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REVIEW

Thermal tolerances of sea turtle embryos: current understanding and future directions

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ABSTRACT: Developing sea turtle embryos only successfully hatch within a relatively narrow temperature range, rendering this immobile life stage vulnerable to the vagaries of climate change. To accurately predict the potential impact of climate change on sea turtle egg mortality, we need to fully understand the thermal tolerance of developing embryos. We reviewed the literature on this topic, and found that published studies interpret the primary literature and subsequent reviews very differently. Based on early literature reviews, the maximum thermal tolerance of sea turtle embryos is frequently cited as either 33 or 35°C. In many sea turtle populations, however, nest temperatures often exceed 35°C by up to several degrees (usually just prior to hatchling emergence) and eggs still hatch successfully. Mean incubation temperatures up to 35°C generally produce hatchlings, although leatherback and olive ridley turtle embryos may be less tolerant of high incubation temperatures than green and loggerhead turtle embryos. Sea turtle embryos are likely to be more sensitive to the duration of time spent at potentially stressful temperatures than to the temperature alone. To complicate matters, developing embryos may change their thermal tolerance as they grow. Overall, we are only beginning to understand how exposure to high temperatures experienced in the field influences embryonic development and hatchling production. This knowledge gap is hampering our ability to predict the impacts of climate change on sea turtle populations, and future work should focus on understanding how temperature and other climatic variables influence embryonic development and, thus, crucial population attributes such as hatchling production.

KEY WORDS: Climate change · Embryonic development · Hatching success · Lethal thermal limits · Marine turtles · Metabolic heating · Thermal mortality · Thermal tolerance

INTRODUCTION

To successfully adapt to environmental changes, species may be forced to shift their geographic ranges or activity patterns; if this is not possible, they may risk going extinct (Hawkes et al. 2009, Witt et al. 2010, Pike 2013). Given that many physiological functions of ectotherms depend on temperature, the vast majority of terrestrial ectotherms may be vulnerable to climate change (Deutsch et al. 2008, Doody & Moore 2010). Many ectotherms have a complex life cycle, where the adult and embryonic stages have different habitat requirements and physiological tolerances to environmental conditions; this vastly complicates the potential impacts of climate change. For example, sea turtles are the most widely distributed reptile taxa (James et al. 2006), and collectively require large areas of oceanic and coastal (both aquatic and terrestrial) habitats for different life stages (Hawkes et al. 2009, Witt et al. 2010). The embryonic stage must occur on land because amniotic eggs need to exchange oxygen through the air for the embryo to develop successfully into a hatchling turtle (Ewert 1985). Unlike the developing embryos of

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viviparous species, the immobile egg stage of oviparous species cannot 'behaviourally buffer' itself against environmental changes (Telemeco et al. 2013a, Pike 2014). A warming environment at nest sites may therefore lead to phenological changes in nesting periodicity, altered sex ratios in species with temperature-dependent sex determination, and possible reductions in hatching success (reviewed by Jourdan & Fuentes in press). Overall, however, the effects of climate change are anticipated to be most dramatic during the egg stage, as opposed to free-living phases of life history (Hawkes et al. 2009, Pike 2014).

Several reviews have highlighted the climatic threats facing the sea turtle reproductive stage during nesting and egg incubation periods (Hawkes et al. 2009, Poloczanska et al. 2009, Hamann et al. 2013, Pike 2014). Along with water and respiratory gases, temperature plays a crucial role for developing embryos (Mortimer 1990, Segura & Cajade 2010), and the influence of temperature on sea turtle embryonic development is well-documented (e.g. Mrosovsky 1980, Miller 1985, Ackerman 1997, Wibbels 2003). Even small changes in temperature within the nest environment can have significant consequences for successful hatching, and could directly influence key sea turtle population dynamics (Hewavisenthi & Parmenter 2002, Wibbels 2003, Poloczanska et al. 2009).

