

Nesting lizards (*Bassiana duperreyi*) compensate partly, but not completely, for climate change

RORY S. TELEMECO,¹ MELANIE J. ELPHICK, AND RICHARD SHINE²

School of Biological Sciences, University of Sydney, NSW 2006, Australia

Abstract. Species in which ambient temperatures directly determine offspring sex may be at particular risk as global climates change. Whether or not climate change affects sex ratio depends upon the effectiveness of buffering mechanisms that link ambient regimes to actual nest temperatures. For example, females may simply lay nests earlier in the season, or in more shaded areas, such that incubation thermal regimes are unchanged despite massive ambient fluctuation. Based on eight years of monitoring nests over a 10-year period in the field at an alpine site in southeastern Australia, we show that, even though lizards (*Bassiana duperreyi*, Scincidae) have adjusted both nest depth and seasonal timing of oviposition in response to rising ambient temperatures, they have been unable to compensate entirely for climate change. That inability stems from the fact that the seasonal progression of soil temperatures, and thus, the degree to which thermal regimes at the time of laying predict subsequent conditions during incubation, also has shifted with climate change. As a result, mean incubation temperatures in natural nests now have crossed the thermal threshold at which incubation temperature directly affects offspring sex in this population.

Key words: *Bassiana duperreyi*; climate change; global warming; nesting behavior; phenology; temperature-dependent sex determination (TSD).

INTRODUCTION

Global temperatures are rising as a result of elevated concentrations of atmospheric, greenhouse gases resulting from human activity since the industrial revolution (IPCC 2007, Rosenzweig et al. 2008). Long-term changes in both temperature and rainfall patterns have occurred at a range of geographic scales (Williams et al. 2003, Willette et al. 2005, IPCC 2007). Current climate models predict a continued warming trend through the twenty-first century, to a degree dependent upon future global socioeconomic policy (Visser 2008). However, even conservative estimates predict an increase of 1.4–5.8°C within this century, with an increase of at least 0.2°C per 10-year period for the next two decades (Hughes 2003, Williams et al. 2003, IPCC 2007).

Understanding the ecological consequences of climate change is vitally important. Climate change has been implicated as a primary cause for reductions in distribution and abundance of many species, and the extinction of at least one taxon, the golden toad (Pounds and Crump 1994, Parmesan 1996, LaVal 2004, Thomas et al. 2004, Araújo et al. 2006). Some biological attributes of species render them particularly vulnerable: for example, reliance on specific habitat features that

will be affected by climate change (e.g., polar bears on ice flows [Stirling et al. 2004]), stenothermic taxa that cannot survive thermal fluctuation (e.g., Antarctic fishes [Van Dijk et al. 1999]), and reliance upon thermal cues to predict future environmental conditions (e.g., Pied Flycatchers [Both et al. 2006]). Of particular concern are species whose basic biology is directly affected by ambient thermal regimes. For example, nest temperatures directly determine offspring sex (as well as other phenotypic traits) in many reptiles (temperature-dependent sex determination, or TSD [Bull 1980]).

Will global warming skew the sex ratios of species with TSD, thereby reducing population viability (Dav-enport 1997, Hawkes et al. 2007)? The answer to this question depends upon the degree to which a given shift in ambient thermal conditions affects nest temperatures (and thus, offspring sex). The link is not direct, because several mechanisms may buffer offspring sex ratios from warming temperatures. For example, females may ameliorate nest temperatures by nesting earlier in the season, by digging deeper nests, or by nesting in shade. Although buffering also could arise via rapid adaptive shifts in the thermal threshold that triggers embryonic sex determination, latitudinal intraspecific comparisons suggest that this trait is highly conservative (Ewert et al. 2005, Doody et al. 2006). Instead, these studies suggest that maternal nest-site selection buffers nest temperatures such that they remain consistent throughout the species' range. By analogy, populations are most likely to respond to a warming world by altering some aspect of plastic nesting behavior. Have such behavioral

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¹ Present address: Department of Biology, University of Central Oklahoma, 100 N. University Drive, Edmond, Oklahoma 73034 USA.

