

Superficial lizards in cold climates: Nest site choice along an elevational gradient

J. SEAN DOODY[†]

Institute for Applied Ecology, University of Canberra, Canberra, Australian Capital Territory, Australia
(Email: sean.doody@anu.edu.au)

Abstract Embryonic conditions may limit the distributions of egg-laying ectotherms, and recent research suggests that nesting mothers of wide-ranging species may use a number of factors to compensate for differing climates. However, while variation in temporal factors across environmental gradients are common or pervasive (i.e. seasonal timing of nesting), similar evidence for spatial factors is rare (e.g. aspect, openness and depth of nest sites). I tested the idea that a wide-ranging lizard, the Australia water dragon (*Physignathus lesueurii*), uses nest depth to counter climate differences along a temperature cline at their cold-end range margin. Two measures of nest depth were significantly, inversely related to elevation across six populations spanning 700 m. Elevation explained 83–86% of the variation in nest depth. These findings support a thermal compensatory mechanism for this pattern, although soil moisture compensation is plausible. My results directly support a recent, untested prediction that the evolution of viviparity in reptiles is preceded by a behavioural shift towards increasingly superficial nest sites in cold climates, followed by selection for increased egg retention to avoid temperature extremes. However, in the present study egg desiccation rates increased with increasing elevation in a dry year, suggesting that increased egg retention may evolve in response to lethal hydric conditions, rather than lethal temperatures. When considered alongside recent research, the present study indicates that water dragons possess several mechanisms for adjusting to climate change.

Key words: climate change, embryonic survival, *Physignathus lesueurii*, range margin, viviparity, water dragon.

INTRODUCTION

Recent, global warming has accelerated research into how organisms might respond to differing climates (Hughes 2000; McCarty 2002; Walther *et al.* 2002; Parmesan & Yohe 2003; Parmeson 2005; Root & Hughes 2005). Although long-term data sets examining trait variation during the warming trend are the most desirable means of gauging climate responses (Strayer *et al.* 1986; Likens 1989), lengthy generation times, logistics and funding cycles favour shorter, more indirect approaches. One useful approach involves identifying responses to environmental gradients across temperature clines in wide-ranging species (Fielding *et al.* 1999; Doody *et al.* 2006). By elucidating patterns in wide space, we can infer processes in deep time (Brown 1995), and predict a species' repertoire for responding to climate change (Fleishman *et al.* 2000; Andrew & Hughes 2004; Doody *et al.* 2006). For example, if a trait exhibits little or no clinal variation, it may not respond to selection induced by climate change.

Elucidating trait variation across temperature gradients should be particularly relevant for oviparous ectotherms, in which environmental temperatures underpin most physiological and developmental processes of not only free-ranging animals but also their immobile embryos (Pough 1980; Shine 2005). Climatic conditions may impose a geographical boundary to successful reproduction (MacArthur 1972; Gaston 2003), and in some cases these boundaries may be determined by the thermal tolerances of egg-bound embryos (Mell 1929; Muth 1980; Shine 1987; Kearney & Porter 2004). Embryonic temperatures influence fitness by affecting embryonic survival and offspring phenotypes, including sex in animals with temperature-dependent sex determination (TSD) (Deeming & Ferguson 1988, 1991; Booth & Thompson 1991). Thus, trait variation along environmental gradients that influences embryonic temperatures is of interest for determining potential climate change responses.

Oviparous mothers that need to provide their broods with similar developmental conditions across a range of climates must compensate for those climates via one of two classes of maternal traits that influence embryonic temperatures (Doody *et al.* 2006). The first includes behaviours underpinning spatial features of

[†]Present address: Department of Botany and Zoology, Australian National University, ACT 0200, Australia

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nests or nest sites (e.g. openness, aspect, depth), while the second includes temporal traits (e.g. seasonal timing of nesting, developmental rate). In the special case of temperature compensation to produce viable offspring sex ratios in TSD animals, the pivotal temperature, or the embryonic temperature that divides the offspring sexes, can also be adjusted across climates (Bull *et al.* 1982; Ewert *et al.* 2005; but see Doody *et al.* 2006).

