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SYMPOSIUM

Parental Effects and Climate Change: Will Avian Incubation Behavior Shield Embryos from Increasing Environmental Temperatures?

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Synopsis A major driver of wildlife responses to climate change will include non-genomic effects, like those mediated through parental behavior and physiology (i.e., parental effects). Parental effects can influence lifetime reproductive success and survival, and thus population-level processes. However, the extent to which parental effects will contribute to population persistence or declines in response to climate change is not well understood. These effects may be substantial for species that exhibit extensive parental care behaviors, like birds. Environmental temperature is important in shaping avian incubation behavior, and these factors interact to determine the thermal conditions embryos are exposed to during development, and subsequently avian phenotypes and secondary sex ratios. In this article, we argue that incubation behavior may be an important mediator of avian responses to climate change, we compare incubation strategies of two species adapted to different thermal environments nesting in extreme heat, and we present a simple model that estimates changes in egg temperature based on these incubation patterns and predicted increases in maximum daily air temperature. We demonstrate that the predicted increase in air temperature by 2100 in the central USA will increase temperatures that eggs experience during afternoon off-bouts and the proportion of nests exposed to lethal temperatures. To better understand how species and local adaptations and behavioral-plasticity of incubation behavior will contribute to population responses to climate change comparisons are needed across more avian populations, species, and thermal landscapes.

Introduction

In the absence of mitigation of greenhouse gas emissions, average annual temperatures are predicted to rise by as much as 2.8°C (5°F) by 2050 in some areas of the USA (US EPA 2015). Climate conditions are expected to become more variable, with more extreme weather events and maximum and minimum temperatures (US EPA 2016). These shifts in climate are predicted to have dramatic effects on flora and fauna, and significant research efforts are underway to determine how these effects will manifest and identify species at greatest risk of extinction.

A major driver of wildlife responses to climate change will be non-genomic effects, like those mediated through parental behavior and physiology (i.e., parental effects; Chakravarti et al. 2016). Phenotypes expressed early in life are the product of both an individual's genotype and the environment in which it developed (Mousseau and Fox 1998; Badyaev and Uller 2009). These environmental effects can cause short- and long-term changes in phenotypic expression (Mousseau and Fox 1998; Badyaev and Uller 2009). Mechanisms of nongenetic inheritance are predicted to contribute importantly to evolutionary responses to rapid environmental change, producing both maladaptive and adaptive phenotypes (Bonduriansky et al. 2012). Currently, the extent to which within and multi-generational

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parental effects will contribute to species' responses to a rapidly changing climate is not well understood (Bonduriansky et al. 2012). However, research in marine invertebrate systems in which these relationships have been more comprehensively and explicitly studied indicate that the parental environment is an important contributor to offspring resilience to ocean warming and acidification (Donelson and Munday 2015; Shama 2015; Chakravarti et al. 2016; Guillaume et al. 2016; Chirgwin et al. 2018).

Little is known about how parental effects will shape responses to climate change in terrestrial vertebrates, although shifts in temperature extremes are expected to be greater in terrestrial systems (US EPA 2016). Relationships between species' adaptation to climate change and parental effects are also poorly studied in species exhibiting extensive parental care (but see Macagno et al. 2018; O'Neill et al. 2018; So and Schwanz 2018). Yet, there could be more opportunity for climate-mediated parental effects in these species since offspring phenotypic development will be tied to parental behavior for extended periods of time, creating a link between parental environment and offspring developmental conditions. These shifts in behavior could retain stability in the developmental environment (Macagno et al. 2018), or behavior could promote adaptive phenotypic plasticity, although there is limited evidence for anticipatory parental effects in animals (Uller et al. 2013).

One mechanism by which climate change and parental care behaviors can shape offspring phenotype is by altering the thermal environment of the offspring. Thermal conditions experienced during embryonic development play an important role in defining offspring traits, hatching success, and offspring fitness in many terrestrial species (Mousseau and Fox 1998; DuRant et al. 2013; Noble et al. 2018). Terrestrial vertebrates have developed ways to control nest environment through behavioral (nest-site selection, physical incubation) and physiological (e.g., internal gestation) means. Species that directly manipulate the thermal environment of developing offspring through behavior provide an excellent opportunity to explore the link between changing climate, parental behavior, offspring phenotype, and ultimately population responses to rising temperatures. Both avian and non-avian reptiles are well-suited for these studies. Indeed, numerous studies explore how the embryonic thermal environment shapes phenotype of non-avian reptiles, and if mothers alter nest-site selection in response to environmental conditions. However, only recently have we started appreciating that the thermal environment of developing avian embryos plays a vital role in determining offspring phenotype of wild birds. Since parental incubation behavior in most avian species determines the thermal environment of developing eggs, this behavior, through its effects on offspring phenotype, may be an important contributor to avian responses to climate change. The purpose of this article is three-fold: (1) to demonstrate that incubation behavior has important implications for avian population responses to climate change; (2) to present a comparison of incubation behaviors in two species adapted to different thermal climates nesting in extreme heat; and (3) to model how rising temperatures will affect exposure of eggs to suboptimal and lethally-hot temperatures.

Incubation behavior as a mediator of avian responses to climate change

Although variability exists across avian species, most avian parents exhibit extensive parental care throughout reproduction and dictate the thermal environment experienced by developing embryos through contact incubation. Shifts in climate that alter incubation behavior could keep nest conditions stable despite changing environmental conditions, but these behavioral shifts can also result in altered nest conditions (e.g., temperature) that have implications for avian phenotypic expression. Furthermore, the ability of birds to make finely-tuned incubation decisions, like delaying an off-bout until air temperature is below/above temperatures suboptimal to embryonic development, may not occur due to physiological or behavioral constraints which could also affect avian phenotype and hatching success. If these different phenotypes experience differential survival and reproduction (Hepp and Kennamer 2012; Nord and Nilsson 2016; Berntsen and Bech 2016), then climate-mediated shifts in incubation behavior and nest conditions will affect avian population dynamics (Fig. 1). Environmental conditions during reproduction will further affect avian population dynamics through costs incurred by parents during incubation (Oswald and Arnold 2012; Martin et al. 2018). Incubating during cold and hot temperatures can increase the cost of incubation, pushing parents to trade-off between self-maintenance and offspring care, and ultimately affect future adult reproductive potential and reproductive phenology (Hepp and Kennamer 1993; 2011; Heaney and Monaghan 1996; Reid et al. 2000, 2002; Amat and Masero 2004; Hanssen et al. 2005; Perez et al. 2008). The numerous endpoints tied to this single parental care behavior suggest that avian incubation behavior