² Corresponding author. E-mail: rics@bio.usyd.edu.au

modifications occurred, and if so have they been able to compensate for current effects of global warming on nest temperatures, and thus on offspring sex ratios? To answer these questions, we need long-term field data on the nesting behavior and subsequent temperatures inside the nests of reptile species with temperature-dependent sex determination. We have gathered such data for montane lizards.

METHODS

Study species and site

Three-lined skinks (*Bassiana duperreyi*) are medium-sized (to 80 mm snout–vent length) terrestrial lizards from cool-climate habitats in southeastern Australia. Females lay clutches of three to nine eggs in early summer, under logs or rocks in open areas exposed to high levels of solar radiation (Shine and Harlow 1996, Shine et al. 2002a). Hatchling phenotypes are strongly influenced by thermal regimes during incubation, both in the field and in the laboratory, but not by hydric variation over the range of soil water-potentials recorded in natural nests (Flatt et al. 2001). *Bassiana duperreyi* is therefore an ideal species for examining the effects of changing environmental temperatures on offspring phenotype because such effects are not confounded by accompanying changes in precipitation. These lizards possess heteromorphic sex chromosomes (XX–XY system), but in cool nests this genetic mechanism is overridden by TSD: eggs incubated at <20°C produce predominately male hatchlings (Shine et al. 2002b, Radder et al. 2008). This sex-determining system appears to enhance offspring fitness because of a sex difference in optimal incubation temperatures: the viability of female offspring is greatly reduced by low-temperature incubation whereas that of males is not (Shine et al. 2002b). The period of thermal sensitivity is prolonged, with *B. duperreyi* embryos sexually labile from the time of oviposition through at least 60% of incubation (Shine et al. 2007).

Our study site in the Brindabella Range (40 km west of Canberra in the Australian Capital Territory) is largely covered by eucalypt forest with occasional open areas of snow-grass (*Poa* spp.). Females move into these open areas for oviposition each summer (Shine and Harlow 1996). We worked in such an area, artificially cleared for overhead hydroelectric power lines, at Picadilly Circus (PC; 1240 m elevation, 148°50' E, 35°21' S). Although this site is more open than the surrounding forest, dense mid- and low-level vegetation is present, resulting in heterogeneous cover at ground level.

Monitoring natural nests

We used miniature thermal data-loggers (thermo-chron iButtons; Dallas Semiconductor, Dallas, Texas, USA; diameter 15 mm, height 6 mm, mass 3.3 g) to monitor temperatures within 112 natural nests (14 ± 2.1 nests/yr [mean \pm SE]) from 1997–1998 through 2006–

2007 summer seasons (10-yr period, data missing for 2003–2004 and 2004–2005 due to intense wildfires in the area in 2003 precluding access at the time of oviposition in both of these years; two-year [e.g., 2004–2005] seasons refer to the southern hemisphere summer which crosses calendar years). Each year, we made trips in early summer (weekly trips, last week of October to first week of December) to locate nests with recently oviposited eggs (<1-week incubation, based on subsequent incubation periods in the laboratory). We searched for nests both within the central cleared area of our site and in the surrounding fringes of eucalypt forest. Minimum and maximum egg depths were recorded for each nest, and data loggers (factory calibrated and preset to record temperature every hour) were placed within nests at their approximate mid-depths. The thermal data loggers were collected 10–12 weeks later and downloaded. Our analysis is based on nine weeks of data per nest, because incubation typically requires about this long under field conditions (Shine and Harlow 1996). We also obtained data from the Australian Bureau of Meteorology for air temperatures recorded at Tidbinbilla Nature Reserve (700 m elevation, 148°94' E, 35°44' S, data recorded daily at 08:00 hours local standard time), 15 km from our study site.