Gradients in timing of reproduction (nesting) across climates are common or even pervasive, occurring in a broad range of animals (Baker 1938; see Iverson *et al.* 1997 for an example in reptiles). In contrast, evidence for gradients in spatial characteristics of nest sites is rare (but see Andrews 2000; Ewert *et al.* 2005). Doody *et al.* (2006) predicted that lizards may excavate shallower nests at higher elevations to compensate for colder temperatures, after finding shallower nests in a higher-elevation species of lizard, compared with a congeneric, lower-elevation species. Moreover, Andrews suggested that this behavioural shift was a precursor to the evolution of viviparity in cold climates: the choice of increasingly superficial nest sites at higher elevations would eventually expose eggs to lethal temperatures, favouring increased egg retention and ultimately the evolution of viviparity. The lack of tests of this hypothesis is presumably due to the difficulty in finding sufficient numbers of squamate reptile nests (Tinkle 1967; Shine 1988; Perry & Dmi'el 1994).

I tested Andrews' central prediction by addressing the idea that water dragons (*Physignathus lesueurii*) use nest depth to counter climate differences along a temperature cline at the cold-end range margin. Although nest depth did not conform to a coarser (latitudinal) gradient in this wide-ranging species (Doody *et al.* 2006), the shallowest nests were found at the coldest site, indicating a possible gradient in nest depth at a finer (elevational) scale. Moreover, recent research demonstrated that the range margin population is thermally challenged: dragons restricted nesting to the most open areas on the warmer side of the gorge, and offspring sex ratios exhibited extreme female bias because of low nest temperatures (Doody *et al.* unpub. data 2009). Specifically, I sampled water dragon nests in six populations along an elevational gradient of 700 m at the cold climate range margin to test the hypothesis that nest depth was inversely related to elevation. I quantified embryonic survival in three of the populations spanning the gradient, allowing me to address the possible mechanism for Andrews' viviparity model. I present these findings within the context of other environmental gradients in the egg stage of this TSD lizard, and briefly discuss implications for climate warming responses, and for the evolution of viviparity in reptiles.

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METHODS

Study species

The water dragon is a large agamid lizard restricted to coastal eastern Australia, where it ranges from Cooktown, Queensland (15°10'24"S, 144°43'38"E) south to near Melbourne, Victoria (37°48'51"S, 144°57'47"E) (Cogger 2000). It generally inhabits rivers and streams from sea level to ~1250 m in elevation (Thompson 1993; Doody *et al.* 2006). Nesting occurs in spring and summer in open areas adjacent to water (Harlow 2001; Doody *et al.* 2006). Nests are excavated and back-filled as in other members of the Agamidae (Greer 1989). The species exhibits TSD, with females produced at lower and higher temperatures, and males produced in a narrow range of intermediate temperatures (Harlow 2004; Doody *et al.* 2006).

Study design and sites

I searched for nests during November to January for two seasons (2006/2007–2007/2008) in the Australian Capital Territory (ACT) and New South Wales (NSW).

Six populations were sampled for nest depth in 19 visits in 2007/2008. These populations were chosen based on elevation and the ability to find sufficient numbers of nests for quantitative analysis. Populations included two sites at (relatively) low elevations (Tuggeranong Creek, ACT, 550 m; Australian National Botanical Gardens, ACT, 600 m), three populations at intermediate elevations (Yarrangobilly River, NSW, 900 m; Gibraltar Falls, ACT, 910 m; Gudgenby River, ACT, 950 m) and one high-elevation population (Blue Water Holes, NSW, 1250 m). There is a predictable gradient in air temperatures along this elevational cline (Fig. 1). Blue Water Holes represents the only known site where nests have been found at elevations >1000 m, and the highest and coldest known site with a substantial population (Doody *et al.* 2006; W. Osborne, pers. comm. 2008; D. Hunter, pers. comm. 2008). The populations are within ~50 km of one another, but are in three different river drainages. Hence our design and results did not reflect pseudoreplication. Embryonic survival data were quantified the previous year in 2006/2007 in 12 visits to three of the sites along the gradient (Australian National Botanic Gardens, Gudgenby River and Blue Water Holes).

Methods and analysis

Nests were found by noting signs of nesting activity and with the aid of a probe designed to locate subter-