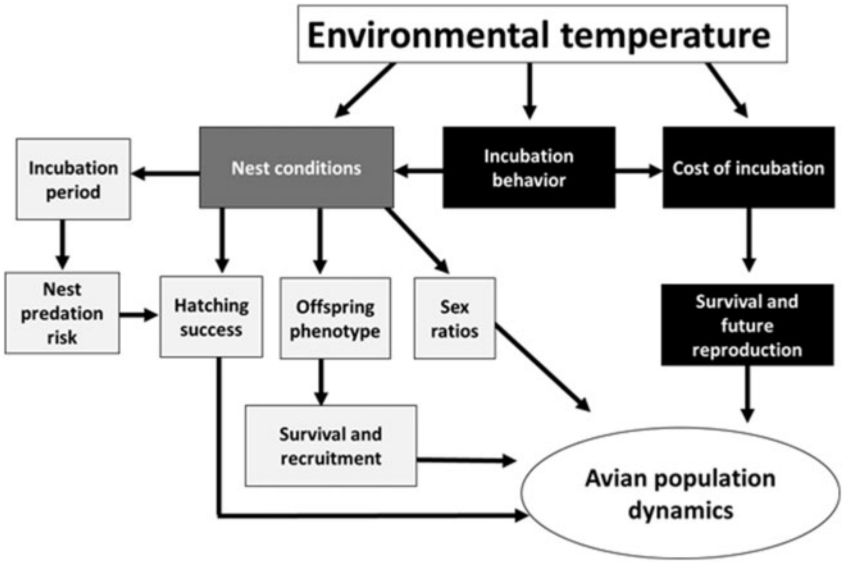

Fig. 1 The direct and indirect pathways through which environmental temperatures can shape avian population dynamics via effects on incubation behavior, costs of incubation, and thermal conditions experienced by the embryos. Black boxes represent effects on parental endpoints, whereas light gray boxes represent effects on offspring endpoints.

will be a critical factor determining how birds respond to and adapt to climate change.

Nest conditions affect hatching success, phenotypes, and sex ratios

Historically, the importance of avian incubation to reproductive success of wild birds was considered in the context of hatching success, incubation period, and nest predation risks (Zicus et al. 1995; Martin et al. 2015). It is now clear that the incubation environment has important implications for other aspects of avian biology (DuRant et al. 2013). Research over the past decade in non-agricultural species representing both ends of the precocial–altricial spectrum demonstrates that temperatures experienced during incubation have dramatic effects on avian offspring phenotypes. These include effects on physiology (e.g., concentrations of developmentally-important hormones, thermoregulation, and immune responses; DuRant et al. 2010, 2012a, 2012b; Nord and Nilsson 2011; Wada et al. 2015), morphology (Hepp et al. 2006; DuRant et al. 2012a), behavior and performance (Hopkins et al. 2011; Bertin et al. 2018; Hope et al. 2018a), growth (Ospina et al. 2018a), and even first-year survival and adult body size (Hepp and Kennamer 2012; Nord and Nilsson 2016; Berntsen and Bech 2016). Interestingly, there is some evidence in poultry that brief exposure to heat stress as embryos can improve heat tolerance of chicks (Piestun et al. 2008; 2009; Willemsen et al. 2010, 2011; Nassar et al. 2015), and exposure to heat stress as a juvenile can increase reproductive output as an adult (Hoffman et al. 2018). In altricial species, which spend significant time in the nest post-hatching, phenotypes may continue to be shaped by the nest thermal environment. Early post-hatch exposure to a thermal challenge that mimics temperature drops that occur when females leave the nest alters bluebird corticosterone responses to stress at fledging (Lynn and Kern 2017, 2018). However, more research is needed to understand how thermal conditions experienced pre- versus post-hatch interact to affect phenotype of altricial offspring. Given the diversity of phenotypic traits affected by incubation temperature, the potential for these effects to shape offspring responses to the post-hatch environment and likelihood of survival, the importance of nest thermal environment must be considered when predicting effects of climate change on avian populations.

In addition to effects on avian offspring phenotype, incubation temperature can also affect secondary sex ratios of non-agricultural avian species. Two species in which incubation temperature-dependent phenotypes have been detected also exhibit temperature dependent sex-biased embryonic mortality (TSEM). These two species, Wood Ducks and Australian Brush Turkey, belong to two different avian families, the Anseriformes and the Galliformes. In both species, greater female embryonic mortality occurs at low incubation temperatures, and chick sex ratios become less skewed toward males as incubation temperature increases (Eiby et al. 2008; DuRant et al. 2016). A recent study also documented a greater proportion of male versus female Zebra Finch chicks hatching at a cooler incubation temperature compared with warmer temperatures (Wada et al. 2018). It is not clear whether this is the result of TSEM, but these data suggest that temperature also may be important in determining sex ratios of passerines. There is also evidence in domesticated poultry that incubation temperature can affect secondary sex ratios (Tzschentke and Halle 2009; Yilmaz et al. 2011; Piestun et al. 2013), but this may not be the result of TSEM (Collins et al. 2013). The effects of pre-hatch nest conditions on avian sex ratios deserves further attention, particularly since many previous studies on sex ratio manipulation in birds have focused on mechanisms occurring pre egg-laying (Krackow 1995; Navara 2013). If TSEM is more widespread among avian species and families, the imminent predicted shifts in climate may contribute importantly to avian population dynamics through this effect alone, especially if differences in sex ratios persist across life stages.

Building connections between the environment, incubation behavior, nest temperatures, and offspring traits

To better estimate the role of parental effects in shaping avian responses to climate change, we first need a better appreciation of the factors shaping avian incubation behavior, their subsequent influence on temperatures experienced by embryos, and effects on offspring traits. While relationships between ambient environmental temperature and parental behavior have been studied (Conway and Martin 2000 a,b), few studies connect the resulting nest conditions with offspring traits. However, it is well-established that temperature can affect incubation behavior. As ambient conditions change, parents modify their behavior, navigating competing demands between self-maintenance and offspring care (Conway and Martin 2000 a,b; Hepp and Kennamer 2011; Coe et al. 2015). For example, off-bouts tend to be shorter for Wood Ducks nesting in colder weather when nests cool rapidly once hens exit the nest box (Hepp and Kennamer 2011). Hens spend more time off the nest as the nesting season progresses and temperatures increase warm (Hepp and Kennamer 2011). Differences in attendance patterns in inclement weather can have important implications for avian development. For instance, in Common Goldeneye (*Bucepha la clangula*) just 13 fewer minutes of parental attendance per day can extend the incubation period (Zicus et al. 1995).

Clutch size also significantly affects incubation behavior and temperatures experienced by the embryos (Tinbergen and Williams 2002; Cooper et al. 2005; Nord and Nilsson 2012; Hepp et al. 2005; Nord and Williams 2015; Hope et al. 2018b; S. F. Hope et al., manuscript under review). In one system, the two most significant drivers of incubation temperature were ambient temperature and clutch size (S. F. Hope et al., manuscript under review). Nests are warmer when ambient temperature is warmer, and smaller clutches are warmer than larger clutches (S. F. Hope et al., manuscript under review), but cool more rapidly (Tinbergen and Williams 2002). Variability in average temperature across eggs within a clutch also is lower in small clutches than large clutches, because eggs in large clutches of the nest experience cooler temperatures when at the periphery than at the center of the nest (S. F. Hope et al., manuscript under review). This finding suggests that phenotypic variation will be greater among chicks produced by large clutches than small clutches. While increased phenotypic variation can benefit the parent's fitness, offspring performance was often greatest at medium incubation temperatures (DuRant et al. 2013; Nord and Nilsson 2016). Interestingly, clutch size tends to decrease throughout the nesting season, even if it is the bird's first nesting event, because ambient incubation at warmer air temperatures, can constrain clutch size as it leads to hatching asynchrony in large clutches (Stoleson and Beissinger 1999). Both the direct effect of ambient temperature on clutch size and the interaction between clutch size and ambient temperature on incubation temperature may contribute importantly to avian reproductive success and offspring phenotypes.