Sea turtle sex is determined during the middle third of embryonic development; a pivotal temperature (generally between ~28 and 31°C, depending on the population and species) produces a 1:1 ratio of males to females (Ackerman 1997, Wibbels 2003). At temperatures below pivotal, males are produced, whereas temperatures above pivotal produce proportionately more females (Yntema & Mrosovsky 1980). A change in temperature as subtle as 0.5°C can alter the offspring sex ratio within a clutch from 1:1 to 1:0 (Hewavisenthi & Parmenter 2002). With climate change, increased temperatures within the nest could therefore create a female bias in the primary sex ratio of some sea turtle populations (Hawkes et al. 2009, Fuentes et al. 2010, Telemeco et al. 2013b), which could lead to complete feminisation of hatchlings by 2070 if extreme climate forecasts materialise (Godley et al. 2001, Glen & Mrosovsky 2004, Hawkes et al. 2007, Fuentes et al. 2010, Laloë et al. 2014). Apart from the effects that elevated temperatures could have on sex ratios, high temperatures can also inhibit successful embryonic development, leading to phenotypic abnormalities or death (Packard et al. 1988, Du & Ji 2003, Maulany et al. 2012a, Telemeco et al. 2013a, Pike 2014). In freshwater turtles, temperature-related abnormalities disrupt the central nervous system, which can influence hypothalamus development and yolk absorption (Micheli-Campbell et al. 2012). Even if the embryo manages to develop successfully, high temperatures within the nest can reduce oxygen levels and disrupt muscle coordination, inhibiting the ability of sea turtles to ascend to the surface and disperse from the nest after hatching (Matsuzawa et al. 2002, Segura & Cajade 2010). High incubation temperatures can also produce smaller-sized hatchlings with reduced locomotor abilities, potentially increasing susceptibility to predation as turtles crawl to the water after emerging from the nest and swim off-shore (Ischer et al. 2009, Segura & Cajade 2010, Booth & Evans 2011, Maulany et al. 2012a, Booth et al. 2013, Read et al. 2013, Wood et al. 2014).

In extreme cases, high incubation temperatures result in embryonic mortality, and can decrease hatching success of nests or lead to complete clutch failure (Matsuzawa et al. 2002, Hawkes et al. 2007, Maulany et al. 2012b). Unlike sex-determining temperatures, for which the pivotal range is known in some detail for most sea turtle species (Wibbels 2003), the upper maximal limit to successful incubation is less well-defined. Estimates of both 33°C (Miller 1997) and 35°C (Ackerman 1997) are frequently cited, but these estimates are based on early studies of natural nest temperatures in the field or artificial incubation experiments at constant temperatures in the laboratory, respectively. The effects of constant and naturally fluctuating temperatures on hatching success and hatchling phenotype can differ substantially (Bowden et al. in press); in some cases, naturally fluctuating thermal regimes can exceed 35°C, particularly over the last 2 wk of incubation, and still produce hatchings (Hewavisenthi & Parmenter 2002, Matsuzawa et al. 2002, Ischer et al. 2009, Booth & Evans 2011, Maulany et al. 2012b, Booth et al. 2013, Read et al. 2013, Wood et al. 2014). Determining the lethal temperature limits to embryonic development is essential to identifying which sea turtle populations are most at risk from embryonic mortality. Here we review the literature to clarify our understanding of how temperature influences sea turtle hatching success and to highlight knowledge gaps that currently limit our ability to predict the impacts of climate change on sea turtle populations. We also briefly discuss some of the potential ways in which sea turtles could adapt to climate change, along with human interventions that could enhance sea turtle population resilience.

REVIEW OF HIGH-TEMPERATURE INCUBATION STUDIES

Hendrickson (1958) first documented natural nest temperatures of green sea turtles *Chelonia mydas* in Malaya and Sarawak; these reached nearly 35°C before turtles successfully hatched. A decade later, Bustard & Greenham (1968) incubated sea turtle eggs in the laboratory under a wide range of constant temperatures, including 15, 20, 27, 32, and 38°C. No eggs hatched from the 38°C incubation treatment, and hatching success was relatively low (60%) at 32°C (Bustard & Greenham 1968). A follow-up study later showed that incubation at both 33 and 35°C resulted in 60% of the eggs hatching (Bustard 1971). Although neither of these early studies provides information on constant temperature incubation between 36 and 37°C, the results suggest that developing embryos can withstand moderately high temperatures (at least 35°C throughout incubation) and still hatch. Bustard (1972) later attempted to narrow down the upper lethal limit by incubating green sea turtle eggs at constant temperatures between 35 and 37°C, but only mentions 'successful hatching' at these temperatures and does not present quantitative results. In stark contrast to incubating eggs, hatchling sea turtles have been reported to survive temperatures exceeding 40°C (Drake & Spotila 2002). This highlights just how truly vulnerable the egg stage is to extreme temperatures (also see Table 1, Fig. 1).

