Climate change and nesting behaviour in vertebrates: a review of the ecological threats and potential for adaptive responses

Journal:	<i>Biological Reviews</i>
Manuscript ID	BRV-02-2016-0024.R2
Manuscript Type:	Original Article
Date Submitted by the Author:	n/a
Complete List of Authors:	Mainwaring, Mark; Lancaster University, Barber, Iain Deeming, Denis; University of Lincoln, School of Life Sciences Pike, David Roznik, Betsy Hartley, Ian
Keywords:	adaptation, nest site selection, nest structure, precipitation, temperature, threats, wind speed

Climate change and nesting behaviour in vertebrates: a review of the ecological threats and potential for adaptive responses

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Running head: Climate change and nesting behaviour

Word count (excluding references): 7280

ABSTRACT

Nest building is a taxonomically widespread and diverse trait that allows animals to alter local environments to create optimal conditions for offspring development. However, there is growing evidence that climate change is adversely affecting nest-building in animals directly, for example via sea level rises that flood nests, reduced availability of building materials, and suboptimal sex allocation in species exhibiting temperature-dependent sex determination. Climate change is also affecting nesting species indirectly, via range shifts into suboptimal nesting areas, reduced quality of nest building environments, and changes in interactions with nest predators and parasites. The ability of animals to adapt to sustained and rapid environmental change is crucial for the long-term persistence of many species. Many animals are known to be capable of adjusting nesting behaviour adaptively across environmental gradients and in line with seasonal changes, and this existing plasticity potentially facilitates adaptation to anthropogenic climate change. However, whilst alterations in nesting phenology, site selection and design may facilitate short-term adaptations, the ability of nest-building animals to adapt over the longer timescales is likely to be influenced by the heritable basis of such behaviour. We urgently need to understand how the behaviour and ecology of nest-building in animals is affected by climate change, and particularly how altered patterns of nesting behaviour affect individual fitness and population persistence. We begin our review by summarising how predictable variation in environmental conditions influences nest-building animals, before highlighting the ecological threats facing nest-building animals experiencing anthropogenic climate change and examining the potential for changes in nest location and/or design to provide adaptive short- and long-term responses to changing environmental conditions. We end by identifying areas that we believe warrant the most urgent attention for further research.

Key words: adaptation, nest-site selection, nest structure, precipitation, temperature, threats, wind speed

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I. INTRODUCTION

Anthropogenic climate change has negatively affected animals and plants across terrestrial and aquatic environments, primarily through advancing phenology, range shifts and community changes (Stenseth *et al.*, 1999; Easterling *et al.*, 2000; Walther *et al.*, 2002; Karl & Trenberth, 2003; Rosenzweig *et al.*, 2008; Fuentes, Hamann & Limpus, 2010a). Whilst the effects on animal reproduction have been extensively studied, empirical studies have focused disproportionately on the later stages of reproduction, particularly when parents are laying and incubating eggs or rearing offspring (Stenseth *et al.*, 1999; Møller, 2012). In contrast, the effects of climate change on the early stages of reproduction, during nest-site selection and nest construction, are far less well understood.

This oversight is of concern because nest construction is a taxonomically widespread behaviour that plays a key role in the reproductive success of many animals. Among the vertebrates, almost all birds, and many species of mammal, reptile, amphibian and fish construct nests of one form or another (Hansell, 2005). Nest construction forms a critically important component of the reproductive cycle because nests create suitable conditions for offspring development (Hansell, 2005; DuRant *et al.*, 2013) where prolonged periods of time spent outside of physiologically acceptable limits can result in abnormal development or even death for offspring developing in nests (DuRant *et al.*, 2013; Howard, Bell & Pike, 2014). Parents are, therefore, under strong selection pressure to build nests that generate suitable microclimates (DuRant *et al.*, 2013; Pike, 2013a). As external environmental conditions become increasingly affected by climate change, the parents' ability to adaptively adjust their nest building behaviour will be a critical determinant of reproductive success.

In this review, we present an overview of the impacts of climate change on the nesting behaviours of vertebrates. We have chosen to include in our definition of nesting behaviours activities that are not only directly related to nest construction, such as the collection of materials by

nest-building birds, but also behaviours, such as incubation, that are integrally linked to nesting. We also distinguish between the selection of sites for nesting – which refers to nests built specifically to serve as a receptacle for eggs and/or offspring – and the occupancy of breeding sites where no nesting behaviour takes place, such as the ephemeral ponds in which many amphibians reproduce. Whilst our review focuses on vertebrates, we also include illustrative examples from invertebrate nest-builders where we consider them to add useful information. To provide a balanced and thorough treatment of the available information we have undertaken a systematic review of the literature. We searched for papers using the Web of Science (1945-present) database using ‘nest’, ‘nesting’, ‘architecture’, ‘climate change’ and all two-word combinations of those search terms, whilst no constraints on the year of publication or language of publication were imposed on those searches. The abstracts of all of the resulting papers were read, and their reference lists were also screened and used to identify further suitable papers. We begin by summarising how predictable variation in environmental conditions – which refer to those well-established changes associated with the advancement of spring in temperate environments and in association with variation in latitude and altitude - influence nest-building animals. We then outline the ecological threats facing nest-building animals under altered environmental conditions resulting from anthropogenic climate change (Easterling *et al.*, 2000) before examining the potential for changes in nest location and/or design to provide adaptive short- and long-term responses to changing environmental conditions. Finally, we highlight areas that we believe warrant the most urgent attention for further research.