As they emerge, a variety of anthropogenic activities and natural factors also affect incubation behavior (Fisher et al. 2006; Snowden 2018; Love et al. 2019). For instance, environmental pollutants, human disturbance, and even pathogen infection can affect parental incubation behavior (Fisher et al. 2006; Snowden 2018; Love et al. 2019), although how these factors relate to changes in nest temperatures is often not known (Snowden 2018; Love et al. 2019). Because climate change is predicted to affect disease emergence and transmission, exposure to pollutants, and human–wildlife interactions (Noyes et al. 2009; Mills et al. 2010), these are all indirect routes through which climate change could affect phenotypes in birds mediated through shifts in incubation.

Incubation behavior of birds nesting in extreme heat

Few studies examine how birds navigate incubation during extreme heat events, and subsequent effects on temperatures experienced by eggs. This is surprising because avian embryos are more acutely susceptible to high temperatures than low temperatures (Webb 1987; Conway and Martin 2000b), and exposure to extreme heat can be physiologically demanding for birds (Amat and Masero 2004; Tieleman et al. 2008; McKechnie and Wolf 2010). Optimal incubation temperatures are thought to range between 35°C and 40°C (Webb 1987). While avian embryos can withstand long periods of exposure below this range, mortality can occur quickly when they are exposed to temperatures above this range (Webb 1987; Conway and Martin 2000b). Avian species nesting in high heat conditions have developed ways to withstand exposure to these hot temperatures, which include choosing cooler nest sites, producing thicker egg shells, and egg shells that reduce heat transfer through solar radiation (Tieleman et al. 2008; Carroll et al. 2015; Maurer et al. 2015; Lahti and Ardia 2016; Carroll et al. 2018). For many species nesting in high heat conditions, parental attendance of the eggs is vitally important in preventing embryonic exposure to lethally hot temperatures. Mourning Doves nesting in the Sonoran Desert keep their eggs below lethal temperatures ($\leq$40°C), despite much higher ambient temperatures, by using evaporative cooling to lower their body temperature when incubating the eggs (Walsberg and Voss-Roberts 1983). In sea birds nesting in exposed sites with high operative temperatures, nest attendance patterns tend to be high across all ambient temperatures, but are greatest when ambient temperatures are low and high, rather than intermediate (AlRashidi et al. 2011; AlRashidi 2016; Snowden 2018). Nest temperature positively correlated with ambient temperature in Least Terns until ambient temperature was above $\sim$32°C, at which point egg temperature was less affected by environmental temperature due to high adult attendance (Snowden 2018). These results suggest that Least Terns invest more in regulating nest temperatures at high ambient temperatures compared with intermediate temperatures to prevent eggs from overheating (Snowden 2018). Least Terns also returned more quickly to their nest after being flushed by disturbance when ambient temperature was high versus intermediate. These data indicate some plasticity of incubation behaviors to fine-scale environmental conditions.

Species differences in incubation behaviors nesting at the extremes: a case study in quail

Perhaps our best opportunity to predict how avian incubation behavior will respond to climate change is through comparative studies of incubation behavior of species inhabiting the edges of their range (Ackerly 2003). Frequently at range edges, individuals are living at their ecological and physiological limits, which can provide insight into the flexibility of incubation and nesting behaviors (e.g., site-selection, nest construction). In some cases, comparisons of closely related species that are adapted to different climates, but overlap in some parts of their ranges could reveal the importance of local adaptations and evolutionary constraints to plasticity in incubation behavior. These studies will be particularly useful if environmental conditions and parental behavior are linked with conditions experienced by the embryos.

A recent study conducted on populations of two species of quail from sister clades at their range overlap in the panhandle of Oklahoma, USA (Carroll et al. 2018) indicate these species use different nesting and incubation strategies. One species, the Scaled Quail (*Callipepla squamata*), is adapted to hot, arid environments, whereas the other species, Bobwhite Quail (*Colinus virginianus*), is adapted to more mesic environments. Populations of these two species coexist at the eastern range edge of the Scaled Quail, and western range edge of Bobwhite Quail. Temperatures during the nesting season in this area are high, and thermal refugia include herbaceous vegetation, shrubs, and yucca. Both species select nest sites that are considerably cooler (6.5°C) than randomly selected sites located within 2 m of the nest (Carroll et al. 2018; also see Carroll et al. 2015). However, operative temperatures at nests during the nesting season as measured by black bulb models can exceed 60°C. Although both species select cooler nest locations, Scaled Quail use nest sites that are 2.8°C cooler than Bobwhite Quail. Scaled Quail also more frequently took incubation recesses when ambient temperatures were cooler, avoiding leaving the nest when ambient temperatures were most extreme. These differences in incubation patterns and nest-sites resulted in bobwhite nests that averaged 1.28°C warmer than Scaled Quail nests (Carroll et al. 2018). Although this is a small difference in average temperature, vastly different phenotypes and sex-biased embryonic mortality occur at temperatures differing by only 0.9–2.0°C (Eiby et al. 2008; DuRant et al. 2013; 2016).

Furthermore, operative nest temperatures were significantly associated with nest success, demonstrating that thermal properties of the nest-site are important to avian reproduction (Carroll et al. 2015, 2018). Interestingly, the two species exhibited opposing patterns: Bobwhite Quail nests with hotter operative temperatures were more likely to fail than

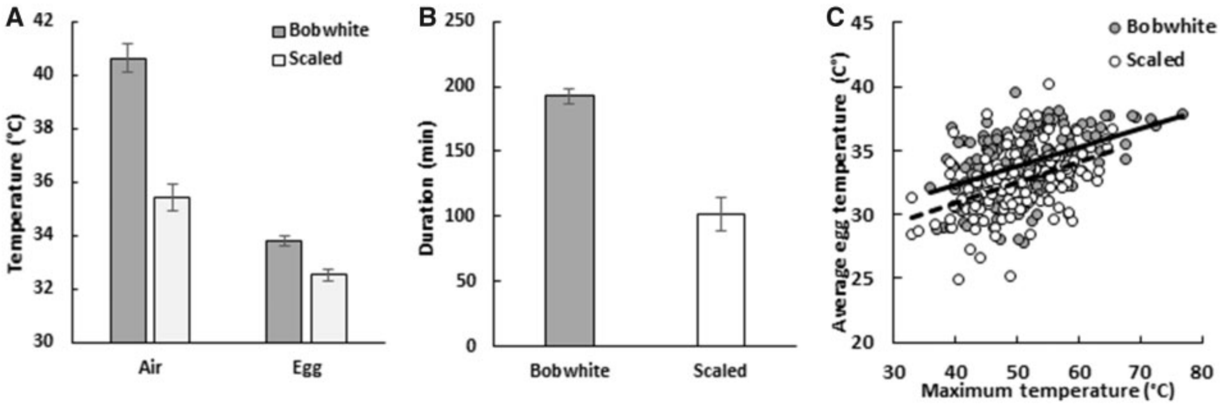

Fig. 2 Bobwhite and Scaled Quail afternoon off-bouts differ in timing and duration, which has implications for temperatures experienced by eggs. (**A**) Operative air temperature ($F_{1,\ 318} = 12.4$; $P < 0.01$) at the start of the afternoon off-bout and average egg temperature ($F_{1,\ 318} = 5.75$; $P = 0.02$) during the afternoon off-bout in Bobwhite and Scaled Quail. (**B**) Duration of the afternoon off-bout in Bobwhite and Scaled Quail ($F_{1,\ 318} = 19.4$; $P < 0.01$). (**C**) Maximum operative daytime temperature significantly affects the average temperature of eggs during the afternoon off-bout in Bobwhite and Scaled Quail (species: $F_{1,\ 310} = 6.40$; $P = 0.01$; maximum temperature: $F_{1,\ 310} = 125.5$; $P < 0.01$). Data were collected throughout the incubation period in 2016 on the Beaver River Wildlife Management Area, Oklahoma following methods described in Carroll et al. (2018), and analyzed using SAS (proc mixed). Nest ID was included as a random effect to account for repeated measurements per nest.