Although some incubating green sea turtle embryos may be able to withstand temperatures up to 37°C for the entire duration of incubation (Bustard 1972), this is not the case for all species (Table 1, Fig. 1). In loggerhead turtles *Caretta caretta* (from Merritt Island, Florida, USA), McGehee (1979) found that 71% of hatchlings emerged when incubated at a constant 32°C, whereas none emerged at 35°C. Yntema & Mrosovsky (1980) also suggested that 35°C may represent a lethal limit for loggerhead turtles (from Georgia, USA). Their results revealed a reduction in hatching success with increasing temperature; no eggs hatched at a constant 36°C, 17% of eggs hatched at 34°C, and 92% of eggs hatched at 32°C (Yntema & Mrosovsky 1980). These early studies revealed distinctly higher thermal tolerances of green turtle eggs than loggerhead eggs, at least at constant incubation temperatures. This difference was initially attributed to their tropical and temperate habitat affinities, respectively (McGehee 1979). Later work by Miller & Limpus (1981) found that only 15% of green sea turtle eggs from Heron Island, Australia, hatched when incubated in a constant 33°C environment, whereas 100% of eggs hatched at 29°C (Miller & Limpus 1981). Research on sympatric green and loggerhead turtles from Mon Repos, Australia, also revealed that green and loggerhead eggs failed to hatch when incubated at constant temperatures above 32°C (Miller 1982). Together, these early studies make it clear that there is substantial variation among species and populations in the maximum constant incubation temperature at which eggs can successfully hatch (Table 1).

Natural nests in the field, by contrast, can fluctuate on a diel basis, and the mean nest temperature often increases as incubation progresses, due to seasonal temperature changes and from metabolic heat produced by late-stage embryos (Hendrickson 1958, Mrosovsky 1994, Booth & Astill 2001, Hewavisenthi & Parmenter 2002, Booth & Freeman 2006, Maulany et al. 2012a). In the past 10 to 15 yr many studies have found that sea turtle eggs can hatch successfully in natural nests that exceed 35°C in the field, although hatching success is substantially reduced above this temperature (Table 1, Fig. 1). Thus, reaching 35°C during natural temperature fluctuations is not universally lethal. For leatherback turtles *Dermochelys coriacea* in Costa Rica, temperatures within hatchery nests can have a mean temperature of 33.6°C and reach up to 36.1°C without negatively affecting hatching success (Wallace et al. 2004). This finding is not surprising for this species, because the embryos can survive temperatures >38°C towards the end of the incubation period as a result of metabolic heating inside the nest (Binckley et al. 1998). On Ascension Island, green turtle nest temperatures average 32.2°C, can exceed 35°C regularly, and reach maximums up to 36.5°C, resulting in a moderate hatching success rate of 57% (Broderick et al. 2001). On Heron Island green turtle nests regularly hatch when nest temperature exceeds 35°C late in incubation (Ischer et al. 2009, Booth et al. 2013). In natural loggerhead turtle nests (which constant-temperature laboratory experiments suggest cannot exceed 35°C; Table 1), temperatures can reach 35.4°C for up to 12 d during the end of incubation, resulting in 40% hatching success (Minabe, Japan; Matsuzawa et al. 2002). At the La Roche Percée loggerhead rookery in New Caledonia, nest emergence success can be >90% in nests where temperature exceeds 35°C for at least 3 d in a row (Read et al. 2013). In flatback sea turtle *Natator depressus* nests on Peak Island, Australia, nest temperatures exceeding 35°C for 6.5 d in several nests (maintaining a maximum of 36.5°C for 8 h) resulted in high hatching success rates, ranging from 84 to

Table 1. Examples of cases in which incubation temperature influences sea turtle egg hatching success. Incubation temperatures exceeding 35°C are in **bold**; this temperature is widely cited as the maximum that can be withstood by developing sea turtle embryos. Studies are presented in chronological order, and we highlight relevant details about the studies in the comments column. The species studied were the green turtle *Chelonia mydas*, loggerhead turtle *Caretta caretta*, flatback turtle *Natator depressus*, leatherback turtle *Dermochelys coriacea*, olive ridely turtle *Lepidochelys olivacea*, and hawksbill turtle *Eretmochelys imbricata*. Fig. 1 shows the same data graphically