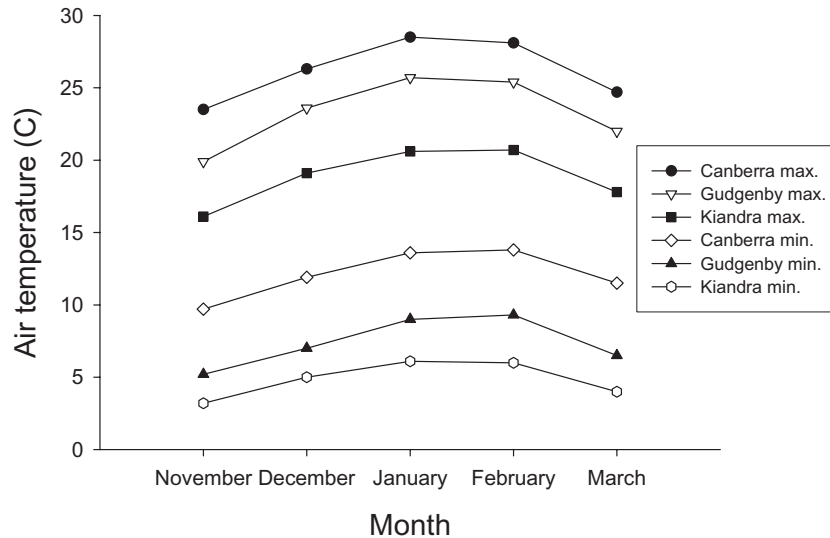


Fig. 1. Mean monthly maximum and minimum air temperatures from three of the study sites spanning the elevations of the six study populations. Canberra = 578 m; Gudgenby = 942 m; Kiandra = 1395 m. Kiandra is the closest station (35 km) to Blue Water Holes.

ranean nest chambers. For each nest, I measured the depth from the surface to the top of the uppermost egg with a ruler, carefully removed the eggs and counted them, and then measured the depth to the bottom of the chamber. The eggs were then carefully replaced at roughly their original depths.

To test for a relationship between depth and elevation both measures of nest depth were regressed against elevation separately (simple linear regression). Clutch size was also regressed against elevation for the following reason. Because clutch size is often related to body size in lizards (Fitch 1970), and nest depth may related to body size (Carr 1952; Iverson *et al.* 1997), any relationship between nest depth and elevation could be confounded by body size. For example, clutch size was positively related to nest depth in a turtle (Nagle *et al.* 2004).

To address the mortality mechanism for Andrews' (2000) model, I quantified embryonic survival. Embryonic survival was quantified at the level of nest, and at the egg level, yielding two estimates. Survival at the nest level was the proportion of successful nests over the total number of nests, and any nest producing at least one successful hatchling was considered successful. Survival at the egg level was the proportion of successful eggs over the total number of eggs, for all nests combined. The majority of unsuccessful eggs were considered to have died from desiccation, as evidenced by shrivelled eggs surrounded by visibly dry soil. However, this may overestimate desiccation rates somewhat because eggs dying of other causes (lethal temperatures, or intrinsic factors) may also become shrivelled post-mortem.

RESULTS

A gradient in air temperatures spanning the elevations of the six study populations was evident (Fig. 1). In 2007/2008 I measured depth in 104 nests in the six populations; numbers ranged from 10 to 37 nests per population (Table 1). Heavy rainfall during the nesting period limited the success in finding nests at some sites in that year. In 2006/2007, I quantified embryonic success for 77 nests; numbers of nests ranged from 15 to 36 per population (Table 2).

Depth to the top egg differed significantly among sites ($F_{5,103} = 17.51$, $P < 0.0001$), and was significantly inversely related to elevation (Fig. 2; $r^2 = 0.862$, $F_{1,5} = 24.99$, $P = 0.007$). Chamber depth also differed significantly among sites ($F_{5,103} = 16.08$, $P < 0.0001$), and was also inversely related to elevation (Fig. 2; $r^2 = 0.828$, $F_{1,5} = 19.24$, $P = 0.012$). Nest depths at the highest elevation site were 26–32% shallower than those at the lowest elevations and 13–21% shallower than depths at intermediate elevations.

Although the lack of replication precluded robust statistical analysis, embryonic success at the level of nest was similar between the low and intermediate elevation sites, but was much lower at the high elevation site (Table 2). Hatchling-level embryonic success was also particularly low at the high elevation site, but was also progressively lower with elevation (Table 2). The majority (>95%) of failed eggs were shrivelled in appearance and surrounded by extremely dry soil conditions, suggesting desiccation. Moreover, in nests with partial success failed eggs were generally at the top of the nest where conditions were drier. In this year, extreme drought conditions prevailed both prior

Table 1. Summary statistics for nest depth and clutch size in the six populations along an elevational cline