The heterogeneous nature of vegetative ground cover at our study site provided ample opportunity for females to select the relative shade over their nests. To determine if females were altering their nest placement in this way, we measured nest canopy cover during years 2002–2003, 2004–2005, and 2005–2006 (one year before and two years after the fires; we were granted access mid-way through the incubation period in 2004–2005). We placed a digital camera with a 180° hemispherical lens (Canon F1 7.5 mm fish-eye lens; Canon, Melbourne, Australia) on nest cover items (rock or log) and took photographs pointing directly upwards ($N = 34$). We used gap light analyzer image-analysis software to extract information on canopy cover from the resulting images (Frazer et al. 1999, Shine et al. 2002a).

Determining date of oviposition

During the years 1998–1999 and 2004–2005 through 2006–2007, we collected 86 gravid female *B. duperreyi* and brought them back to the University of Sydney, where they were housed in separate cages (each $22 \times 13 \times 7$ cm) and allowed to oviposit. Each cage contained moist vermiculite (for oviposition), a shelter site, and a water dish. The lizards were fed on live crickets three times a week. In order to replicate natural conditions, the room was kept at 20°C with a 12-h light : 12-h dark photoperiod. A thermal gradient of 20–35°C within each cage was maintained for 8 h per day via an under-floor heating element; cage temperature fell to ambient room temperature (20°C) overnight (see Shine and Harlow 1996 for details). All cages were inspected twice daily for eggs.

Analyses

We used the software program Statview 5 (SAS Institute, Cary, North Carolina, USA) to analyze all data. Data sets were checked to ensure they conformed to the requirements of statistical tests. We used linear regression to analyze nest temperatures, ambient air temperatures, mean nest depth, % canopy cover, and date of oviposition over time. In order to analyze nest temperatures over time, we determined mean weekly temperature, mean temperature over the entire 9-week period eggs were in the nests, and mean temperature for a 7-week calendar period in which all nests had eggs (16 December–2 February). Linear regression was also used to analyze the effects of mean nest depth on week-1 nest temperature. We used ANCOVAs to determine how well temperatures at the time of oviposition, and nest depth, predicted mean nest temperatures over time. Early and late year groups were factor levels while week-1 nest temperature and mean nest depth were covariates. The “early” group included years 1, 2, 3, 4, and 5 (1997–1998 to 2001–2002) and the “late” group included years 6, 9, and 10 (2002–2003, 2005–2006, and 2006–2007). Data for years 7 and 8 were missing due to fire damage at PC. The seasonal temperature pattern for year 5 departed from the norm seen in other years, but including or deleting it did not change the statistical outcome of analyses. For this reason, it was removed when constructing graphs but grouped with early years (which it most resembled) for statistical analysis.

RESULTS

Climate change

Mean ambient air temperatures in summer (from 16 December through 2 February) showed a warming trend of $\sim 1.5\text{--}1.7^\circ\text{C}$ over the 10-yr period we examined ($r^2 = 0.03$, $df = 446$, $P = 0.0003$; Fig. 1a). This trend mirrors that seen in analyses based on larger geographic areas (mean summer temperatures in New South Wales from 1950–2007 [Commonwealth of Australia 2008]). Temperatures increased at the same annual rate in each month across the summer season, resulting in the advancement of spring thermal progression (Fig. 2).

Nest temperatures

Temperatures in natural lizard nests increased by $\sim 1.5^\circ\text{C}$ over the 10-yr period we examined (Fig. 1b). Regression analysis of nest temperatures over the summer period (7 weeks, 16 December–2 February) as well as mean nest temperature over the 9-week period eggs are in the nest, revealed a warming trend (respectively, $r^2 = 0.111$, $df = 111$, $P = 0.0003$, Fig. 1b; $r^2 = 0.04$, $df = 110$, $P = 0.034$). The warming effect was most marked late in the incubation period: nest temperatures during the first week after eggs were laid did not vary significantly among years ($r^2 = 0.01$, $df = 111$, $P = 0.3$), whereas nest temperatures at the time of hatching rose by $\sim 3.0^\circ\text{C}$ (Fig. 3). Thus, the relationship