Reference	Species	Incubation temperatures and egg hatching success (%)	Location	Comments
Hendrickson (1958)	*C. mydas*	'... nearly 35°C just before hatching'	Malaya and Sarawak	Natural nests. No mention of hatching success.
Bustard & Greenham (1968)	*C. mydas*	32°C = 60% 38°C = 0%	Heron Island, Australia	Constant temperature incubation. Authors conclude eggs successfully incubate from 25 to 35°C, including natural temperature fluctuations and metabolic heating.
Bustard (1971)	*C. mydas*	33°C = 60% 35°C = 60%	Heron Island, Australia	Constant temperature incubation.
Bustard (1972)	*C. mydas*	**35–37°C**	Capricon Bunkers, Australia	Constant temperature incubation. No mention of hatching success apart from 'successful incubation'.
McGehee (1979)	*C. caretta*	32°C = 71% **35°C = 0%** **38°C = 0%**	Merritt Island, Florida, USA	Constant temperature incubation.
Yntema & Mrosovsky (1980)	*C. caretta*	30°C = 93% 32°C = 92% 34°C = 17% **36°C = 0%**	Little Cumberland Island, Georgia, USA	Constant temperature incubation. Authors stated that favourable conditions range from 26 to 32°C.
Yntema & Mrosovsky (1982)	*C. caretta*	32°C = 92% 34°C = 17% **36°C = 0%**	Little Cumberland Island, Georgia, USA	Constant temperature incubation.
Miller & Limpus (1981)	*C. mydas*	29°C = 100% 33°C = 15%	Heron Island, Australia	Constant temperature incubation.
Miller (1982)	*C. caretta* *C. mydas* *N. depressus*	32°C = 70% 32°C = 40% 32°C = 90%	Mon Repos, Australia	Constant temperature incubation. Author notes that 'hatching occurred from eggs incubated at constant temperatures between 25°C and 33°C'. Although eggs were incubated at set temperatures exceeding 32°C, hatching success rates were not provided.
Binckley et al. (1998)	*D. coriacea*	31°C = 45.5% 31.5°C = 54.6% 32°C = 50% 33°C = 0%	Guanacaste, Costa Rica	Constant temperature incubation. Natural nests can exceed **38°C** during the final third of development and successfully produce hatchlings.
Broderick et al. (2001)	*C. mydas*	Mean: 32.2°C, max.: **36.5°C** = 57% Mean: 29.9°C, max.: **35.7°C** = 82% Mean: 29.5°C, max.: 34.9°C = 85%	Ascension Island	Natural nests.
Godley et al. (2001)	*C. caretta*	Max.: 34.9°C	Alagadi, northern Cyprus	Natural nests. No mention of hatching success other than hatching success decreased with higher mean nest temperatures.
Matsuzawa et al. (2002)	*C. caretta*	Nest temperatures at **35.4°C** for 12 d = 40%	Minabe, Japan	Natural nests. High temperatures experienced in the final period of incubation.

Table 1 (continued)

Reference	Species	Incubation temperatures and egg hatching success (%)	Location	Comments
Hewavisenthi & Parmenter (2002)	*N. depressus*	**>35°C** for up to 6.5 d, **36.5°C** for 0.3 d = 84–95 %	Peak Island, Australia	Natural nests.
Wallace et al. (2004)	*D. coriacea*	Mean: 33.6°C, range: 32.1–**36.1**°C	Guanacaste, Costa Rica	Natural nests relocated to a hatchery. No hatching success rates are provided other than the statement that maximum temperature did not affect hatching success.
Dobbs et al. (2010)	*E. imbricata*	Mean: 34.6°C, range: 33.5–**36.0**°C Mean: 34.7°C, range: 33.6–**35.7**°C ≥50 %	Milman Island, Australia	Natural nests.
Valverde et al. (2010)	*L. olivacea*	Mean: 34.2°C, 20 d **>35°C** = 19 % Mean: 33.7°C, 30 d **>35°C** = 4 % Mean: 33.9°C, 30 d **>35°C** = 5 % Mean: 33.1°C, 14 d **>35°C** = 4 % Mean: 34.4°C, 20 d **>35°C** = 2 %	Ostional Beach, Costa Rica	Natural nests.
Weber et al. (2012)	*C. mydas*	Mean: 33.6°C = 18 % Mean: 33.4°C = 25–57 %	Ascension Island	Natural nests.
Maulany et al. (2012a)	*L. olivacea*	Mean: 32.4°C, max.: **35.7°C** = 62 % Mean: 31.6°C, max.: **36.3°C** = 54 %	East Java, Indonesia	Natural nests.
Read et al. (2013)	*C. caretta*	**>35°C** for 3 consecutive d = 90 %	La Roche Percée, New Caledonia	Natural nests.

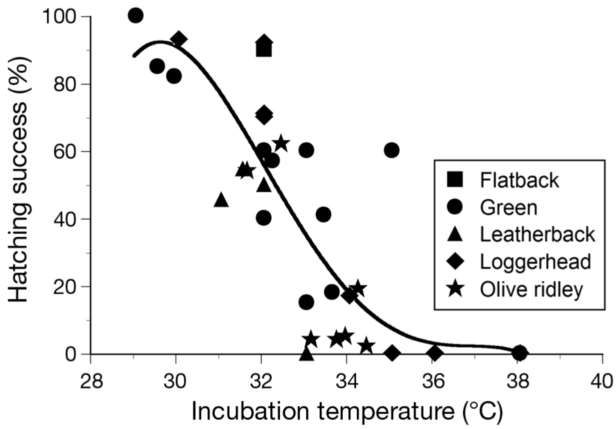

Fig. 1. Relationship between incubation temperature and hatching success for sea turtle eggs, shown by species. We plotted data from studies in Table 1 that incubated eggs under constant or mean temperatures and present quantitative hatching success data. Trend line shows a 4th order polynomial fit to the entire dataset. Scientific names of species, see Table 1

95 % (Hewavisenthi & Parmenter 2002). These data suggest that the lethal limit for this species could be at, or above, 37°C near the end of incubation, and that near-term flatback embryos can withstand temperatures exceeding 35°C for extended periods. Such high temperatures have also been recorded in hawksbill sea turtle *Eretmochelys imbricata* nests; at least 1 successful nest averaged 34.6°C and ranged from 33.5 to 36.0°C (Dobbs et al. 2010).