II. ENVIRONMENTAL CONDITIONS INFLUENCING NEST LOCATION AND DESIGN

The location and design of nests is expected to be under strong selection since they act together to generate a suitable physiological microhabitat for developing offspring, with suboptimal nest conditions adversely affecting productivity (e.g. Ardia, Pérez & Clotfelter, 2008; Pérez *et al.*, 2008;

reviewed by Ar & Sidis, 2002; DuRant *et al.*, 2013; Howard, Bell & Pike, 2014). In some species, parents can regulate the nest microclimate through behavioural interventions, such as altering patterns of incubation in birds or egg fanning in fish. However, such behaviours are typically energetically costly (FitzGerald, Guderley & Picard, 1989; Ar & Sidis, 2002; DuRant *et al.*, 2013) and may have higher costs than those involved in nest building (Mainwaring & Hartley, 2013). Therefore, costly incubation behaviours may be minimised by the parents by altering nest location and design (Vinyoles, Côté & de Sostoa, 2002; Hansell, 2005), as the cost of nest building is less than the cost of incubation (Mainwaring & Hartley, 2013). Nest characteristics should, therefore, vary adaptively in relation to predictable environmental conditions.

Before constructing a nest, the parent(s) must decide where to build (Hansell, 2005; Møller, 2012). In addition to selecting sites based on their structural characteristics, animals also select sites with a specific microclimate, by either increasing or limiting exposure to factors such as sunlight, moisture or water flow. In temperate environments, optimal temperatures for offspring development are usually higher than ambient temperatures and so nests are often located in sites that warm up quicker and lose heat more slowly than sites selected at random (Roper *et al.*, 2003; Rockweit *et al.*, 2012). The converse applies in tropical environments (Edelman, 2011; Refsnider *et al.*, 2014). For aquatic ectotherms, including fish such as three-spined sticklebacks (*Gasterosteus aculeatus*), the selection of a nest site typically reflects a trade-off between taking advantage of water flows to ventilate eggs with oxygenated water, which reduces the energetic demands of behavioural ventilation (FitzGerald, Guderley & Picard, 1989; Smith & Wootton, 1999), and the risk of washout from water currents (Vinyoles, Côté & de Sostoa, 2002; Rushbrook *et al.*, 2010). Meanwhile, those animals that are sensitive to desiccation choose sites that remain moist until offspring are able to leave the nests; for example, some terrestrial-nesting amphibians such as the red-crowned toadlet (*Pseudophryne australis*) and the South American pepper frog (*Leptodactylus labyrinthicus*) excavate basins into which they deposit eggs, which maintain moisture and protect eggs and larvae against drying out (Wells, 2007).

Nest material can regulate nest microclimates, which is probably more important to ectotherms than endotherms given that the latter are unable to provide heat for the nest contents themselves. Temperatures are, therefore, often warmer and more stable inside the nests of birds (pectoral sandpipers (*Calidris melanotos*): Reid *et al.*, 2002) than at locations immediately outside of nests. Nest microclimates can be regulated in a variety of ways, for example: birds often line their nests with good insulating material, such as feathers (Hilton *et al.*, 2004), amphibians can nest in thick vegetation that retains moisture (Wahl, Harris & Nelms, 2008), and some anurans, e.g. spotted grass frogs (*Limnodynastes tasmaniensis*), create foam nests by beating their mucus secretions into a froth, which protects their eggs against desiccation (Seymour & Roberts, 1991). While nest materials can help to create suitable microclimates for offspring, environmental conditions can be variable, so nest location and design also plays a key role in maintaining suitable conditions for offspring viability (Ardia, Pérez & Clotfelter, 2008).

In temperate environments, mammals (Edelman, 2011), reptiles (Kushlan & Jacobsen, 1990) and birds (Mainwaring & Hartley, 2008) can adjust nest design adaptively so that nest microclimates remain relatively constant even as spring advances and ambient temperatures increase. Moreover, environmental conditions often vary predictably with latitude and/or altitude and nest-site selection and nest design varies accordingly. Birds (Crossman, Rohwer & Martin, 2011; Mainwaring *et al.*, 2012) and rodents (Shump, 1978) breeding in northerly locations build better insulated nests than conspecifics farther south. Reptiles, such as water dragons (*Physignathus lesueurii*), select more open nest sites at cooler latitudes (Doody *et al.*, 2006) and water dragons and western painted turtles (*Chrysemys picta bellii*) build shallower nests at higher altitudes (Doody, 2009; Refsnider *et al.*, 2013) to create the optimal thermal microclimates for offspring development. In the tropics, Hawaiian honeycreepers (*Hemignathus virens virens*) breeding at high altitudes increase nest exposure to the warmth of the sun by building on the outer parts of tree canopies whereas individuals breeding at lower altitudes built inside the canopy, closer to the main tree trunk (Kern & van Riper, 1984). In three-spined sticklebacks, nest construction is influenced by water

flow; individuals building nests under flowing water conditions up-regulate the expression of genes encoding the synthesis of spiggin, a secreted glue used in nest building (Seear *et al.*, 2014) and secrete more into nests (Rushbrook *et al.*, 2010) in comparison to individuals building in still waters.