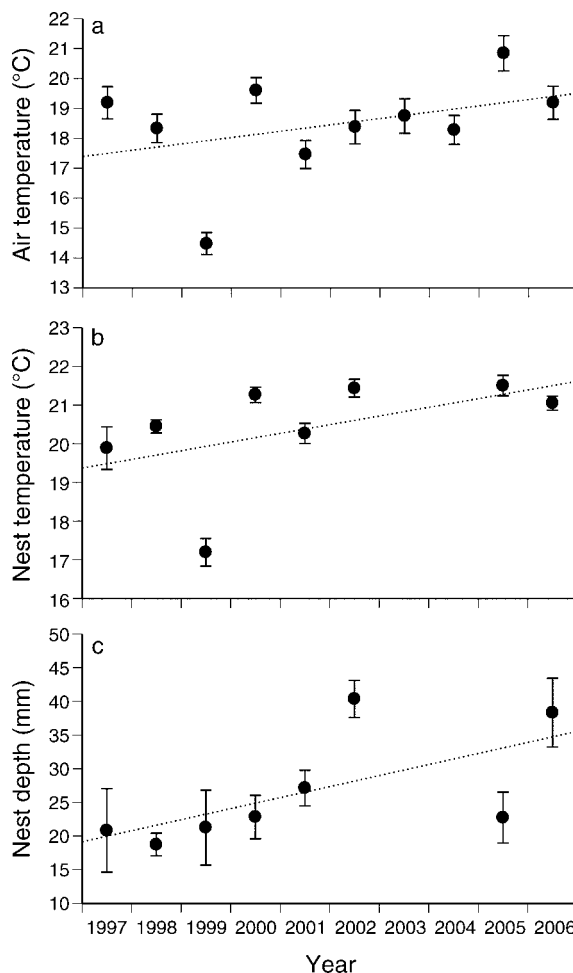


FIG. 1. Shifts over a 10-year period in (a) mean annual air temperature at Tidbinbilla Nature Reserve (15 km from Picadilly Circus, Australia) during the period all lizard nests had eggs present (16 December–2 February; data were collected each day at 08:00 hours local standard time); (b) mean temperatures within natural *Bassiana duperreyi* nests at Picadilly Circus during the period when all nests had eggs present; and (c) mean nest depth. Years are the first calendar year of each season.

between mean nest temperatures in week 1 and week 9 differed between early and late years (interaction, $F_{1,107} = 7.822$, $P = 0.006$). Nest depth did not affect mean 9-week nest temperature (nest depth, $F_{1,98} = 0.82$, $P = 0.37$), although early vs. late years differed in mean thermal regimes even if nest depth was included as a covariate in the analysis ($F_{1,98} = 5.5$, $P = 0.02$). This warming trend meant that over the course of our study, mean nest temperatures each year crossed the 20°C threshold for temperature effects on sex determination in this species. In the early years, nests remained below 20°C for the entire sex-labile period, whereas in later years nests exceeded 20°C for approximately one-third of the sex-labile period (Fig. 3).

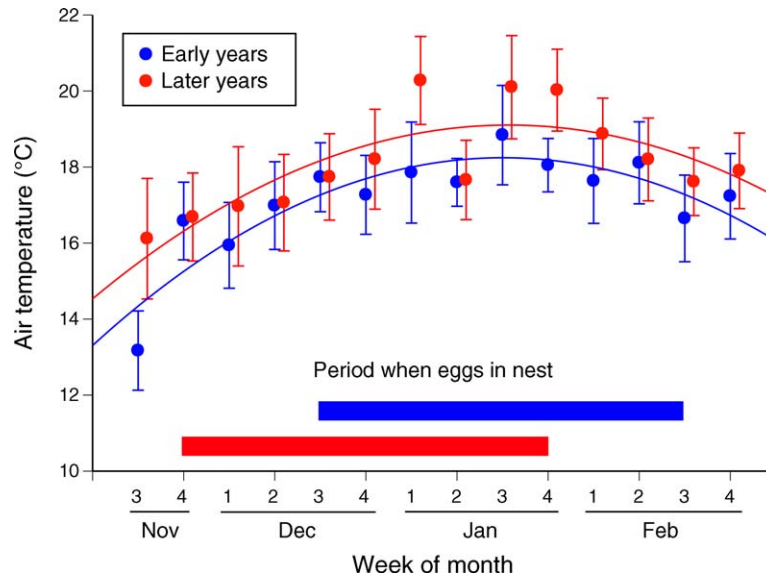


FIG. 2. Mean weekly air temperatures at Tidbinbilla Nature Reserve (15 km from Picadilly Circus; data collected at 08:00 hours local standard time) during the *Bassiana duperreyi* reproductive period. Data are grouped by early (years 1, 2, 3, 4) and late (years 6, 9, 10) years. Lines are fitted polynomial trend lines.