Studies of incubation temperatures within natural nests provide important information on the temperature range that sea turtle embryos can withstand and at which they can successfully hatch, but have not yet determined whether temperature fluctuation and stage of embryonic development interact, such that the thermal tolerance of embryos changes during incubation. Research on olive ridley sea turtles *Lepidochelys olivacea* has come closest to answering these questions, by investigating hatching success relative to the duration of time spent above 35°C. Valverde et al. (2010) found that mean incubation temperatures >35°C on Ostional Beach, Costa Rica, did not produce hatchlings. When the maximum incubation temperatures exceeded 35°C, the number of days spent above 35°C decreased hatching success (with a maximum of 37.13°C in the third trimester; Table 1). These results suggest that some of the olive ridley embryos within a clutch can survive temperatures exceeding 37°C for short periods, if the mean temperature for the whole incubation period is below 35°C.

Olive ridley nests in hatcheries in East Java, Indonesia, show a similar pattern (Maulany et al. 2012a,b). Nests that reached a maximum of 35.7°C, but averaged 32.4°C, showed 61.6% hatching success, and those that reached 36.3°C (with the last 10 d of incubation >35.5°C) showed a 54.2% hatching success at a mean temperature of 31.6°C (Maulany et al. 2012a). However, the hatchlings that emerged from nests that reached temperatures >34°C for at least 3 d showed a reduction in locomotor performance, suggesting that high incubation temperatures had sublethal effects (Maulany et al. 2012a). Other authors have also suggested that earlier embryonic stages may be more sensitive to high temperatures (e.g. Birchard 2004). It is likely that high temperatures have the largest effect on sea turtle embryos during the first 2 trimesters of development, although this requires further experimentation.

INFLUENTIAL LITERATURE REVIEWS ON HIGH-TEMPERATURE INCUBATION

Three early reviews of the embryology of sea turtles summarise the optimal incubation temperatures or maximum thermal limits of sea turtle eggs (Miller 1985, 1997, Ackerman 1997). These studies each focused on different aspects of the thermal environment, leading to very different conclusions. For example, Miller (1985, p. 272) concludes that 'Under natal beach conditions, the eggs incubate at temperatures between 24° and 33°C', whereas Ackerman (1997, p. 85) concludes that 'The thermal tolerance range (TTR) for development of sea turtle embryos incubated at constant temperature appears to fall between about 25 to 27°C and 33° to 35°C...'

Miller (1985) explicitly refers to natural incubation conditions in the field and (potentially) to the temperature range at which hatching success is optimal, by citing studies demonstrating successful embryonic development at temperatures above 33°C, with a maximum of 35 to 37°C reached during late incubation (i.e. Hendrickson 1958, Caldwell 1959, Bustard 1972). Later, however, Miller (1997, p. 67) also states that 'eggs held at temperatures greater than 33°C for extended periods do not hatch', which some authors have interpreted as the putative upper thermal limit to embryonic development (Table 2). Ackerman (1997) specifically refers to the temperatures that embryos can physiologically tolerate, and thus provides a higher value of 35°C (note, however, that the minimum temperature provided by Ackerman [1997] is a degree higher than that provided by Miller [1985]). Ackerman (1997) references Ewert (1985), who in turn references Bustard's (1971) study reporting that green turtle eggs can tolerate temperatures up to 35°C (Table 1).

Our review of the literature found that many subsequent studies cite Ackerman (1997) and Miller (1985 and/or 1997) interchangeably, or have taken some of their conclusions out of context (e.g. Table 2). Miller (1985) explicitly refers to natal beach conditions rather than lethal limits, which does not imply that 33°C is fatal for sea turtle embryos, but only that many nesting beaches do not reach this temperature (Table 1). Under climate change, natal beach conditions are likely to become warmer, and thus Ackerman's (1997) review of the absolute physiological tolerances of developing embryos is the more relevant early review, compared to the description of the range of natural incubation conditions provided by Miller (1985) (Table 2).

SYNTHESIS OF HIGH-TEMPERATURE INCUBATION STUDIES

Several studies have reported hatchlings successfully emerging from sea turtle eggs incubated at mean temperatures >30°C (Table 1, Fig. 1). Hatching success declines substantially as the mean incubation temperature exceeds 29°C (Fig. 1). The highest recorded mean incubation temperature that resulted in hatchlings being produced is 35°C, from green turtles (Fig. 1). Experiments on loggerhead turtle eggs incubated at 35 and 36°C, and green turtle eggs incubated at 38°C, did not produce any hatchlings (Table 1, Fig. 1). The limited data available suggest that leatherback and olive ridley embryos could have lower thermal tolerances than green and loggerhead turtles (Fig. 1), but this warrants further testing. Importantly, data on high-incubation temperatures and resultant hatching success are lacking for flatback turtles *Natator depressus*, hawksbill turtles, and Kemp's ridley turtles *Lepidochelys kempii*, which limit the generalisations that can be made about all sea turtle species (Table 1, Fig. 1).

METABOLIC HEATING AND NEST TEMPERATURES

When sea turtle embryos are developing rapidly during the period of internal organ differentiation, metabolic heat is produced and transferred to the nest chamber (Hendrickson 1958). The nest cham-

Table 2. Example of oversimplified statements about the thermal tolerance of sea turtle eggs from seminal papers, based upon information available at the time of publication. *C. caretta*: *Caretta caretta*

Reference	Statement about thermal tolerance	Discrepancy with primary literature
Miller (1997, p. 67)	'…eggs held at temperatures greater than 33°C for extended periods do not hatch.'	Bustard (1971) found that eggs can hatch at 35°C. Ackerman (1997, p. 85) states that 'The thermal tolerance range (TTR) for development of sea turtle embryos incubated at constant temperature appears to fall between about 25 to 27°C and 25 to 35°C...'
Hewavisenthi & Parmenter (2002, p. 307)	Paper cites Miller (1985) as evidence that 33°C is the 'upper tolerance limit'.	Miller (1985, p. 272) states that 'Under natal beach conditions, the eggs incubate at temperatures between 24–33°C.' There is no specific mention of an upper limit.
Miller et al. (2003, p. 136)	'The maximum temperature for successful incubation is 33°C [for *C. caretta*] in eastern Australia (Limpus et al. 1985)'.	Limpus et al. (1985) incubated eggs between 25 and 32°C and made no mention of 33°C. In addition, Limpus et al. (1985) state that incubation above 31°C is the lethal limit and reference Limpus et al. (1983), who incubated eggs at temperatures up to 32°C, but refer to unpublished data for an upper lethal limit of 34°C.
Hamann et al. (2007, p. 480)	33°C is 'near the upper limits for incubation survival' (Miller 1997).	Miller (1997) states that 'Under natal beach conditions, the eggs incubate at temperatures between 24–33°C.' There is no mention of an upper limit.
Dobbs et al. (2010, p. 14)	Paper cites Miller (1985) as evidence for '...a lethal threshold of incubation temperature at approximately 34°C...'	Miller (1985) states that 'Under natal beach conditions, the eggs incubate at temperatures between 24–33°C.' There is no mention of an upper limit.
Fuentes et al. (2012, p. 58)	Paper cites Miller (1985) as evidence for 34°C as the 'upper thermal threshold'.	Miller (1985) states that 'Under natal beach conditions, the eggs incubate at temperatures between 24–33°C.' There is no mention of an upper limit.
Maulany et al. (2012a, p. 2658)	'Continuous incubation of sea turtle eggs at temperatures above 34°C is fatal (Miller 1997).'	Miller (1997, p. 67) states that 'eggs held at temperature greater than 33°C for extended periods do not hatch'. Bustard (1971) found that eggs can hatch at 35°C.

ber often retains this heat (Wallace et al. 2004), which can increase nest temperatures above that of the surrounding substrate (Table 3). The extent of metabolic heating can also vary by position within the clutch (Standora et al. 1982). Metabolic heating mainly occurs during the latter third of incubation (Table 3), when embryos may be less susceptible to negative effects caused by exposure to high temperatures (e.g. as hypothesised by Birchard 2004). In the context of climate change, metabolic heating may have the most influence when nest temperatures are near the pivotal sex-determining temperature or near 35°C, and at risk of exceeding lethal levels. Examples of vulnerable beaches include Ostional Beach, Costa Rica (Valverde et al. 2010); Senri Beach, Japan (Matsuzawa et al. 2002); Wembrak Beach, Indonesia (Tapilatu & Tiwari 2007); and Alas Purwo National Park, Indonesia (Maulany et al. 2012b). In these cases, metabolic heating may drive nest temperatures to lethal limits, or at least high enough to cause sublethal effects (e.g. reduced locomotor ability).