cooler nests, whereas cooler Scaled Quail nests were more likely to fail than warmer nests. Although more research is required to understand this relationship, it suggests that Scaled Quail are very effective at selecting nest sites with high insulative properties and in exhibiting incubation patterns that prevent exposure of their eggs to lethally hot temperatures. Most likely this is because Scaled Quail have evolved to reproduce in hot, arid climates. These data also hint at behavioral and physiological constraints in the non-desert adapted species. Bobwhite Quail frequently took afternoon incubation recesses when operative temperatures near the nest were above 40°C (Fig. 2A, C), temperatures considered lethal for many avian embryos, and rarely nested in the coolest nest substrates even when they were available (Carroll et al. 2018). Bobwhite Quail also took off-bouts that were nearly 80 min longer in the afternoon than Scaled Quail (Fig. 2B).

These data on quail clearly indicate that parental behavior buffers against exposure to extreme heat, but this ability varies across species and individuals. These data also raise several interesting questions: (1) How will species and local adaptations influence parental incubation behaviors? (2) How will shifts in incubation behavior correspond to offspring phenotypes and fitness? (3) How plastic are incubation behaviors to extreme heat? In regards to plasticity of incubation behaviors, it is possible that birds shift the timing or duration of an off-bout based on exposure to temperature maximums. General weather patterns often correlate with nesting behaviors (described above and Conway and Martin 2000a; AlRashidi et al. 2011; Vincze et al. 2013, 2017), indicating some plasticity to incubation behaviors. However, it is often not clear how these behaviors respond to fine-scale or discrete intervals of high ambient temperature (Snowden 2018). For instance, do quail modify timing of off-bouts in relation to maximum daily temperatures, which typically occur between 13:30 and 16:00 h? The timing of the afternoon off-bout, which typically occurs between 15:00—19:00 h (Carroll et al. 2018) critically-influences temperatures experienced by embryos (Figure 2), including exposure to lethal temperatures, and could result in severe parent–offspring conflict. Parents, at the risk of exposing offspring to lethal temperatures, may leave the nest earlier to seek better thermal refugia or seek out food and water to maintain homeostasis. Alternatively, birds may choose to stay on nests until after maximum highs are reached, and ambient temperature begins to fall. Parents in this case would be favoring offspring survival over self-maintenance. Some research suggests that parents make incubation decisions based on energetic constraints to the parent versus outcome for the offspring (Ardia et al. 2009). This idea is supported by data indicating that shading of eggs provides more benefit to the incubating adult (increased air flow and cooling) than the eggs (Downs and Ward 1997; Brown and Downs 2003). These lines of evidence suggest that self-maintenance will drive incubation patterns of birds affected by climate change.

To illustrate this point, we tested for relationships between maximum operative temperatures near the nest and the timing and duration of afternoon off-bouts, but they were only weakly related (in both cases $R^2 \leq 0.03$) and not statistically significant (in both cases $F \leq 3.04$; $P \geq 0.08$). Instead, parents typically stayed on the nest until after peak temperature occurred (Carroll et al. 2018), but not necessarily until temperature was below lethal limits to the embryo. Although further work is needed to determine how responsive incubation behavior is to fine-scale shifts in temperature, this suggests that hotter days will both expose eggs to warmer, and sometimes lethal temperatures in the afternoon, and increase incubation costs to females (see below climate simulation scenario). In this case study, incubation costs are likely to be greater in Bobwhite Quail. Bobwhite Quail select warmer nest sites on average than Scaled Quail, and begin gular fluttering, an indication of heat stress, on nests at cooler air temperatures than Scaled Quail (35°C for Bobwhite versus more than 40–45°C for Scaled Quail; Guthery 2000; Henderson 1971). Although gular fluttering is very effective at relieving heat load through evaporative cooling, it also greatly increases rates of evaporative water loss and can increase risk of dehydration (McKechnie and Wolf 2010). In this region, annual mean surface air temperature is predicted to increase by 1.5–2.2°C by the year 2050 and ~5.0°C by 2100, which will represent a significant burden to Bobwhite Quail incubating in this area (US EPA 2015).

In addition to affecting hatching success and adult condition, incubation decisions will also presumably affect offspring phenotype through effects on the thermal environment of the developing embryo. If exposure to high incubation temperatures promote tolerance to heat stress post-hatch (described in section "Nest conditions affect hatching success, phenotypes, and sex ratios"), as noted in some poultry studies, then it may be advantageous for embryos to be exposed to short periods of high temperature during embryonic development (Piestun et al. 2008, 2009; Willemsen et al. 2010, 2011, Nassar et al. 2015). Such an effect may contribute to the persistence of Bobwhite Quail in this region even if surface air temperatures continue to rise. Alternatively, embryonic exposure to high temperatures could result in poor hatching success, or chicks with suboptimal phenotypes (as predicted in DuRant et al. 2013), and contribute to already declining Bobwhite Quail populations. Nonetheless, how exposure to high temperatures during development shapes offspring resilience to heat in birds requires further attention.

Will current incubation patterns protect against rising air temperatures?: modeling effects of climate change on quail nest conditions

The next step to better understanding how incubation behavior will affect responses of avian populations to climate change is to build models estimating egg temperature using existing incubation patterns and simulated increases in air temperature. We did this using the behavioral patterns of quail across different daily maximum temperatures and the effects of those behaviors on egg temperatures to estimate the effects of increasing environmental temperatures on temperatures experienced by eggs. We focused on the afternoon off-bout because this is when eggs can be exposed to lethally hot temperatures. For simplicity, our models work under the assumption that quail maintain consistent behavioral and physiological responses to ambient temperature and do not adjust nesting phenology, nest locations, or nesting behavior in response to long-term shifts in ambient temperature. To model the effects of increasing global temperature on nest conditions for the two quail species we (1) examined empirical relationships between daily maximum ambient temperature (Ta_{max}) and quail nest conditions in Oklahoma; (2) used these relationships to simulate nest temperature profiles of 10,000 simulated nests of each species in each of 11 years (2006–16), based on the observed Ta_{max} profiles in those years; and (3) conducted additional simulations using those temperature profiles increased by a static 2°C and 4°C.