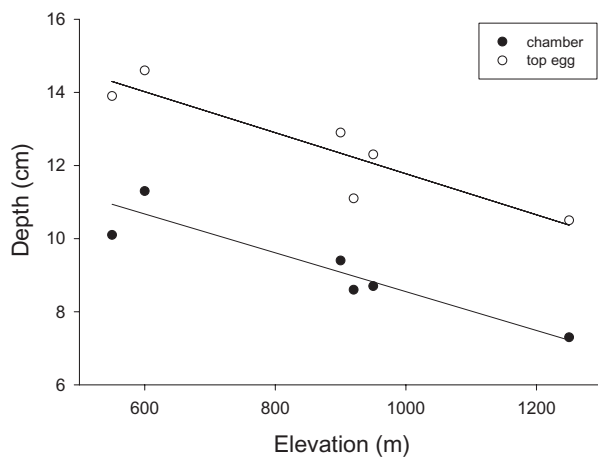
| Population/site | Elevation (m) | Number of nests | Depth to top egg (cm) | Chamber depth (cm) | Clutch size |
|---------------------|---------------|-----------------|-----------------------|--------------------|-------------|
| Tuggeranong Creek | 550 | 10 | 10.1 ± 1.47 | 13.9 ± 1.23 | 7.4 ± 2.99 |
| ANBG | 600 | 37 | 11.3 ± 1.64 | 14.6 ± 1.89 | 7.8 ± 2.95 |
| Yarrangobilly River | 900 | 10 | 9.4 ± 1.59 | 12.9 ± 1.26 | 9.7 ± 3.74 |
| Gibraltar Falls | 910 | 10 | 8.6 ± 1.47 | 11.1 ± 1.48 | 5.3 ± 2.79 |
| Gudgenby River | 950 | 22 | 8.7 ± 1.79 | 12.3 ± 2.17 | 7.5 ± 2.24 |
| Blue Water Holes | 1250 | 15 | 7.3 ± 1.12 | 10.5 ± 1.15 | 8.7 ± 2.52 |

Data are means ± 1 SD. ANBG, Australian National Botanic Gardens.

Table 2. Embryonic survival in *Physignathus lesueurii* at three sites along an elevational cline

| Population/site | Elevation (m) | Nest-level embryonic survival (# of nests) | Egg-level embryonic survival (# of eggs) |
|------------------|---------------|--|--|
| ANBG | 600 | 0.94 (36) | 0.89 (272) |
| Gudgenby River | 950 | 0.96 (26) | 0.77 (202) |
| Blue Water Holes | 1250 | 0.27 (15) | 0.32 (160) |

ANBG, Australian National Botanic Gardens. Nest-level embryonic survival is the proportion of nests producing at least one successful hatchling; egg-level embryonic survival is the proportion of successful eggs for all nests combined.

**Fig. 2.** Relationships between elevation and two measures of depth in *Physignathus lesueurii* nests.

to and during the time eggs were in the ground. For example, during the period of August 2006 through January 2007 Canberra received 102 mm of rain compared with the long-term average of 341 mm, and the same station recorded only 4 mm of rain for October 2006 (Australian Bureau of Meteorology 2006/2007). An important caveat for these data is that the nesting area at Australian National Botanic Gardens (ANBG) is artificially irrigated, possibly reducing the probability of desiccation for most nests at the site.

Clutch size differed significantly among sites ($F_{5,103} = 2.87$, $P = 0.018$). However, clutch size was not related to elevation ($r^2 = 0.04$, $F_{1,5} = 0.163$, $P = 0.707$), or to either measure of nest depth (top egg: $r^2 = 0.00$, $F_{1,5} = 0.00$, $P = 0.996$; chamber depth: $r^2 = 0.03$, $F_{1,5} = 0.118$, $P = 0.748$).

DISCUSSION

The predictable reduction in nest depth with elevation in water dragons near the cold-end range margin suggests that wide-ranging oviparous animals that excavate subterranean nests may be able to compensate for differing climates by 'adjusting' nest depth. Specifically, higher-elevation mothers apparently countered cooler temperatures by nesting more superficially (Fig. 1; Fig. 2; but see below). The mean daily range in nest temperatures in water dragons at the highest elevation is significantly inversely proportionate to nest depth (Doody *et al.* unpub. data 2009), and shallower reptile nests often experience both higher mean temperatures and greater daily variation in temperatures than deeper nests (Ewert 1979; Packard & Packard 1988). Collectively, these contribute to warmer conditions in shallower nests (Georges *et al.* 1994; Valenzuela 2001). The supposition that water dragons used nest depth to compensate for cool developmental temperatures is supported by evidence that the species is temperature-limited at the range margin (Blue Water Holes). At this site, dragons restrict nesting to the warmer, north-facing side of the gorge (Doody *et al.* unpub. data 2009). The resulting cohorts are heavily female-biased (95% in typical climate years), and experiments with data loggers in artificial nests indicated that nesting on the cool side would lead to the production of an exclusively female cohort at best, and complete embryonic failure at worst. Dragons at the cold range margin also nest in the most open areas against bedrock, presumably to achieve higher embryonic temperatures. At a more continental scale, the species compensates for climate differences in nest temperatures across its range chiefly through canopy

openness, although some compensation is achieved via timing of nesting (Doody *et al.* 2006).