The susceptibility of sea turtles eggs to lethal temperatures may depend on the species, and even on differences within species in terms of egg and clutch sizes. Smaller clutches, which have a higher surface area to mass ratio, may be able to more readily release metabolic heat to the surrounding environment, and thus experience lower core temperatures when compared to larger egg clutches (Hendrickson 1958, Hewavisenthi & Parmenter 2002). Likewise, greater metabolic heating has been demonstrated in nests with a larger clutch mass in green turtles (Booth & Astill 2001). Sea turtles with smaller clutch sizes (e.g. leatherback and flatback turtles; Van Buskirk & Crowder 1994) may be least likely to reach lethal thermal limits if excess heat is lost to surrounding sand. These 2 species also produce the largest eggs (Miller 1985), which can improve hatching success, presumably by reducing water loss during incubation (Gutzke & Packard 1985). However, increased egg size may also correlate with increased metabolic heating, causing Booth & Astill (2001, p. 79) to note that 'the total amount of metabolic heat produced by a clutch will depend on the biomass of embryos within the clutch and this is a function of the egg size and number of eggs in the clutch.' Therefore, a smaller clutch may only release more metabolic heat

Table 3. Summary of the effects of metabolic heating on sea turtle nest temperatures, shown for each third of the incubation period. In cases where standard deviations were presented in the text we converted them to standard errors for consistency

Species	Metabolic heating (°C, ±SE) by incubation stage First third	Middle third	Last third	Reference
Caretta caretta	−0.6 ± 0.10	0.2 ± 0.2	1.64 ± 0.56	Zbinden et al. (2006)
	0.1 ± 0.1	0.2 ± 0.1	0.9 ± 0.1	Godley et al. (2001)
	–	~0.6–0.7	2.5–3.5	Maloney et al. (1990)
	–	–	3.0	Maxwell et al. (1988)
Chelonia mydas	–	–	2.0–4.0	Booth & Freeman (2006)
	~0.1	0.68–1.27	3.0–4.0	Broderick et al. (2001)
	~0.3	~0.3–1.2	~1.6–2.3	Carr & Hirth (1961)
	–	–	3.0–5.0	Booth & Astill (2001)
	~0.1	~1.5–3	~5.0	Bustard (1972)
	–	–	6.0	Standora et al. (1982)
	–	–	5.0–6.0	Bustard & Greenham (1968)
	–	–	6.0	Hendrickson (1958)
Dermochelys coriacea	–	–	4.0–8.0	Binckley et al. (1998)
	~0.5	~0.8	0.82 ± 0.09	Godfrey et al. (1997)
Eretmochelys imbricata	–	1.1	3.4	Glen & Mrosovsky (2004)
	–	–	~5.0	Raj (1976)
Natator depressus	–	–	0.5	Hewavisenthi & Parmenter (2002)

if the eggs themselves are also small. The literature for sea turtles on the effects of egg size on metabolic heating is limited, however (e.g. Table 3), and thus this topic requires further investigation.

POTENTIAL OF TURTLES TO ADAPT TO INCREASING NEST TEMPERATURES

The ability of sea turtles to cope with contemporary climate change will depend on their adaptability to increasing temperatures, which could include changes in phenology (Weishampel et al. 2004, Pike et al. 2006, Telemeco et al. 2013b), changes in nesting beach or nest-site choice (Weber et al. 2012), latitudinal advantages (Hawkes et al. 2007, Pike 2014), and, potentially, the thermoregulation of individual embryos inside of the egg (as has been documented in Chinese pond turtles *Chinemys reevesii*; Zhao et al. 2013). The pace at which contemporary climate change is occurring could be more rapid than the adaptation of sea turtles to such change (Hamann et al. 2013). For instance, the timing of breeding is often affected by the climatic conditions at feeding sites, which can be more than a thousand kilometres from nesting rookeries (Plotkin 2003, Polovina et al. 2004). Any phenological shifts in the timing of nesting for a whole population could therefore take generations (Hamann et al. 2007). However, changes in phenology over much shorter time periods have already been reported, with sea turtle populations nesting earlier when ocean temperatures are warmer (reviewed by Hamann et al. 2013).

Recent evidence suggests that some sea turtle populations could be adapted to warmer local incubation environments than other populations. On Ascension Island, green turtle nests incubating within the warmer black sands survive better at hotter incubation temperatures then those laid in cooler pale sands (Weber et al. 2012). Even if sea turtles begin selecting beaches which provide cooler nest temperatures (e.g. as a result of the sand colour, grain size, beach orientation, canopy shading, etc.; Ackerman 1997, Moran et al. 1999, Booth & Freeman 2006, Poloczanska et al. 2009), the pace of adaptation may be unable to keep up with current levels of rapid warming. Sea turtle populations at higher latitudes, however, may fare better than those at lower, tropical latitudes, because the temperatures at high latitudes may become more favourable as temperatures increase, whereas those in tropical locations may exceed lethal levels (Hawkes et al. 2009, Pike 2014).