The location and design of nests, therefore, can be adjusted adaptively in response to predictable variation in environmental conditions. This suggests that individuals may be capable of altering characteristics of their nests within their own lifetimes as environmental conditions change; for longer lived animals this may mean that they are able to respond plastically to anthropogenic climate change (Møller & Nielsen, 2015). The extent of this plasticity and the propensity for adaptation is important because suboptimal conditions within the nest adversely affect offspring. For example, in birds, both high (Murphy, 1994; Mainwaring & Hartley, 2016) and low (Dawson, Lawrie & O'Brien, 2005b) ambient temperatures, high wind speeds (Ritz, Hahn & Peter, 1995) and high levels of precipitation (Keller & van Noordwijk, 1994) negatively impact the growth of offspring. In species with temperature-dependent sex determination (TSD), meanwhile, suboptimal nest temperatures affect the sex of the offspring (reptiles: Hawkes *et al.*, 2007; Mitchell *et al.*, 2008; Laloë *et al.*, 2014; birds: Göth & Booth, 2005; reviewed by Mitchell & Janzen, 2010). This highlights the need for a better understanding of how nest site characteristics affect nest-building animals.

III. DIRECT ECOLOGICAL THREATS FACING NEST-BUILDING ANIMALS

(1) Nest flooding as a result of sea level rise and tropical storms

Climate driven increases in air and sea temperature have resulted in sea level rises (Rosenzweig *et al.*, 2008; Fuentes, Hamann & Limpus, 2010a). Current projections suggest that – under realistic

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2 195 future climate scenarios (RCP2.6 - RCP4.5) – global mean sea level rises for the period 2081–2100
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4 196 of between 0.26-0.63m are expected, compared to 1986–2005 (Church *et al.* 2013). This provides a
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6 197 direct increase in the risk of flooding for animals nesting in proximity to high tide lines, such as
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8 198 seabirds and shorebirds (van de Pol *et al.*, 2010; Bonter *et al.*, 2014), crocodilians (Kushlan &
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10 199 Jacobsen, 1990) and sea turtles (Fuentes, Hamann & Limpus, 2010a; Dewald & Pike, 2014; Pike,
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12 200 Roznik & Bell, 2015). A vulnerability assessment of the impact of climate change on green turtles
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14 201 (*Chelonia mydas*) on the Great Barrier Reef showed that, in the short-term, the flooding of nests as
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16 202 a direct result of sea level rise poses the greatest threat to reproduction (Fuentes, Hamann &
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18 203 Limpus, 2010a). Illustratively, the experimental flooding of green turtle eggs in saltwater for 1 or 3
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20 204 hours reduced their viability by less than 10%, whereas flooding for 6 hours reduced their viability
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22 205 by 30% (Pike, Roznik & Bell, 2015). This suggests that more frequent nest inundation associated
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24 206 with sea-level rise will increase variability in sea turtle hatching success due to impacts of saltwater
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26 207 inundation on developing embryos. Additionally, long-term sand temperatures are predicted to rise
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28 208 to levels that will severely bias sea turtle hatchling sex ratios towards females or even increase
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30 209 embryonic mortality (Fuentes, Hamann & Limpus, 2010a). However, these risks are not always
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32 210 disastrous; extreme flooding events were found to have had no effect on the survival, recruitment or
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34 211 annual population growth rates of adult female painted turtles (*Chrysemys picta*) living in
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36 212 freshwater habitats (Jergenson *et al.*, 2014). Many internationally important shorebird populations
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38 213 nest on the coast, just above mean high tide lines, or on low lying islands and salt marshes.
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40 214 Illustratively, a modelling study found that 11 percent of Kentish plover (*Charadrius alexandrinus*)
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42 215 nests are likely to be inundated under any rise of sea level in the Farasan Islands in Saudi Arabia,
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44 216 whilst 26 percent of nests will be flooded if sea level rises by one metre (AlRashidi *et al.*, 2012).
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46 217 | Meanwhile, North American tidal marshes are home to clapper rails (*Rallus crepitans*) and willets
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48 218 (*Tringa semipalmata*) which breed on the marshes in significant numbers (Wiest *et al.*, 2016),
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50 219 whilst important numbers of common redshanks (*Tringa totanus*) breed on British saltmarshes
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52 220 (Malpas *et al.*, 2013). The nests of such species are safe from flooding under normal high tides, but
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they are vulnerable to the larger storm surges that result from extreme weather events (Easterling *et al.*, 2000). Such events occurred more frequently on the Wadden Sea between the period 1971 - 2008, which experienced the maximum high tide levels increasing at twice the rate of the mean high tide level (van de Pol *et al.*, 2010). This increased the flooding risk for a range of shorebirds and – most worryingly – reduced the reproductive output of Eurasian oystercatchers (*Haematopus ostralegus*) below the level required for their population to remain stable (van de Pol *et al.*, 2010). Sensitivity analyses showed that whilst shorebirds could potentially adapt to the risk of flooding effectively by nesting at more elevated sites on the salt marsh, they continued to exhibit preferences for nesting lower down the salt marsh, which is closer to the feeding grounds on the water's edge and affords better views of predators because of the shorter vegetation. Thus, the lower parts of the salt marsh may have been acting as an 'ecological trap', as the birds reduced their fitness by nesting there (van de Pol *et al.*, 2010). Further research is urgently required to examine how extreme weather events, which are predicted to become more frequent and/or intense in a changing climate (Easterling *et al.*, 2000), affect such populations and particularly those species endemic to offshore islands. Seabirds breeding on offshore islands are particularly vulnerable because such islands are usually low lying and are thus susceptible to small sea level rises. Illustratively, nearly 75 percent of the global breeding population of Laysan albatrosses (*Phoebastria immutabilis*) breed on the Midway Atoll, a low lying atoll within the Hawaiian archipelago, and a sea level rise of two metres is predicted to result in anywhere between 10-100 percent of the albatross nests being flooded (Reynolds *et al.*, 2015).