Although the chief finding of the present study supports a thermal compensatory mechanism for the variation in depths, the gradient in nest depth could also be explained by soil moisture, the other major environmental condition important to developing reptile eggs (Packard & Packard 1988; Deeming 2004). Although soil moisture data are not available for the sites, a clinal pattern in rainfall exists across the study populations. For example, mean monthly rainfall amounts for November to February are 58.0, 65.5 and 94.8 mm for ANBG (600 m), Gudgenby (950 m) and Kiandra (1395 m), respectively (Kiandra is 35 km from, and 145 m above, Blue Water Holes). Lizards may dig the deepest nests at ANBG/Canberra because this is the driest site, and deeper nests are more moist (e.g. Brown & Shine 2006). This idea receives some support from the finding that nest depth is deepest in Canberra across a more coarse (latitudinal) cline that includes Sydney and Brisbane (Doody *et al.* 2006), two warmer sites which receive more summer rainfall than Canberra (Australian Bureau of Meteorology). Data on soil moisture are needed to clarify the potential for hydric compensation to explain the observed variation in nest depth. In the present study, however, embryonic survival was lowest at the highest elevation because of desiccation in a very dry year (Table 2), suggesting that soil moisture did not increase with elevation. The high desiccation rate of embryos at the coldest site may be a result of lizards nesting only on the warm (north-facing) side of the gorge, where soils are conspicuously drier than the cold side (Doody *et al.* unpub. data 2009).

The cold climate hypothesis for the evolution of viviparity in reptiles posits that egg retention can compensate for the effects of decreasing temperature on the rate of embryonic development with increasing elevation or latitude (Tinkle & Gibbons 1977; Shine 1985; Andrews 2000). Andrews (2000) suggested a variant of the model in which lizards nest more superficially at higher elevations to achieve warmer egg temperatures: eventually, at some critical elevation, the effectiveness of this behavioural compensation would be offset by increasing embryonic mortality because of temperature extremes (see also Shine *et al.* 2003). At this stage, an increase in the length of egg retention would be adaptive because it would reduce the time the eggs were at risk. A central, untested assumption of this hypothesis is the existence of elevational gradients in nest depth in cold-climate, oviparous lizards that excavate nests. Prior to the present study evidence for this relationship was anecdotal: *Sceloporus virgatus* nested ~6 cm deep at 1800 m elevation, while the related *S. aeneus* nested ~2 cm deep at 2800 m (Andrews 2000). The environmental gradient in nest depth for *P. lesueurii* in the present study supports the

key prediction of the Andrews model (Fig. 2). As far as I know, this intraspecific pattern has not been reported in other reptiles or oviparous ectotherms.

The suggested adaptive mechanism for why viviparity evolves in this model is protection from temperature extremes offered by egg retention (Andrews 2000; Shine *et al.* 2003; Shine 2004). However, in the present study egg desiccation rates increased with increasing elevation in a dry year (Table 2), suggesting that a decrease in soil moisture with shallower depths at higher elevations may be the key mechanism selecting for increased egg retention, rather than extreme temperatures. While early works implicated the hydric environment in the evolution of viviparity (Weekes 1935; Neill 1964; Shine & Berry 1978), this was dismissed in later studies (e.g. Andrews 2000), and hydric conditions were said to have a permissive or partial role in still others (Packard 1966; Guillette *et al.* 1980; Shine & Thompson 2006). More specifically, however, researchers have suggested that hydric conditions are unlikely to select for increased egg retention and viviparity because (i) hydric conditions are less likely to vary clinally than temperatures (Shine & Thompson 2006), and because (ii) short periods of retention (an evolutionary intermediate) would not enhance the survival of eggs, assuming that extreme dry conditions are typical of the entire incubation period (Andrews 2000). Theoretically, however, small increments in egg retention could translate into increased embryonic survival by protecting embryos during drier early periods of external development, especially if those periods are somewhat predictable. Further research along elevational clines is needed to determine the relative roles of temperature, moisture and gas exchange on embryonic survival at different depths, and thus, their potential contribution to the evolution of viviparity in reptiles.

By what means did water dragons adjust nest depth? Elevational differences in nest depth may reflect genetic-based, among-generation changes, or simply behavioural compensation. My data cannot distinguish between these possibilities, for which experimental data are needed. There has been a surprising lack of manipulative studies investigating nest site choice in ectothermic animals, and this has left important questions unanswered. For example, we do not know which proximate mechanisms reptile mothers use to select appropriate nest site conditions. Some authorities contend that reptiles use direct cues, such as substrate temperature, while others favour indirect cues, such as aspect and canopy openness (Stoneburner & Richardson 1981; Schwartzkopf & Brooks 1987; Janzen 1994; Morjan & Valenzuela 2001). Unfortunately, no study has attempted to disentangle these auto-correlated factors. An understanding of the proximate cue(s) used by nesting mothers would be essential for understanding the evolution of nest site choice across

environmental gradients, and its potential role in climate change responses.

The present data and recent related research (Doody *et al.* 2006; Doody *et al.* unpub. data 2009) collectively indicate that water dragons possess several mechanisms for adjusting to climate change, although we know little about the species' ability to evolve relative to the *rate* of climate change (adequate variability and heritability of traits in question). Snapping turtles also nested in more open areas in cooler climates, and exhibited predictable, clinal variation in pivotal temperatures, or the temperatures dividing offspring sexes (Ewert *et al.* 2005). In contrast, pivotal temperatures did not differ across climate extremes in water dragons, suggesting that the trait may be conserved and that dragons may be unable to compensate for climate warming to produce viable sex ratios by shifting their pivotal temperatures (Doody *et al.* 2006). Although direct tests of these predictions may be hindered by long generation times, clinal variation in some of these traits suggests that the potential for adjustment does exist.

Successful reproduction may be the key factor limiting the distributions of some oviparous animals, and the embryos of water dragons and many other wide-ranging species have successfully met with the challenge of differing environments. We would predict that these species would be more likely to persist in the face of imminent climate warming, not only because of their large range size, but because of variation in nest site choice behaviour (Doody *et al.* 2006). However, research is needed to test the competing hypotheses that the egg *vs.* the adult stage sets the boundaries of geographical distributions in water dragons and in other oviparous, ectothermic animals.

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REFERENCES

- Andrew N. R. & Hughes L. (2004) Species diversity and structure of phytophagous beetles along a latitudinal gradient: predicting the potential impacts of climate change. *Ecol. Entomol.* **29**, 527–42.
- Andrews R. M. (2000) Evolution of viviparity in squamate reptiles (*Sceloporus* spp.): a variant of the cold climate model. *J. Zool. (London)* **250**, 243–53.
- Australian Bureau of Meteorology (2006/2007). Monthly Climate Summaries [Cited 1 April 2008.] Available from URL: <http://www.bom.gov.au/climate/current/month/act/archive/index.shtml>
- Baker J. R. (1938) The relation between latitude and breeding season in birds. *Proc. Zool. Soc. Lond.* **108A**, 557–82.
- Booth D. T. & Thompson M. B. (1991) A comparison of reptilian eggs with those of megapode birds. In: *Egg Incubation, Its Effect on Embryonic Development in Birds and Reptiles* (eds D. C. Deeming & M. W. J. Ferguson) pp. 325–44. Cambridge University Press, Cambridge.
- Brown J. H. (1995) *Macroecology*. University of Chicago Press, Chicago.
- Brown G. & Shine, R. (2006) Effects of nest temperature and moisture on phenotypic traits of hatchling snakes (*Tropidonophis mairii*, Colubridae) from tropical Australia. *Biol. J. Linn. Soc.* **89**, 159–68.
- Bull J. J., Vogt R. C. & McCoy C. J. (1982) Sex-determining temperatures in turtles: a geographic comparison. *Evolution* **36**, 326–32.
- Carr A. (1952) *Handbook of Turtles*. Comstock Publ. Assoc., Ithaca, New York.
- Cogger H. (2000) *Reptiles and Amphibians of Australia*. Reed New Holland, Sydney.
- Deeming D. C. (2004) *Reptilian Incubation: Environment, Evolution, and Behaviour*. Nottingham University Press, Nottingham.
- Deeming D. C. & Ferguson M. W. J. (1988) Environmental regulation of sex determination in reptiles. *Phil. Trans. Roy. Soc. Lond.* **322B**, 19–39.
- Deeming D. C. & Ferguson M. W. J. (1991) Physiological effects of incubation temperature on embryonic development in reptiles and birds. In: *Egg Incubation, Its Effect on Embryonic Development in Birds and Reptiles* (eds D. C. Deeming & M. W. J. Ferguson) pp. 147–71. Cambridge University Press, Cambridge.
- Doody J. S., Guarino E., Georges A., Corey B., Murray G. & Ewert M. (2006) Nest site choice compensates for climate effects on sex ratios in a lizard with environmental sex determination. *Evol. Ecol.* **20**, 307–20.
- Ewert M. A. (1979) The embryo and its egg: development and natural history. In: *Turtles: Perspectives and Research* (eds M. Harless & H. Morlock) pp. 333–413. John Wiley and Sons, New York.
- Ewert M. A., Lang J. W. & Nelson C. (2005) Geographic variation in the pattern of temperature-dependent sex determination in the American snapping turtle (*Chelydra serpentina*). *J. Zool. (Lond.)* **265**, 81–95.
- Fielding C. A., Whittaker J. B., Butterfield J. E. L. & Coulson J. C. (1999) Predicting responses to climate change: the effect of altitude and latitude on the phenology of the Spittlebug *Neophilaenus lineatus*. *Funct. Ecol.* **13**, 65–73.
- Fitch H. S. (1970) Reproductive cycles in lizards and snakes. *Univ. Kansas Mus. Nat. Hist. Misc. Publ.* **52**, 1–247.
- Fleishman E., Fay J. P. & Murphy D. D. (2000) Upsides and downsides: contrasting topographic gradients in species richness and associated scenarios for climate change. *J. Biogeog.* **27**, 1209–19.
- Gaston K. J. (2003) *The Structure and Dynamics of Geographic Ranges*. Oxford University Press, Oxford.
- Georges A., Limpus C. J. & Stoutjesdijk R. (1994) Hatchling sex in the marine turtle *Caretta caretta* is determined by proportion of development at a temperature, not daily duration of exposure. *J. Exp. Zool.* **270**, 432–44.
- Greer A. (1989) *The Biology and Evolution of Australian Lizards*. Surrey Beatty, Sydney.
- Guillette L. J. Jr., Jones R. E., Fitzgerald K. T. & Smith H. M. (1980) Evolution of viviparity in the lizard genus *Sceloporus*. *Herpetologica* **38**, 94–103.