Human management interventions may possibly help sea turtles adapt to climate change (reviewed by Fuentes et al. 2012). First and foremost, reducing anthropogenic threats is necessary to provide sea turtles the best opportunity for survival during contemporary climate change. Protecting incubating eggs from lethally high temperatures, and ensuring the production of male offspring, are important secondary goals (Fuentes et al. 2012). Measures which will help achieve these goals include manipulating vegetation cover to alter nest temperature, artificially incubating eggs at desired temperatures, adding sand of different thermal properties, cooling the sand using sprinklers, and protecting natural beach features by limiting human development (Fuentes et al. 2012). Nearly all of these strategies could be effective in some instances, but identifying the underlying climate change threat to individual nesting beaches is key to selecting the most appropriate strategy (Fuentes et al. 2012).

CONCLUSIONS AND FUTURE DIRECTIONS

Observational field studies and laboratory experiments have contributed useful information to understanding the relationship between hatching success of sea turtle embryos and temperature. Existing data reveal strong differences in lethal temperature thresholds within and among populations, depending (at least partially) on turtle species, geographic location, environmental temperatures, and nest depth (Table 1, Fig. 1). The lethal limit or threshold temperature for sea turtle embryos is usually cited as ranging between 33 and 35°C, with both Miller (1997) and Ackerman (1997) as common references. However, it is much less commonly acknowledged that embryos can and do survive temperatures above these limits. Overall, developing sea turtle embryos rarely hatch when the mean incubation temperature is 35°C, and, when embryos survive temperatures 1 to 2°C above this, hatchlings are only produced when these high temperatures are reached during the latter part of incubation. The exact lethal limit of sea turtles will most likely never be known, unlike the sex-determining temperature, given that it is not just the temperature but also the duration at that temperature which dictates hatching success (Valverde et al. 2010). Nevertheless, more accurate data on each species and their respective nesting beaches are required to make meaningful predictions of hatching success under climate change. Because experiencing optimal incubation temperatures is fundamental to successful embryonic development (Hamann et al. 2007), and high temperatures are predicted to have the greatest effect on sea turtle nesting as a result of climate change (Fuentes et al. 2011), knowledge of these processes and the effects of climate change require more fundamental research.

Given the rapidly growing literature on climate change in sea turtles (reviewed by Hawkes et al. 2009), it is surprising that more research has not been done on the effects of temperature on embryonic developmental limits. Many researchers are hesitant to conduct potentially lethal experiments on eggs of species of conservation concern; however, with the increasing population trends of many rookeries worldwide this may begin to change. Collecting a few hundred eggs for experiments that could substantially advance our ability to forecast the spatial and temporal impacts of climate change, and better understand the risks of negative impacts on populations and species is certainly justified because the knowledge benefits (when shared with the scientific community) likely outweigh any potential demographic effects to individual nesting beaches.

Experimental studies that use artificial incubators to mimic realistic nest temperatures can be used to tackle much more complicated questions about sea turtle embryology (Bowden et al. in press), but have some disadvantages because these experiments are unable to imitate natural nest conditions and thus may be less accurate (Telemeco et al. 2013b). The use of constant temperature incubation experiments has also been questioned with respect to its effects on metabolic heating, and whether this would influence embryonic development (McGehee 1979). For sea turtles, natural fluctuations in nest temperatures and metabolic heating are generally quite predictable, especially when the nests are located deep underground, which may allow easier replication in the laboratory. Once physiological tolerances are known, other sources of temperature variation (e.g. effects of nest depth and intra-clutch thermal gradients) can be modelled. Far more difficult to replicate in the laboratory are the potentially important interactions between temperature and oxygen partial pressure in nests (which tend to drop more rapidly at higher temperatures), which could help us understand the physiological limits of embryonic development.

Many of the current knowledge gaps we highlight can be addressed by focusing on the factors that modulate the relationship between temperature and survival, rather than on attempting to generalise a lethal temperature for embryonic development. Experimentally defining temperature survival curves for individual species, and populations within species, will help determine the plasticity of this trait across the range of a species, and thus the potential for embryonic responses to climate change. Determining how heritable this variation is could lead to novel insights on population resilience. Understanding relationships between incubation temperature and oxygen tension within the nest could also provide important mechanistic insights into how temperature influences sea turtle embryonic development. Advancing our current state of knowledge of this topic will substantially improve our ability to understand the impacts of climate change on globally distributed marine megafauna that are entirely dependent upon coastal terrestrial environments for successful reproduction.

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