(2) Availability of nesting sites and building materials

Climate change is likely to alter the availability of nesting sites and some building materials. For example, there is evidence that the availability of scrub and trees as nesting and foraging sites for some bird species has declined. As ambient over-winter temperatures have progressively increased

with climate change, reductions in snow cover have enabled increased numbers of elk (*Cervus canadensis*) to occupy North American woodlands throughout the winter months. Browsing activity of these elk populations have reduced the growth of saplings and limited their availability as nesting sites in the subsequent summer months (Martin & Maron, 2012). Experimentally excluding elk from woodland plots reversed long-term declines in both plant and bird populations, strongly supporting the hypothesis that increased winter browsing by large herbivores is responsible for reducing the availability of scrub and trees as nest sites for passerine birds (Martin & Maron, 2012). For amphibians, which depend on freshwater for reproduction, there is a risk that the availability of suitable damp habitat might become limiting as a result of droughts (Stewart, 1995; Walls, Barichivich & Brown, 2013). Amphibian reproduction is tightly linked to environmental conditions but this relationship differs between species. Whilst the phenology of amphibians nesting in permanent bodies of water is primarily related to temperature, amphibians nesting in ephemeral pools and terrestrial habitats respond more strongly to precipitation which maintains their breeding sites (reviewed by Blaustein *et al.*, 2010).

Climatic changes that affect the availability of water or moisture pose a great threat to amphibians globally since, without suitable nest sites, they are unable to reproduce. For terrestrial-nesting amphibians, soil moisture is the most important factor in successful reproduction. For example, the Puerto Rican coquí frog (*Eleutherodactylus coqui*) deposits eggs in terrestrial nests, and the eggs hatch directly into small froglets and generally live for less than one year; thus, this species is susceptible to periods of drought that decrease the availability of their nesting sites. One study found that their population size declined during a prolonged drought in northeast Puerto Rico, with the abundance of frogs in one year being negatively related to the period of the longest dry spell in the previous year (Stewart, 1995). Amphibians that nest in temporary ponds and intermittent streams are also particularly vulnerable to changes in temperature and precipitation because aquatic nesting sites can dry up as a result of decreased precipitation and increased rates of evapotranspiration (Blaustein *et al.*, 2010; Walls, Barichivich & Brown, 2013).

Such changes in the availability of nesting sites can limit successful reproduction (Semlitsch, 1987; Palis, Aresco & Kilpatrick, 2006) and lead to population declines and even local extinctions (Daszak *et al.*, 2005; McMenamin, Hadly & Wright, 2008) in amphibian populations.

The materials used to build nests may also become scarcer following a change in climate. For example, the availability of bryophytes, which are used as nesting material by many passerine birds in Europe and North America (Breil & Moyle, 1976), may be reduced under warmer climates because associated increases in soil nutrient cycling favour the growth of vascular plants (Tulp, Schekkerman & de Leeuw, 2012). Increasing temperature and decreasing rainfall may alter the availability of mud (Tomiałojć, 1992), an important structural material for many nesting birds (Møller, 2006) and, for some species, such as white-winged choughs (*Corcorax melanorhamphos*) and apostlebirds (*Struthidea cinerea*) i.e. the 'Struthideidae' family of mud nesting birds in Australia, the only material (Rowley & Russell, 2009).

While it is likely that climate change will limit the availability of nesting materials for some species, it may increase opportunities for others. In the Baltic Sea, increased growth of filamentous algae in coastal areas, driven by increasing spring temperatures and the input of agricultural nitrates, has reduced competition among male three-spined sticklebacks for nest sites (Candolin, 2004). Since the availability of nest sites and nesting material normally limits the proportion of males that can successfully engage in reproduction, this suggests a relaxation of sexual selection at impacted sites (Candolin, 2004), which has been confirmed in experimental studies (Heuschele & Candolin, 2010). Consequently, there may be unexpected and profound implications of climate change for the availability of nesting opportunities, with consequences for the distribution of reproductive success at the population level.

(3) Suboptimal sex allocation in species with temperature-dependent sex determination

Environmental conditions experienced during embryonic development have population-scale

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2 299 consequences in taxa for which offspring sex is irreversibly determined by thermal regimes
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4 300 experienced during development (reptiles: Mrosovsky, Hopkins-Murphy & Richardson, 1984;
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6 301 Janzen, 1994; Hawkes *et al.*, 2007; Mitchell *et al.*, 2008; Schwanz & Janzen, 2008; Hays *et al.*,
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8 302 2010; Fuentes, Limpus & Hamann, 2010b; Pike, 2014; Simoncini *et al.*, 2014; Laloë *et al.*, 2014;
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10 303 amphibians: Eggert, 2004; megapode birds: Göth & Booth, 2005; reviewed by Mitchell & Janzen,
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12 304 2010). For species with temperature-dependent sex determination (TSD), equal numbers of male
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14 305 and female offspring are produced at a pivotal temperature, whereas higher or lower ambient
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16 306 temperatures result in consistent sex ratio bias (Mitchell & Janzen, 2010). In many reptiles, nest
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18 307 temperature changes as small as ~1°C can radically alter hatchling sex ratios, with increasing
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20 308 temperatures leading to female-bias in hatchling sex ratios in sea turtles (Janzen, 1994; Eggert,
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22 309 2004; Hawkes *et al.*, 2007; Schwanz & Janzen, 2008; Laloë *et al.*, 2014;) and male-bias in tuatara
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24 310 (Mitchell *et al.*, 2008) and caiman (Simoncini *et al.*, 2014). At the relatively cool, northerly extent
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26 311 of their breeding range in North America, loggerhead sea turtles (*Caretta caretta*) currently produce
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28 312 58% female hatchlings, with models predicting a 7.5°C ambient temperature increase resulting in
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30 313 100% female broods (Hawkes *et al.*, 2007). For warmer, more southerly populations of both
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32 314 loggerhead sea turtles (Pike, 2014) and green turtles (Fuentes, Limpus & Hamann, 2010b) that
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34 315 currently produce 90% females, 100% female broods are predicted with as little as 1°C of warming.
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36 316 So, in this case, it seems that climate change could increase the intensity of sexual selection, rather
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38 317 than reduce it, but the viability of populations of animals with TSD will rely on their ability to adapt
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40 318 to further increases in ambient temperatures (Fuentes, Limpus & Hamann, 2010b; Pike, 2014).
41
42 319 Reassuringly though, there is evidence that the sensitivity of crocodilian embryos to incubation
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44 320 temperatures varies considerably between individuals, and the presence of such variation strongly
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46 321 suggests that the species will be able to cope in a changing climate (Deeming & Ferguson, 1989).
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48 322 Moreover, species with TSD are also likely to be able to influence the environmental conditions
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50 323 experienced in the nest by choosing appropriate nesting sites and by adjusting nest depth, as
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52 324 discussed below.
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IV. INDIRECT ECOLOGICAL THREATS FACING NEST-BUILDING ANIMALS