- Harlow P. S. (2001) The ecology of sex-determining mechanisms in Australian agamid lizards. PhD thesis, Macquarie University, Sydney.
- Harlow P. S. (2004) Temperature-dependent sex determination in lizards. In: *Temperature-Dependent Sex Determination in Vertebrates* (eds N. Valenzuela & V. A. Lance) pp. 42–52. Smithsonian Institution Press, Washington, DC.
- Hughes L. (2000) Biological consequences of global warming: is the signal already apparent? *Trends Ecol. Evol.* **15**, 56–61.
- Iverson J. B., Higgins H., Sirurulnik A. & Griffiths C. (1997) Local and geographic variation in the reproductive biology of the snapping turtle (*Chelydra serpentina*). *Herpetologica* **53**, 96–117.
- Janzen F. J. (1994) Vegetational cover predicts the sex ratio of hatchling turtles in natural nests. *Ecology* **75**, 1593–9.
- Kearney M. & Porter W. P. (2004) Mapping the fundamental niche: physiology, climate, and the distribution of a nocturnal lizard. *Ecology* **85**, 3119–31.
- Likens G. E. (1989) *Long-Term Studies in Ecology: Approaches and Alternatives*. Springer-Verlag, New York.
- MacArthur R. H. (1972) *Geographical Ecology: Patterns in the Distributions of Species*. Princeton University Press, Princeton.
- McCarty J. P. (2002) Ecological consequences of recent climate change. *Conserv. Biol.* **15**, 320–31.
- Mell R. (1929) *Beitrage zur Fauna Sinica. IV. Grundzuge einer okologie der chinesischen retilien und einer herpetologischen tiergeographie Chinas*. Walter de Gruyter, Berlin.
- Morjan C. L. & Valenzuela N. (2001) Is ground-nuzzling by female turtles associated with surface temperatures? *J. Herpetol.* **35**, 668–72.
- Muth A. (1980) Physiological ecology of desert iguana (*Dipsosaurus dorsalis*) eggs: temperature and water relations. *Ecology* **61**, 1335–43.
- Nagle R. D., Lutz C. L. & Pyle A. L. (2004) Overwintering in the nest by hatchling map turtles (*Graptemys geographica*). *Can. J. Zool.* **82**, 1211–8.
- Neill W. T. (1964) Viviparity in snakes: some ecological and zoogeographical considerations. *Am. Nat.* **98**, 35–55.
- Packard G. C. (1966) The influence of ambient temperature and aridity on modes of reproduction and excretion of amniote vertebrates. *Am. Nat.* **100**, 677–82.
- Packard G. C. & Packard M. J. (1988) The physiological ecology of reptilian eggs and embryos. In: *Biology of the Reptilia. Vol. 16. Ecology B. Defense and Life History* (eds C. Gans & R. B. Huey) pp. 523–605. Alan R. Liss, New York.
- Parmesan C. & Yohe G. (2003) A globally coherent fingerprint of climate warming impacts across natural systems. *Nature* **421**, 37–42.
- Parmeson C. (2005) Biotic response: range and abundance changes. In: *Climate Change and Biodiversity* (eds T. E. Lovejoy & L. Hannah) pp. 41–60. Yale University Press, London.
- Perry G. & Dmi'el R. (1994) Needles and haystacks: searching for lizard eggs in a coastal sand dune. *Amphib-Reptil.* **15**, 395–401.
- Pough F. H. (1980) The advantages of ectothermy for tetrapods. *Am. Nat.* **115**, 92–112.