We examined empirical relationships between daily Ta_{max} and mean daily egg temperature during the afternoon offbout (Te), for nests with ≥5 daily measurements (Bobwhite: $N = 16$, Scaled Quail: $N = 8$). Ta_{max} was determined using data from a weather station in Guymon, Oklahoma (74 km west of the study site), and Te was determined using thermal probes disguised as eggs that were inserted into quail nests (see Carroll et al. 2018 for additional details). Across both quail species, Te was consistently linearly related to Ta_{max}, but the slope and intercept of these relationships varied among nests (Fig. 3A, B), likely reflecting differences in nest substrate, shading, aspect, and individual variation in parental incubation behavior. For both species, average slope was similar (0.368) and there was a very strong linear relationship between slope and intercept of this relationship (Fig. 3C). However, the two species differed in the degree of variability around this relationship with Bobwhite being more variable (mean SD Te = 1.73 [±0.60]) than Scaled Quail (mean SD Te = 1.50 [±0.25]), but this

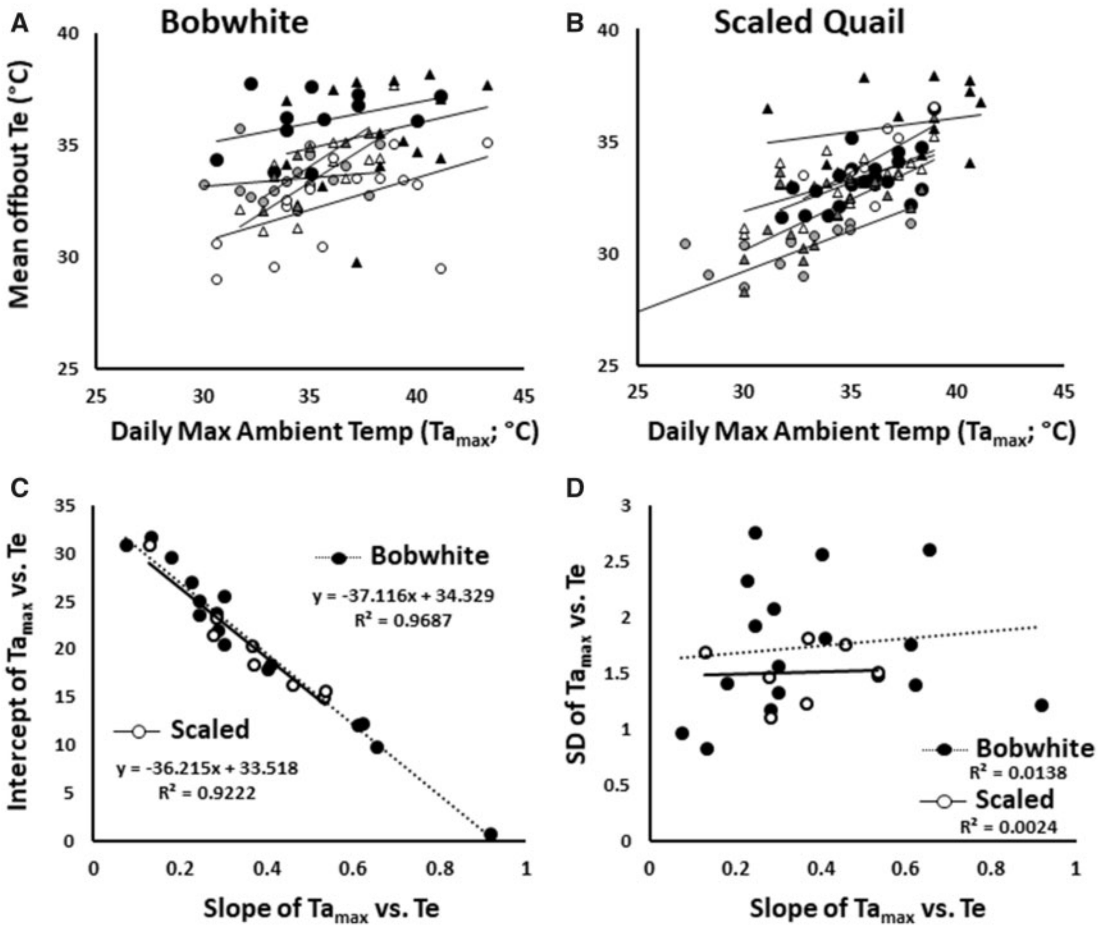

Fig. 3 Empirical relationships between daily maximum ambient temperature (Ta_{max}) and mean offbout egg temperature (Te) for quail in Oklahoma. Ta_{max} versus Te regressions for six representative (**A**) Bobwhite and (**B**) Scaled Quail nests. Regressions of (**C**) slope versus intercept and (**D**) slope versus SD of Ta_{max} versus Te for the two quail species.

variability was not related to slope for either species (Fig. 3D).

We conducted stochastic simulations using 11 years (2006–16) of empirical daily Ta_{max} data from the weather station in Guymon, Oklahoma, to generate nest temperature (Te) profiles for 10,000 simulated nests for each species. For each simulated nest, we selected a random nest initiation date between 15 April and 9 July, and continued incubation for 23 days thereafter (thus, nesting season lasting from 15 April to 31 July). We then generated a Ta_{max} versus Te relationship (slope, intercept, and variability [SD]) for each nest and used that relationship to derive a Te profile for that nest through incubation. Specifically, for each simulated nest, we drew a slope of the relationship between Ta_{max} and Te from a normal distribution characterized by the mean and SD of the empirical data for that species (Bobwhite mean [±SD] slope = 0.368 [±0.225]; Scaled Quail = 0.368 [±0.139]), used the regression equations from Fig. 3C to assign a corresponding intercept for that slope, and drew an SD from a normal distribution based on the mean and SD of the Ta_{max} versus Te SD for each species. For each nest on each day during incubation, we used that nest's regression equation to set the corresponding mean Te from Ta_{max}, and then used that mean and the nest's SD to assign a Te value for that day. We repeated this process using the same annual Ta_{max} profiles increased by a static 2°C and 4°C, temperatures that approximately correspond to predictions for 2050 and 2100 for this region (US EPA 2015). We calculated the mean Te for each nest and then the grand mean Te across the 11 years for each species. Finally, for each year and species, we calculated the proportion of nests experiencing at least 1 day with Te >40°C during the afternoon off-bout, a common threshold for adverse effects in avian embryos (Webb 1987; Conway and Martin 2000b; Reyna and Burggren 2012).

As expected, Scaled Quail nests maintained cooler temperatures during afternoon off-bouts than

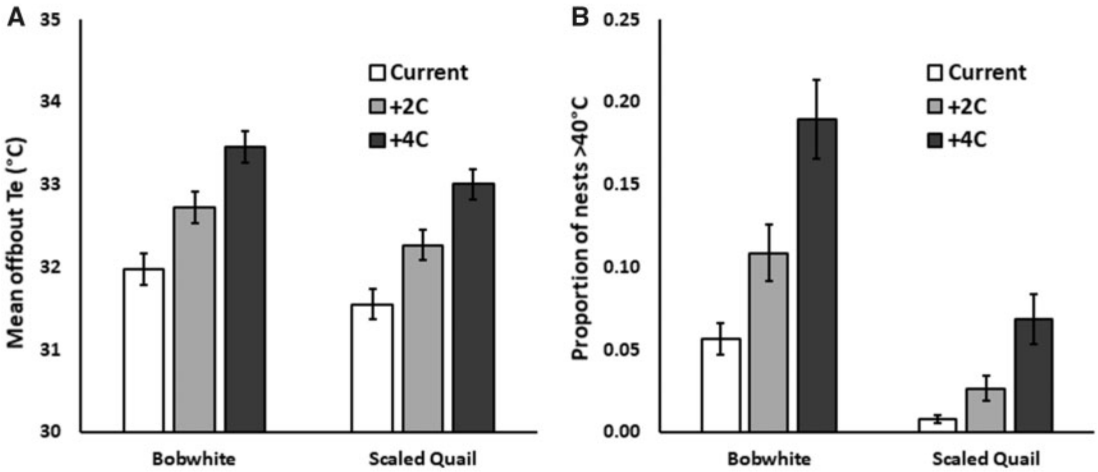

Fig. 4. Predicted effects of climate change on Bobwhite and Scaled Quail nest conditions in Oklahoma. (**A**) Change in mean daily afternoon offbout egg temperature (*Te*) of simulated quail nests under scenarios of (1) current daily maximum ambient temperature profiles during the quail nesting season from 2006 to 2016; (2) a static increase in daily maximum ambient temperature of +2°C; and (3) +4°C. (**B**) Change in proportion of nests experiencing at least one day with mean offbout *Te* exceeding 40°C under the three climate change scenarios. Means represent mean across 10 years (± 1 SE), each with 10,000 simulated nests for each species. Incubation conditions of each simulated nest were generated based on empirical relationships between daily maximum ambient temperature and *Te* in the field (see text).

Bobwhite in a given simulation (Fig. 4A). Under current climate conditions, average *Te* for Scaled Quail during afternoon off-bouts across the 11 years was 31.55°C, whereas average *Te* for Bobwhite was 31.98°C. A static 2°C and 4°C increase in Ta_{max} increased average *Te* for Scaled Quail to 32.27°C and 33.01°C, respectively. Bobwhite nests consistently averaged 0.45°C greater than Scaled Quail nests for each climate simulation. Reflecting higher mean *Te* and *Te* variability during afternoon off-bouts, a greater percentage of simulated Bobwhite nests (5.7%) experienced at least 1 day with *Te* exceeding 40°C than did simulated Scaled Quail nests (0.8%) under current climate (Fig. 4B). Increasing the daily Ta_{max} profile by 2°C and 4°C increased the percentage of Bobwhite nests exceeding 40°C to 10.9% and 19.0%, respectively, and Scaled Quail nest to 2.7% and 6.9%, respectively. Our model did not incorporate increases in stochastic events, like heat waves or drought, both of which are predicted to increase in frequency and significantly affect avian reproduction (McKechnie and Wolf 2010). Thus, effects of climate change on nest conditions are probably greater than predicted by our model, assuming birds do not shift nesting phenology to avoid these hot conditions. Earlier nesting has occurred in a number of avian species in response to rising spring temperatures (Dunn and Winkler 1999; Both et al. 2004), but these behavioral effects are also associated with consequences for avian reproduction (Both et al. 2006, 2009). Although our model simulations are subject to several simplifying assumptions, they suggest that changes in global temperature could have severe consequences for reproduction in birds and that those effects may be mediated by nest site selection and incubation behavior. These effects may be most pronounced in species at the edge of their geographic ranges, as is the case with Bobwhite in this case study.

Concluding remarks

The data in quail suggest that in some species there may be limitations on plasticity of incubation behavior to high maximum temperatures, such that parents do not engage in behaviors that would better protect the incubating embryos. Ambient temperature also was not always the best predictor of incubation behavior of Orange-Crowned Warblers, a desert-adapted species nesting in extreme heat (Conway and Martin 2000b). Thus, incubation behavior may not prevent exposure of avian nests to suboptimal and lethally hot temperatures as surface air temperatures rise. As predicted by our model, in the absence of shifting nesting phenology or nest-site selection, more avian nests will be exposed to lethally hot temperatures. Exposure to hotter temperatures during an off-bout may also affect average incubation temperatures, since previous work indicates that relatively small differences in attendance patterns when ambient temperatures are extreme can affect developmental rates (Zicus et al. 1995). However, to best understand how local adaptations and behavioral-plasticity of incubation behavior will contribute to population responses to climate change, comparisons are needed across more avian populations, species, and thermal landscapes. When predicting how these effects will shape avian population dynamics, we must relate shifts in behavior to conditions experienced by embryos, and, ideally, to important offspring traits. Currently, more data are needed for species across diverse avian families on temperature-induced phenotypes, temperature-dependent shifts in secondary sex ratios, and whether these effects persist across life stages or generations.

Monitoring incubation behavior of birds and relating this to fine-scale environmental and incubation conditions requires data on incubation patterns, ambient temperature, and egg temperature and can be complicated to analyze. A recently developed program, NestIQ, facilitates analysis of these data, which capitalizes on the flexibility and speed of machine learning algorithms (W. D. Hawkins and S. E. DuRant, manuscript under review). The algorithm in NestIQ detects changes in incubation behavior, and the program overlays these shifts with changes in environmental and egg temperatures. NestIQ and similar tools can aid conservation efforts, because they do not require programming knowledge in order to analyze complicated data sets, and can easily be adapted to diverse incubation scenarios. Such tools are necessary to better understand how animals interact with their environment and predict how disturbance can disrupt behavior.

In studying the connections between the environment, incubation behavior, and population-level processes, avian biologists will achieve two goals. The first benefit is that avian biologists stand to gain a better appreciation of the factors driving ecological and evolutionary processes in birds. Already incubation strategies are thought to play an important role in life history trade-offs (Cooper et al. 2005; Martin 2008, Martin et al. 2007, 2015, 2018), but these studies rarely incorporate the effects of temperature on avian phenotypes as a selecting pressure on avian reproductive traits (but see Martin et al. 2011). The second, more urgent goal is better conservation of avian populations experiencing rapid environmental change. Parental care behaviors are vital to offspring development, phenotype, and fitness; therefore, it is imperative we consider the plasticity of these behaviors and their influence on offspring outcomes when estimating population responses to climate change.

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References

Ackerly DD. 2003. Community assembly, niche conservatism, and adaptive evolution in changing environments. Int J Plant Sci 164:S165–S184.

AlRashidi M. 2016. The Challenge of Coping in an Extremely Hot Environment: a Case Study of the Incubation of Lesser Crested Terns (*Thalasseus bengalensis*). Waterbirds 39:215–21.

AlRashidi M, Kosztolányi A, Shobrak M, Küpper C, Székely T. 2011. Parental cooperation in an extreme hot environment: natural behaviour and experimental evidence. Anim Behav 82:235–43.

Amat JA, Masero JA. 2004. How Kentish plovers, *Charadrius alexandrinus*, cope with heat stress during incubation. Behav Ecol Sociobiol 56:26–33.

Ardia DR, Pérez JH, Chad EK, Voss MA, Clotfelter ED. 2009. Temperature and life history: experimental heating leads female Tree Swallows to modulate egg temperature and incubation behaviour. J Anim Ecol 78:4–13.

Badyaev AV, Uller T. 2009. Parental effects in ecology and evolution: mechanisms, processes and implications. Philos Trans R Soc B 364:1169–77.

Berntsen HH, Bech C. 2016. Incubation temperature influences survival in a small passerine bird. J Av Biol 47:141–145.

Bertin A, Calandreau L, Meurisse M, Georgelin M, Palme R, Lumineau S, Houdelier C, Darmaillacq AS, Dickel L, Colson V, et al. 2018. Incubation temperature affects the expression of young precocial birds' fear-related behaviours and neuroendocrine correlates. Sci Rep 8:1–11.

Bonduriansky R, Crean AJ, Day T. 2012. The implications of nongenetic inheritance for evolution in changing environments. Evol Apps 5:192–201.

Both C, Artemyev AV, Blaauw B, Cowie RJ, Dekhuijzen AJ, Eeva T, Enemar A, Gustafsson L, Ivankina EV, Jarvinen A, et al. 2004. Large-scale geographical variation confirms that climate change causes birds to lay earlier. Proc R Soc Lond B 271:1657–62.

Both C, Bouwhuis S, Lessells CM, Visser ME. 2006. Climate change and population declines in a long-distance migratory bird. Nature 441:81–3.

Both C, van Asch M, Bijlsma RG, van den Burg AB, Visser ME. 2009. Climate change and unequal phenological changes across four trophic levels: constraints or adaptations?. J Anim Ecol 78:73–83.

Brown M, Downs CT. 2003. The role of shading behaviour in the thermoregulation of breeding crowned plovers (*Vanellus coronatus*). J Therm Biol 28:51–8.

Carroll JM, Davis CA, Elmore RD, Fuhlendorf SD. 2015. A ground-nesting galliform's response to thermal heterogeneity: implications for ground-dwelling birds. PLoS One 10:e0143676.

Carroll R, Davis CA, Fuhlendorf SD, Elmore RD, DuRant SE, Carroll JM. 2018. Avian parental behavior and nest success influenced by temperature fluctuations. J Therm Biol 74:140–8.

Chakravarti LJ, Jarrold MD, Gibbin EM, Christen F, Massamba-N'Siala G, Blier PU, Calosi P. 2016. Can trans-generational experiments be used to enhance species resilience to ocean warming and acidification? Evol Appl 9:1133–46.

Chirgwin E, Marshall DJ, Sgrò CM, Monro K. 2018. How does parental environment influence the potential for adaptation to global change? Proc R Soc B Biol Sci 285: 20181374.

Coe BH, Beck ML, Chin SY, Jachowski CMB, Hopkins WA. 2015. Local variation in weather conditions influences incubation behavior and temperature in a passerine bird. J Avian Biol 46:385–94.

Collins KE, Jordan BJ, McLendon BL, Navara KJ, Beckstead RB, Wilson JL. 2013. No evidence of temperature-dependent sex determination or sex-biased embryo mortality in the chicken. Poult Sci 92:3096–102.

Conway CJ, Martin TE. 2000a. Evolution of passerine incubation behavior: influence of food, temperature, and nest predation. Evolution 54:670–85.

Conway CJ, Martin TE. 2000b. Effects of ambient temperature on avian incubation behavior. Behav Ecol 11:178–188.

Cooper CB, Hochachka WM, Butcher G, Dhondt AA. 2005 Seasonal and latitudinal trends in clutch size: Thermal constraints during laying and incubation. Ecology 86:2018–31.

Donelson JM, Munday PL. 2015. Transgenerational plasticity mitigates the impact of global warming to offspring sex ratios. Glob Chang Biol 21:2954–62.

Downs CT, Ward D. 1997. Does shading behavior of incubating shorebirds in hot environments cool the eggs or the adults? Auk 114:717–24. doi: 10.2307/4089291

Dunn PO, Winkler DW. 1999. Climate change has affected the breeding date of tree swallows throughout North America. Proc R Soc Lond B 266:2487–90.

DuRant SE, Moore IT, Hepp GR, Hopkins BC, Hopkins WA. 2010. Slight differences in incubation temperature affect early growth and stress endocrinology of Wood Duck (*Aix sponsa*) ducklings. J Exp Biol 213:45–51.

DuRant SE, Hopkins WA, Hawley DM, Hepp GR. 2012a. Incubation temperature affects multiple measures of immunocompetence in young Wood Ducks (*Aix sponsa*). Biol Lett 8:108–11.

DuRant SE, Hopkins WA, Wilson AF, Hepp GR. 2012b. Incubation temperature affects the metabolic cost of thermoregulation in a young precocial bird. Funct Ecol 26:416–22.

DuRant SE, Hopkins WA, Hepp GR, Walters JR. 2013. Ecological, evolutionary, and conservation implications of incubation temperature-dependent phenotypes in birds. Biol Rev 88:499–509.

DuRant SE, Hawley DM, Carter AW, Kirkpatrick LT, Navara KJ, Hopkins WA. 2016. Incubation temperature causes skewed sex ratios in a precocial bird. J Exp Biol 219:1961–4.

Eiby YA, Wilmer JW, Booth DT. 2008. Temperature-dependent sex-biased embryo mortality in a bird. Proc R Soc B Biol Sci 275:2703–6.

Fisher SA, Bortolotti GR, Fernie KJ, Bird DM, Smits JE. 2006. Behavioral variation and its consequences during incubation for American kestrels exposed to polychlorinated biphenyls. Ecotoxicol Environ Saf 63:226–35.

Guillaume AS, Monro K, Marshall DJ. 2016. Transgenerational plasticity and environmental stress: do paternal effects act as a conduit or a buffer? Funct Ecol 30:1175–84.

Guthery FS. 2000. On Bobwhites. College Station, TX: Texas A & M University Press.

Hanssen SA, Hasselquist D, Folstad I, Erikstad KE. 2005. Cost of reproduction in a long-lived bird: incubation effort reduces immune function and future reproduction. Proc R Soc B 272:1039–46.

Heaney V, Monaghan P. 1996. Optimal allocation of effort between reproductive phases: the trade-off between incubation costs and subsequent brood rearing capacity. Proc R Soc B 263:1719–24.

Henderson CW. 1971. Comparative temperature and moisture responses in Gambel's and Scaled Quail. Condor 73:430–6.

Hepp GR, Kennamer RA. 1993. Effects of age and experience on reproductive-performance of wood ducks. Ecology 74:2027–36.

Hepp GR, Kennamer RA. 2011. Date of nest initiation mediates incubation costs of Wood Ducks (*Aix sponsa*). Auk 128:258–64.

Hepp GR, Kennamer RA. 2012. Warm is better: incubation temperature influences apparent survival and recruitment of Wood Ducks (Aix sponsa) PLoS One 7:1–6.

Hepp GR, Hayes Folk T, Manlove CA. 2005. Nest temperature, incubation period, and investment decisions of incubating Wood Ducks *Aix sponsa*. J Avian Biol 36:523–30.

Hepp GR, Kennamer RA, Johnson MH. 2006. Maternal effects in Wood Ducks: incubation temperature influences incubation period and neonate phenotype. Funct Ecol 20:307–14.

Hoffman AJ, Finger JW, Wada H. 2018. Early stress priming and the effects on fitness-related traits following an adult stress exposure. J Exp Zool Part A Ecol Integr Physiol 329:323–30.

Hope SF, Kennamer RA, Moore IT, Hopkins WA. 2018a. Incubation temperature influences the behavioral traits of a young precocial bird. J Exp Zool Part A Ecol Integr Physiol 329:191–202.

Hope SF, DuRant SE, Beck ML, Hallagan JJ, Kennamer RA, Hopkins WA. 2018b. Free-moving artificial eggs containing temperature loggers reveal remarkable within-clutch variance in incubation temperature. J Avian Biol 49:1–8.

Hopkins BC, Durant SE, Hepp GR, Hopkins WA. 2011. Incubation temperature influences locomotor performance in young Wood Ducks (*Aix sponsa*). J Exp Zool Part A Ecol Genet Physiol 315 A:274–9.

Krackow S. 1995. Potential mechanisms for sex ratio adjustment in mammals and birds. Biol Rev 70:225–41.

Lahti DC, Ardia DR. 2016. Shedding light on bird egg color: pigment as Parasol and the Dark Car Effect. Am Nat 187:547–63.

Love AC, DuRant SE. 2019. Does prior infection shape reproductive investment and parental effects in birds? Integr Comp Biol 59:E141–E141.

Lynn SE, Kern MD. 2017. Ecologically relevant cooling early in life alters prefledging adrenocortical response in free-living songbirds. Physiol Biochem Zool 90:118–23.

Lynn SE, Kern MD. 2018. Interactions of body temperature and nutritional status on hypothalamo-pituitary-adrenal axis activity in pre-thermoregulatory eastern bluebird chicks (*Sialia sialis*). Gen Comp Endocrinol 267:82–9.

Martin TE. 2008. Egg size variation among tropical and temperate songbirds: an embryonic temperature hypothesis. Proc Nat Acad Sci U S A 105:9268–71.

Martin TE, Arriero E, Majewska A. 2011. A trade-off between embryonic development rate and immune function of avian offspring is revealed by considering embryonic temperature. Biol Lett 7:425–428.

Macagno ALM, Zattara EE, Ezeakudo O, Moczek AP, Ledón-Rettig CC. 2018. Adaptive maternal behavioral plasticity and developmental programming mitigate the transgenerational effects of temperature in dung beetles. Oikos 127:1319–29.

Martin TE, Auer SK, Bassar RD, Niklison AM, Lloyd P. 2007. Geographic variation in avian incubation periods and parental influences on embryonic temperature. Evolution (NY) 61:2558–69.

Martin TE, Oteyza JC, Boyce AJ, Lloyd P, Ton R. 2015. Adult mortality probability and nest predation rates explain parental effort in warming eggs with consequences for embryonic development time. Am Nat 186:223–36.

Martin TE, Ton R, Oteyza JC. 2018. Adaptive influence of extrinsic and intrinsic factors on variation of incubation periods among tropical and temperate passerines. Auk 135:101–13.

Maurer G, Portugal SJ, Hauber ME, Mikšík I, Russell DGD, Cassey P. 2015. First light for avian embryos: eggshell thickness and pigmentation mediate variation in development and UV exposure in wild bird eggs. Funct Ecol 29:209–18.

McKechnie AE, Wolf BO. 2010. Climate change increases the likelihood of catastrophic avian mortality events during extreme heat waves. Biol Lett 6:253–6.

Mills JN, Gage KL, Khan AS. 2010. Potential influence of climate change on vector-borne and zoonotic diseases: a review and proposed research plan. Envrion Health Perspect 118:1507–14.

Mousseau TA, Fox CW. 1998. Maternal effects as adaptations. New York: Oxford University Press.

Nassar M, Halle I, Plagemann A, Tzschentke B. 2015. Detection of long-term influence of prenatal temperature stimulation on hypothalamic type-ii iodothyronine deiodinase in juvenile female broiler chickens using a novel immunohistochemical amplification protocol. Comp Biochem Phys 179A:120–4.

Navara KJ. 2013. The role of steroid hormones in the adjustment of primary sex ratio in birds: compiling the pieces of the puzzle. Integr Comp Biol 53:923–37.

Noble DWA, Stenhouse V, Schwanz LE. 2018. Developmental temperatures and phenotypic plasticity in reptiles: a systematic review and meta-analysis. Biol Rev 93:72–97.

Nord A, Williams JB. 2015. The energetic costs of incubation. In: Deeming DC and Reynolds SJ, editors. Nests, eggs, and incubation: new ideas about avian reproduction. Oxford: Oxford University Press. p. 152–70.

Nord A, Nilsson J. 2011. Incubation temperature affects growth and energy metabolism in Blue Tit nestlings. Am Nat 178:639–51.

Nord A, Nilsson J. 2012. Context-dependent costs of incubation in the pied flycatcher. Anim Behav 84:427–36.

Nord A, Nilsson JA. 2016. Long-term consequences of high incubation temperature in a wild bird population. Biol Lett 12.

Noyes PD, McElwee MK, Miller HD, Clark BW, Van Tiem LA, Walcott KC, Erwin KN, Levin ED. 2009. The toxicology of climate change: environmental contaminants in a warming world. Env Int 35:971–86.

O'Neill LG, Parker TH, Griffith SC. 2018. Nest size is predicted by female identity and the local environment in the blue tit (*Cyanistes caeruleus*), but is not related to the nest size of the genetic or foster mother. R Soc Open Sci 5.

Ospina EA, Merrill L, Benson TJ. 2018. Incubation temperature impacts nestling growth and survival in an open-cup nesting passerine. Ecol Evol 8:3270–9.

Oswald SA, Arnold JM. 2012. Direct impacts of climatic warming on heat stress in endothermic species: seabirds as bioindicators of changing thermoregulatory constraints. Integr Zool 7:121–36.

Perez JH, Ardia DR, Chad EK, Clotfelter ED. 2008. Experimental heating reveals nest temperature affects nestling condition in Tree Swallows (*Tachycineta bicolor*). Biol Lett 4:468–71.

Piestun Y, Shinder D, Ruzal M, Halevy O, Brake J, Yahav S. 2008. Thermal manipulations during broiler embryogenesis: effect on the acquisition of thermotolerance. Poult Sci 87:1516–25.

Piestun Y, Halevy O, Yahav S. 2009. Thermal manipulations of broiler embryos-the effect on thermoregulation and development during embryogenesis. Poult Sci 88:2677–88.

Piestun Y, Druyan S, Brake J, Yahav S. 2013. Thermal treatments prior to and during the beginning of incubation affect phenotypic characteristics of broiler chickens post-hatching. Poult Sci 92:882–9.

Reid JM, Monaghan P, Ruxton GD. 2000. Resource allocation between reproductive phases: the importance of thermal conditions in determining the cost of incubation. Proc R Soc B 267:37–41.

Reid JM, Monaghan P, Nager RG. 2002. Incubation and the costs of reproduction. In: Deeming DC, editor. Avian incubation: behavior, environment, and evolution. New York: Oxford University Press. p. 314–25.

Reyna KS, Burggren WW. 2012. Upper lethal temperatures of Northern Bobwhite embryos and the thermal properties of their eggs. Poult Sci 91:41–6.

Shama L. 2015. Bet hedging in a warming ocean: predictability of maternal environment shapes offspring size variation in marine sticklebacks. Glob Chang Biol 21:4387–400.

Snowden R 2018 Least Tern nest thermoregulation in response to environmental temperature and human disturbance (Master's thesis).

So CKJ, Schwanz LE. 2018. Thermal plasticity due to parental and early-life environments in the jacky dragon (*Amphibolurus muricatus*). J Exp Zool Part A Ecol Integr Physiol 329:308–16.

Stoleson SH, Beissinger SR. 1999. Egg viability as a constraint on hatching synchrony at high ambient temperatures. J Anim Ecol 68:951–62.

Tieleman BI, van Noordwijk JF, Williams JB. 2008. Nest site selection in a hot desert: trade-off between microclimate and predation risk. Condor 110:116–24.

Tinbergen JM, Williams JB. 2002. Energetics of incubation. In: Deeming DC, editor. