assessed for eligibility

(lab-based

n = 30; field-based n =69)

Records excluded

(lab-based studies n = 15; field-based studies n = 57)

## **Eligibility**

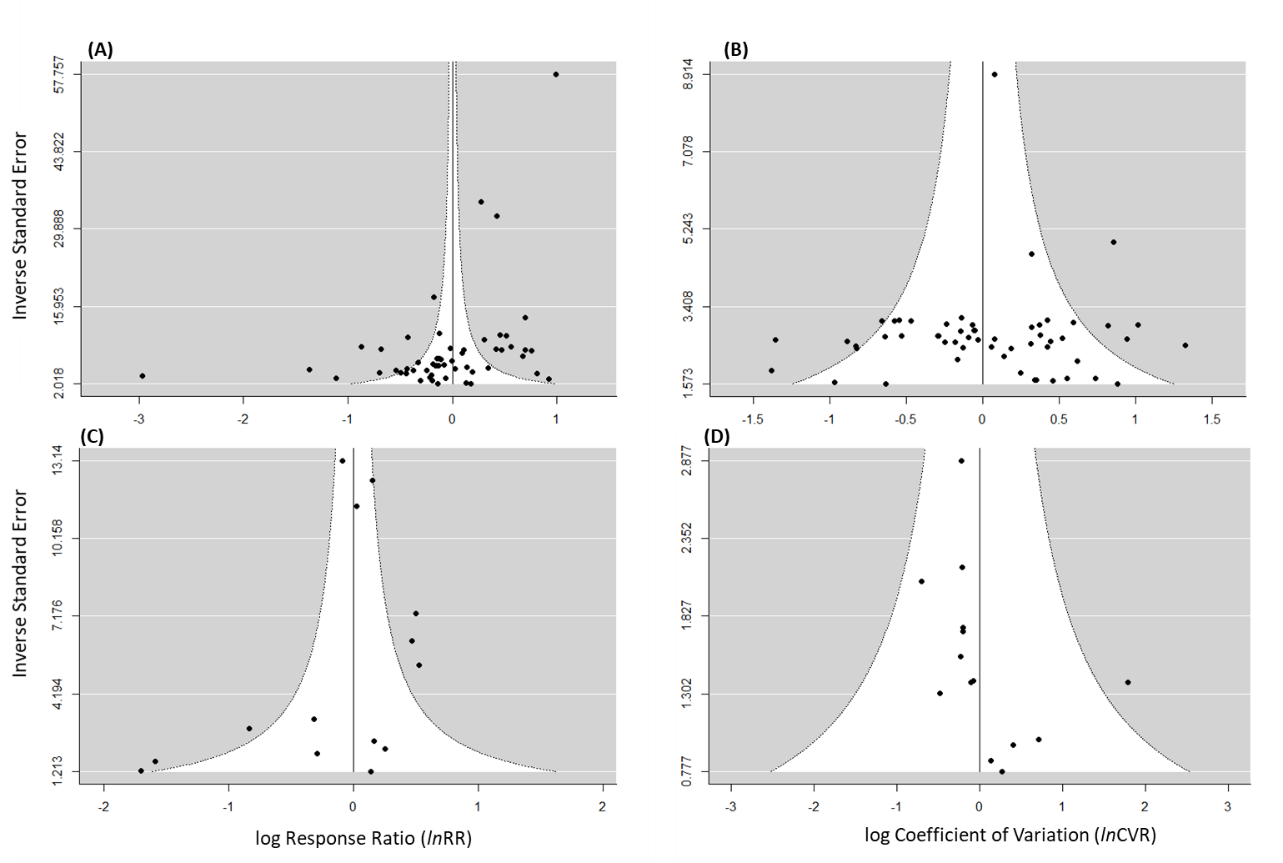
## **Identification**

## **Included**

Studies included in quantitative synthesis

(lab-based studies n = 15; field-based studies n=12)

**Fig. S1: Preferred reporting items for systematic reviews and meta-analyses (PRISMA) flow-chart showing the systematic search for literature on the effects of increasing water temperature on dive durations in ectothermic vertebrates**. Included are all search terms, how many entries were identified and the step-by-step screening description of the selection of the data based on a pre-determined selection criteria (see main text) for inclusion in the meta-analysis.

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**Fig. S2: Funnel plots for the distribution of effect sizes around the meta-analytic mean, for meta-analysis of mean differences (*ln*RR, A,C) and variance differences (*ln*CVR, B,D) in laboratory-based (A,B) and field-based studies (C,D).** The y-axis represents the precisions of the estimates (inverse of the standard error). Values are shown as raw effect sizes.