In addition to the direct threats highlighted above [and summarized in table 1](#), climate change may also indirectly affect nest-building animals via range shifts into suboptimal nesting areas, altered construction conditions in aquatic environments, and changes in the frequency and types of interactions with nest predators and parasites.

(1) Range shifts into suboptimal nesting areas

Increases in ambient temperature have led to the distributions of many (sub) tropical and temperate species heading poleward (Walther *et al.*, 2002; Hicking *et al.*, 2006). Whilst marine turtles range widely throughout many of the world's oceans and seas during the non-breeding season, they are confined to beaches located relatively close to the equator during the breeding season (Pike, 2013a). The distribution of many species of breeding turtles is linked tightly to ambient environmental conditions, with several endangered species nesting only within particularly narrow niches (Pike, 2013a). Consequently, whilst increasing ambient temperatures predict an expansion of the breeding distribution of turtles by enabling them to nest farther from the equator, there is evidence that they are expanding into areas that ultimately reduce their reproductive success, in terms of hatchling survival, as a consequence of human disturbance and competition from larger and thus more dominant turtle species (Pike, 2013a, 2013b). The distribution of breeding turtles is tightly linked to environmental conditions, and critically endangered Kemp's Ridley (*Lepidochelys kempii*) and flatback turtles (*Natator depressus*) nest within particularly narrow thermal and wider climatic niches as compared to the five other sea turtle species (Pike, 2013a, 2013b). Increasing temperature is therefore predicted to expand the turtles' breeding distribution by enabling them to nest further

from the equator as temperatures there warm (Pike, 2013a, 2013b). In some cases, subordinate species may suffer due to increased levels of competition from dominant species, such as humans, and bringing them into closer proximity to humans. There is evidence of this in Kemp's Ridley turtles, which traditionally nested only along a thousand kilometres or so of the Mexican coastline; as temperatures have increased over the past three decades their breeding range has expanded as far north as the Atlantic coast of Florida (Pike, 2013a). In comparison to the traditional nesting area, the Florida coastline is densely populated by humans, exposing these turtles to negative impacts from human development that could have fitness consequences (Pike, 2013b). Whilst this study suggests that vagile species may be able to adapt to changing global climates by moving polewards, it is important to consider that where settlement decisions are based primarily on ambient temperature, then no other behavioural changes are required to facilitate these range shifts. In this scenario, changes in the environment are actually being met with no actual change in the animal itself and instead, changes are occurring because the movements of animals. Consequently, further studies could usefully examine the consequences of such range expansions in other species inhabiting other habitats to assess the effects of such shifts more generally because without any changes in the animal itself, they are likely to eventually run out of options.

(2) Altered construction conditions in aquatic environments

Climate change-induced warmer water temperatures are directly associated with lower concentrations of dissolved oxygen, and eutrophication can further reduce oxygen availability in aquatic environments. Eutrophication occurs when water is unnaturally enriched by nutrients, such as nitrogen and phosphorus, which increases the growth of aquatic plants and subsequently depletes oxygen within water. Eutrophication has been directly linked to population declines in fish, amphibians and mammals, and the negative impacts are predicted to become more severe under changing environmental conditions (Peltzer *et al.*, 2008; Moss *et al.*, 2011). Many amphibians

already live under naturally hypoxic conditions, which can adversely affect the development and survival of their eggs and larvae (Peltzer *et al.*, 2008) and these effects may become more pronounced in a changing climate (Rome, Stevens & John-Alder, 1992). Empirical studies have examined how eutrophication-induced changes in habitat structure and water clarity influences the nest building behaviour of male three-spined sticklebacks in the Baltic Sea. When compared to conspecifics building nests under non-eutrophic conditions, male sticklebacks in turbid 'algal bloom' water took longer to build nests, and when completed, these nests were also smaller and had wider entrances (Wong, Tuomainen & Candolin, 2012). Since wide nest entrances facilitate the ventilation of nests but also increase the susceptibility of eggs to predation (Jones & Reynolds, 1999) and the risk of losing paternity to 'sneaker males' (Svensson & Kvarnemo, 2003), the design of nests built under eutrophic conditions may reflect the outcome of a trade-off by male builders.

Another study took advantage of spatial variability in the intensity of algal blooms by comparing nest building behaviour in three-spined stickleback populations exposed to different levels of eutrophication over three decades. When males from these different populations were allowed to construct nests under standardized conditions in the laboratory, those from more eutrophic areas built nests faster than males from less eutrophic areas, though the design and composition of their nests did not differ (Tuomainen & Candolin, 2013). Stickleback nests function as extended phenotypic signals of the male builder's quality and play a role in sexual selection (Barber *et al.*, 2001), meaning that despite variation in construction periods, males may be unwilling to alter the design of nests as it could impair their ability to attract females (Tuomainen & Candolin, 2013). In contrast, a more recent study has shown that male three-spined sticklebacks do adjust the compactness of their nests in response to changing dissolved oxygen levels by building more compact nests in high dissolved oxygen conditions. Further, females then exhibited strong environmentally-dependent mate choices, choosing more compact nests in high dissolved oxygen conditions and choosing looser nests when oxygen levels were lowered (Head, Fox & Barber, 2016). Although these studies report contrasting effects of eutrophication, they demonstrate the

potential for eutrophication to impact nest-building behaviours in fish. Further research could usefully examine how eutrophication affects nest construction in aquatic environments and, more generally, how pollutants alter nest construction in all ecosystems.

(3) Changes in the frequency and types of interactions with nest predators and parasites

Avoiding predation presents a continual challenge for most animals and climate change may affect the predator-prey interactions of nesting species through changes in the abundance of nest predators or egg/nestling prey, the predation process itself or through trophic cascades and regime shifts (Bretagnolle & Hanneke, 2010; Prop *et al.*, 2015). Climate change may generate altered patterns of predation on nests. In an experimental study of artificial birds' nests, levels of predation on baited nests in the southern Appalachian mountains (USA) increased with increasing ambient temperatures, with those placed on the ground experiencing the greatest predation rates by opossum (*Didelphis virginiana*) and other predators (Lumpkin, Pearson & Turner, 2012). An agent-based modeling study demonstrated that warmer ambient temperatures alter the nest predation behaviour of rat snakes (*Pantherophis* spp.) on birds, increasing the level and altering the diurnal pattern of nest predation, and shifting from targeting field- to forest-nesting species (DeGregorio *et al.*, 2015). Studies of long-term field data also suggest that higher ambient temperatures are linked to increased nest predation on North American passerines by both snake and bird (but not mammal) predators (Cox, Thompson & Reidy, 2013). In the Arctic, polar bears (*Ursus maritimus*) have traditionally hunted seals on the sea ice during winter, but with increasing ambient temperatures driving the earlier loss of sea ice, polar bears have responded by switching to alternative terrestrial prey. This has included a recent shift towards consuming an ever-increasing number of the eggs of ground- and cliff-nesting seabirds, such as common eiders (*Somateria mollissima*) and thick-billed murre (*Uria lomvia*) (Carthey & Banks, 2014; Iverson *et al.* 2014).

Climate changes is therefore capable of altering both the extent of nest predation and the

suite of predators involved, generating novel pressures on nest-building animals. As well as providing ideal conditions for developing offspring, nests also provide an ideal environment for parasites to reproduce so host species have evolved a wide range of defenses against nest parasites (Clayton & Moore, 1997; Banning *et al.*, 2008). However, whilst such defenses do limit parasites (Clayton & Moore, 1997), they may become less effective if host-parasite interactions become altered under climate change (Merino & Møller, 2010). Since climatic conditions influence the abundance of parasites in birds' nests in complex ways (Dawson, Hillen & Whitworth, 2005a; Martínez-de la Puente *et al.*, 2009), further research is required to examine how climate-induced increases and possibly decreases in the abundance and virulence of parasites (Merino & Møller, 2010) influence nest building behaviour in an attempt to mitigate any negative effects of parasites. Furthermore, because avian brood parasites frequently use nest characteristics to locate host nests (Moskát & Honza, 2000), climate change-induced alterations in the phenology of brood parasites and hosts (Douglas *et al.*, 2010), the prevalence and virulence of brood parasites (Møller *et al.*, 2011) and/or the defences hosts are able to mount against brood parasites (Berkowic *et al.*, 2015) may all impact nest building behaviour.

V. THE POTENTIAL FOR ADAPTIVE RESPONSES

The observed capacity of animals, but primarily birds and reptiles, to adjust their patterns of nest site selection and construction behaviour may give some optimism for their ability to respond appropriately to ongoing climate change (summarized in Fig. 1). The observed changes may result from phenotypic plasticity (Merilä & Hendry, 2014), whereby animals make changes to their behaviour and / or physiology during the course of their lifetime. Alternatively, changes may result from rapid evolutionary changes, via selection on choice of nest site or on construction behaviour (Carlson, Cunningham & Westley, 2014), potentially allowing species to respond within a few generations. In this respect, there is likely to be a differentiation between shorter-lived and longer-

lived organisms; whereas longer lived organisms tend to adapt to climate change via phenotypic plasticity (Merilä & Hendry, 2014), organisms with shorter generation times, and greater *per capita* reproductive output, may have greater potential to respond through evolutionary changes (Balanya *et al.*, 2006). Thus, ‘generation time’ may well influence the ways in which nest building species can adapt to ongoing climate change, and ultimately their capacity to persist under altered climate scenarios. However, the genetic basis of nest building behaviours is poorly understood at present. Whilst some studies provide evidence [for](#) nesting behaviour having a large genetic component (Lee, 1973; Kolbe & Janzen, 2002; Møller, 2006), others have not (Brommer, Rattiste & Wilson, 2008; McGaugh *et al.*, 2010) and so further research could usefully examine such issues in greater detail. Animals may be able to adapt to ongoing climate change via alterations in their nesting phenology, patterns of nest site selection and changes in nest design and we consider each of these aspects below.