Nesting behavior

Females oviposited in the laboratory from mid-November through early December with laying date becoming progressively earlier (oviposition date 48.9 ± 4.1 days from 1 November for 1998–1999, 37.2 ± 0.7 for 2004–2005, 42.2 ± 0.8 for 2005–2006, and 12.1 ± 1.2 for

2006–2007; $r^2 = 0.16$, $df = 85$, $P < 0.0001$; Fig. 2). Data collected prior to our study at a nearby site (Coree Flats, elevation 1050 m, $148^\circ 48' E$, $35^\circ 17' S$, ~ 9 km from PC) indicate that this trend for increasingly early oviposition has been going on for a much longer period (Pengilley 1972). Pengilley (1972) reported that in 1968, female *B.*

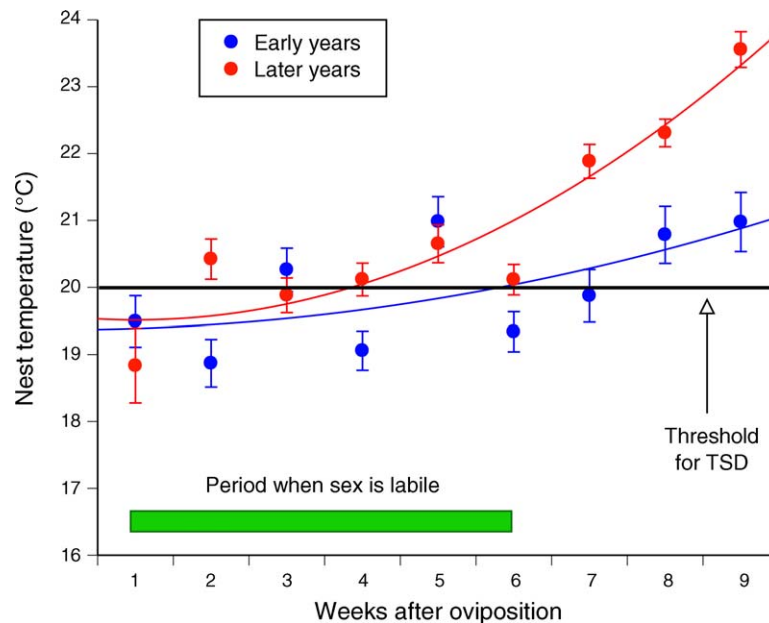


FIG. 3. Mean weekly temperatures of *Bassiana duperreyi* nests at Picadilly Circus grouped by early (years 1, 2, 3, 4) and late (years 6, 9, 10) years, showing nest temperatures relative to the 20°C temperature threshold, below which offspring sex is temperature dependent and above which offspring sex is genetically determined. “TSD” indicates temperature-dependent sex determination. Lines are fitted polynomial trend lines.

duperreyi oviposited from late December through early January, nearly a month later than the latest oviposition that we observed.

In the field, females placed eggs in progressively deeper nests but not shadier nests (respectively, $r^2 = 0.08$, $df = 98$, $P = 0.0055$, Fig. 1c; and $r^2 = 0.006$, $df = 32$, $P = 0.67$). Mean canopy openness was relatively stable at 67% (SE = 1.20%), whereas mean nest depth increased by ~15 mm over our 10-yr study period (Fig. 1c). However, as noted above, this change in nest depth was not responsible for annual variation in mean 9-week nest temperature.