- Root T. L. & Hughes L. (2005) Present and future chronological changes in wild plants and animals. In: *Climate Change and Biodiversity* (eds T. E. Lovejoy & L. Hannah) pp. 61–9. Yale University Press, London.
- Schwartzkopf L. & Brooks R. J. (1987) Nest-site selection and offspring sex ratio in painted turtles, *Chrysemys picta*. *Copeia* **1987**, 53–61.
- Shine R. (1985) The evolution of viviparity in reptiles: an ecological analysis. In: *Biology of the Reptilia. Vol. 15.* (eds C. Gans & F. Billett) pp. 605–94. John Wiley and Sons, New York.
- Shine R. (1987) Reproductive mode may determine geographic distributions in Australian venomous snakes (*Pseudechis*, Elapidae). *Oecologia* **71**, 608–12.
- Shine R. (1988) Parental care in reptiles. In: *Biology of the Reptilia, Vol. 16.* (eds C. Gans & R. B. Huey) pp. 275–325. Alan R. Liss Inc., New York.
- Shine R. (2004) Does viviparity evolve in cold climate reptiles because pregnant females maintain stable (not high) body temperatures? *Evolution* **58**, 1809–18.
- Shine R. (2005) Life-history evolution in reptiles. *Ann. Rev. Ecol. Evol. Syst.* **36**, 23–46.
- Shine R. & Berry J. F. (1978) Climatic correlates of live-bearing in squamate reptiles. *Oecologia* **33**, 261–8.
- Shine R. & Thompson M. B. (2006) Did embryonic responses to incubation conditions drive the evolution of reproductive modes in squamate reptiles? *Herpetol. Monogr.* **20**, 159–71.
- Shine R., Elphick M. & Barrott E. G. (2003) Sunny side up: lethally high, not low, nest temperatures may prevent oviparous reptiles from reproducing at high elevations. *Biol. J. Linn. Soc.* **78**, 325–34.
- Stoneburner D. L. & Richardson J. I. (1981) Observations on the role of temperature on loggerhead turtle nest site selection. *Copeia* **1981**, 238–41.
- Strayer D., Gutzenstein J. S., Jones C. G. *et al.* (1986) Long-term ecological studies: an illustrated account of their design, operation, and importance to ecology. *Occas. Publ. Inst. Ecosystem Stud.* **2**, 1–38.
- Thompson M. B. (1993) Estimate of the population structure of the eastern water dragon, *Physignathus lesueurii* (Reptilia: Agamidae), along riverside habitat. *Wildl. Res.* **20**, 613–9.
- Tinkle D. W. (1967) The life and demography of the side-blotched lizard, *Uta stansburiana*. *Misc. Publ. Mus. Zool. Univ. Michigan* **132**, 1–182.
- Tinkle D. W. & Gibbons J. W. (1977) The distribution and evolution of viviparity in reptiles. *Misc. Publ. Mus. Zool. Univ. Mich.* **154**, 1–55.
- Valenzuela N. (2001) Constant, shift, and natural temperature effects on sex determination in *Podocnemis expansa* turtles. *Ecology* **82**, 3010–24.
- Walther G. R., Post E., Convey P. *et al.* (2002) Ecological responses to recent climate change. *Nature* **416**, 389–95.
- Weekes H. C. (1935) A review of placentation among reptiles with particular regard to the function and evolution of the placenta. *Proc. Zool. Soc. Lond.* **1935**, 625–45.