Adaptation to climate change via changes in nesting phenology seem logical as some of the most well documented responses to climate change include advances in the timing of a range of events, such as tree bud bursts, flowering dates, [and](#) the migratory journeys and egg laying dates of birds (Stenseth *et al.*, 1999; Walther *et al.*, 2002). Such adaptive changes in the phenology of reproduction have usually resulted from phenotypic plasticity. In the context of nest building, adaptive changes in nesting phenology enable animals to time their reproduction to coincide with the period of maximal food availability, as has been demonstrated in insectivorous birds in temperate environments, such as blue tits (*Cyanistes caeruleus*), to coincide with favourable weather conditions for reproduction (Merilä & Hendry, 2014). Meanwhile, reptiles with TSD systems may be able to increase the proportion of male hatchlings, or even restore sex ratios to parity, by nesting earlier in the season when ambient temperatures are cooler, as demonstrated in loggerhead turtles (Hawkes *et al.*, 2007). However, other studies indicate that such shifts will be insufficient, and predict 100% female hatchlings regardless of any realistic advances in nesting date (Godley *et al.*, 2001; Telemeco, Abbott & Janzen, 2013) or changes in nest depth (Telemeco,

Elphick & Shine, 2009; Refsnider & Janzen, 2012) of turtles and lizards. For example, the latter studies suggest that an ambient temperature increase of 4°C over the twenty-first century, which is within realistic long term projections (IPCC, 2014), would require an advance in nest date by about 20 days and, whilst such shifts are plausible, thermal reaction norms in lizards encompass shifts of only 10 days (Telemeco, Abbott & Janzen, 2013). Thus, whilst shifts in nesting phenology undoubtedly facilitate adaptive responses to climate change, they seem unlikely to be sufficient to enable species with TSD to fully adapt, with serious implications for the viability of their populations. Whilst rapid evolutionary changes in nesting phenology may yet enable some turtles to adapt, the evidence for such evolutionary rescue is ambiguous (Carlson, Cunningham & Westley, 2014).

In addition to changes in nesting phenology, adaptive plasticity in the locations in which nests are built may provide other means for animals to adapt to climate change, and importantly, such changes can occur over rapid timescales that facilitate adaptation within the lifetimes of individuals. In tropical and sub-tropical environments, optimal temperatures for offspring development are usually lower than the highest ambient temperatures, meaning that nests should be located in cooler sites than sites selected at random (Hansell, 2005; Refsnider & Janzen, 2010). Empirical studies in warm regions support this idea, with mammals, birds and some large reptiles excavating underground burrows that almost completely eliminate their exposure to direct sunlight (Edelman, 2011; Pike & Mitchell, 2013). Ground-nesting birds inhabiting arid environments preferentially select nest sites close to vegetation so that they are in the shade from the midday sun, when daily temperatures are hottest, as demonstrated in grasshopper sparrows (*Ammodramus savannarum*) and eastern meadowlarks (*Sturnella magna*) (Long, Jensen & With, 2009). Both birds (Long, Jensen & With, 2009) and reptiles (Telemeco, Elphick & Shine, 2009; Telemeco, Abbott & Janzen, 2013) breeding in hot environments preferentially choose progressively cooler sites over time, meaning that further changes over both ecological and evolutionary timescales are possible (Refsnider & Janzen, 2010). However, there is likely to be a limit to the ability of vertebrates

breeding in hot environments to keep their nests cooler than ambient temperatures through [nest](#) placement alone and this presents an interesting avenue for further research.

Whilst changes in the location of nests may provide a way in which nesting animals can adapt to climate change, simultaneous adjustments of nest design may also contribute to such adaptation. The creation of a suitable microclimate for offspring is an important function of nests and increasing ambient temperatures are likely to benefit animals in temperate environments by reducing the requirement for nest insulation. By contrast, animals in tropical environments may adaptively alter their nest design to reduce temperatures experienced by offspring. This is particularly relevant to those species with TSD, where increasing temperatures have already biased hatchling sex ratios, although adaptive changes in the location and design of nests can shift hatchling sex ratios towards parity (Janzen, 1994; Mitchell & Janzen, 2010). An observational study of three-lined skinks (*Bassiana duperreyi*) showed that despite digging deeper nests in more shaded locations over time, these actions were not sufficient to keep the nest temperatures below the level at which equal numbers of males and females are produced (Telemeco, Elphick & Shine, 2009). This inability to respond has occurred because soil temperatures have increased with climate change and the shifts in nest design have been insufficient for the skinks to respond (Telemeco, Elphick & Shine, 2009). Only one experimental study has examined how nest depth may enable animals to reduce the temperature within nests. That study tested the hypothesis that, by digging deeper nests, painted turtles would create cooler microclimates for their eggs that would subsequently produce equal numbers of male and female hatchlings (Refsnider *et al.*, 2013). However, the creation of experimentally deepened nests had no effect on temperatures experienced within nests and thus had no effect on hatchling sex ratios or the subsequent size or survival of those hatchlings (Refsnider *et al.*, 2013). Thus, the limited evidence to date suggests that changes in nest design will not enable animals to fully adapt to a changing climate (Telemeco, Elphick & Shine, 2009; Mitchell & Janzen, 2010; Refsnider & Janzen, 2012; Refsnider *et al.*, 2013; Telemeco, Abbott & Janzen, 2013). There is, therefore, a need for more experimental studies that examine how changes in the design and

composition of nests may enable animals to respond and adapt to ongoing climate change.

In summary, animals can adapt to ongoing climate change via phenotypic plasticity (Merilä & Hendry, 2014) or through rapid evolutionary changes via selection on nest construction behaviour (Carlson, Cunningham & Westley, 2014). There is a need to develop a better understanding of the evolutionary constraints facing animals, and the relative roles of plasticity and rapid evolutionary changes in any measurable changes in behaviour. There is evidence from a range of taxa such as birds (Long, Jensen & With, 2009) and reptiles (Hawkes *et al.*, 2007; Telemeco, Elphick & Shine, 2009) that individuals are able to adaptively change aspects of nest-site selection and construction behaviour during their lifetimes and so can respond to ongoing climate change in the short-term via phenotypic plasticity. Meanwhile, animals could also respond to climate changes via rapid evolutionary changes in nest construction behaviour. However, whilst there is evidence that the nest construction behaviour of mammals (Lee, 1973) and reptiles (Kolbe & Janzen, 2002) and the design of the completed nests of birds (Møller, 2006) do have a large genetic component, other studies have only found a low level of inheritance (Brommer, Rattiste & Wilson, 2008; McGaugh *et al.*, 2010), suggesting that there are differences between species in levels of heritability. Thus, the ability of animals to adapt in the longer term to climate change via heritable changes in their nest building behaviour is unclear and offers a fruitful area for further research.

VI. CONCLUSIONS

(1) Anthropogenic climate change is affecting nest-building animals across a range of taxa (Table 1). The effects are disparate and include direct threats from sea level rise that flood nests, reductions in nest site availability and of some building materials, and suboptimal sex allocation in species with TSD. Indirect threats include range shifts into suboptimal nesting areas, altered nest construction conditions in aquatic environments, and changes in predator-prey and host-parasite interactions. Behavioural plasticity in nesting phenology, nest-site selection and nest design may

help to ameliorate the effects of climate change, but there is evidence to suggest that, in some cases, changes in nest design are insufficient to rapidly adapt to climate change.

(2) Climate change is influencing the nesting behaviour of animals, and further research is needed to fully understand how they may be affected by additional changes in environmental conditions. So far, the majority of research has focused upon birds and reptiles (especially those with TSD), with less focus on mammals, fishes and amphibians. Consequently, there is a need to balance research efforts across taxa to better understand broad patterns of climate change impacts. Second, the majority of empirical studies to date have been observational and further experimentation is required; studies that manipulate environmental conditions or the availability of nest-building materials would be particularly informative. More specifically, further studies that search for evidence of nest-building being the specific point of failure of species responding to climate change are needed because they are currently in limited supply (but see e.g. Palis *et al.*, 2006; McMenamin, Hadly & Wright, 2008), at least partly because of the difficulties associated with performing manipulative experiments on nest building behaviour. Thus, experiments that examine links between climate change, nest-building, and reduced species or population success would be extremely valuable. Third, studies that examine the relative contributions of phenotypic plasticity and rapid evolution in allowing individuals to change their nest characteristics are urgently needed. Finally, theoretical modeling could usefully inform empiricists how further changes in environmental conditions may affect the ability of animals to construct their nests and help to identify the limits of potential adaptive responses.

VII. ACKNOWLEDGEMENTS

We thank Jim Reynolds for useful discussions and anonymous reviewers for their insightful comments.

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For Review Only

Fig. 1. The potential for adaptive short- and long-term responses to climate change in birds and reptiles via nest building behaviour. Note that other taxa are not included because there are an insufficient number of studies available from which to make sound conclusions.

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Fig. 1.

Table 1. Summary of the main impacts of climate change on the nesting behaviour of vertebrates, split by taxonomic group, and some illustrative examples.

Taxonomic group	Direct effects and examples	Indirect effects and examples
Reptiles	<p>Turtle nest flooding from sea level rises and tropical storms (Fuentes, Hamann & Limpus, 2010a; Pike, Roznik & Bell, 2015)</p> <p>Skewed sex ratios in species with temperature dependent sex determination (Hawkes <i>et al.</i>, 2007; Laloë <i>et al.</i>, 2014)</p>	<p>Range shifts into suboptimal nesting areas such as those that more populated by humans (Pike, 2013a, 2013b)</p>
Birds	<p>Seabird nest flooding from sea level rises and tropical storms (van de Pol <i>et al.</i>, 2010)</p> <p>Decreasing snow cover results in increased increased elk grazing and fewer vegetative nest sites (Martin & Maron, 2012)</p> <p>Skewed sex ratios in megapodes with temperature dependent sex determination (Göth & Booth, 2005)</p>	<p>Higher nest predation rates on geese by polar bears that are unable to hunt seals on shrinking sea ice (Iverson <i>et al.</i>, 2014)</p> <p>Changes in ectoparasite abundance induce changes in nesting behaviours to counteract them (Dawson, Hillen & Whitworth, 2005a)</p> <p>Changes in the abundance of avian brood parasites induce changes in nesting to counteract them (Møller <i>et al.</i>, 2011)</p>
Fish	<p>Polluted sea water reduces competition for nest sites in three-spined sticklebacks (Candolin, 2004)</p>	<p>Eutrophication reduced water clarity lowers ability to build sexually selected elaborate nests (Tuomainen & Candolin, 2013)</p>
Amphibians	<p>Droughts reduce the availability of ephemeral waterbodies as nesting sites (Walls, Barichivich & Brown, 2013)</p> <p>Skewed sex ratios in species with temperature dependent sex determination (e.g. Eggert, 2004)</p>	