DISCUSSION

Female ectotherms have the potential to buffer their progeny from the effects of climate change through active thermoregulation in viviparous species, and through nest site choice in oviparous species (Shine and Harlow 1996). Behavioral mechanisms such as these are ideal for buffering against relatively rapid climate change because they can be modified by individuals on a short-term basis. Therefore before conclusions on the effects of climate change on reproductive life-history traits can be made, we must understand such behavioral responses to climatic variation.

At our study site, air temperatures during the reproductive season of *B. duperreyi* increased by ~1.5°–1.7°C over a 10-year period from 1997 to 2006 (Fig. 1a). Temperatures inside natural lizard nests showed a similar increase over this period (Fig. 1b). Meanwhile, females adjusted their nesting behavior by digging deeper nests (Fig. 1c) and ovipositing earlier (especially when compared to Pengilley's 1968 records; Fig. 2). However, consistent with reports in a freshwater turtle (Janzen and Morjan 2001), nest canopy cover did not vary suggesting this aspect of nest-site choice may be genetically fixed. Over the time course of our own study, modifications in nest depth and timing were sufficient to maintain a relative constancy in overall mean nest temperatures in the first week after laying (Fig. 3). However, these shifts failed to compensate for the rapid warming experienced later in the incubation period: nests have become warmer overall, especially late in development (Fig. 3).

The shift in thermal regimes of natural nests over the last decade has crossed a biologically significant threshold in this species: the temperature at which offspring sex is directly affected by thermal cues rather than by offspring genotype (20°C [Shine et al. 2002b]). In the early years of our study, eggs within field nests spent their first six weeks of development below 20°C, at temperatures low enough to override heteromorphic sex chromosomes and thus, produce male-biased hatchling sex ratios. Due to climate change, nests laid in more recent years at the same site rarely fell below this thermal threshold for more than two or three weeks after the eggs were laid (Fig. 3). Incubation at these temperatures results in a hatchling sex ratio nearing

50:50, with offspring sex determined by genotype (Shine et al. 2002b). The effects of such a shift on population viability remain unclear.

Sex is not the only fitness-relevant phenotypic trait of hatchlings that is influenced by nest temperature in *B. duperreyi*. For example, higher mean incubation temperatures result in smaller, faster hatchlings in both sexes (Shine and Harlow 1996, Shine et al. 1997, Shine 2002, 2004). The slope of seasonal warming while eggs are in nests (a trait that has shifted markedly over recent years; Figs. 2 and 3) also can influence hatchling phenotypes (independent of mean nest temperatures, Shine 2004) as well as the timing of hatching. Not only are females now ovipositing earlier, but the duration of incubation has shortened as a direct result of hotter nest conditions. Because an increase in mean incubation temperature from 22° to 30°C more than halves incubation period in *B. duperreyi* (Shine and Harlow 1996), rising temperatures will result in hatchlings emerging much earlier than they once did. Similar shifts in hatching dates as a result of climate change have been noted in other reptiles as well as in many other taxa including insects, amphibians, and birds (Beebee 1995, Crick and Sparks 1999, Visser and Holleman 2001, Weishample et al. 2004, Both et al. 2006, Doody et al. 2006, Visser 2008). The phenology of resources upon which the hatchlings depend (e.g., prey availability, vegetation structure) also may shift with hatchling emergence in response to global warming, but may not (Stenseth and Mysterud 2002, Visser et al. 2004). Our data suggest that female *B. duperreyi* continue to use the same thermal cue to time oviposition, but that this cue fails to predict subsequent thermal conditions within the nest (Figs. 2 and 3). Other subsequent environmental conditions such as food availability, rainfall, or predator abundance may have shifted as well, plausibly affecting hatchling fitness.

A changing climate will have profound effects on ecosystems. In order to aid policy makers, we must better understand the effects of current climate change. Our study suggests that female *B. duperreyi* are unable to behaviorally buffer their progeny against warming nest temperatures; and one result of that inability has been a shift in the prevailing mode of sex determination within natural nests. This result suggests that although many TSD species have persisted under a wide range of ambient thermal conditions over millions of years (Morjan 2003, Ewert et al. 2005, Doody et al. 2006), they may have difficulty adjusting within the time frame enforced by current rates of climate change.

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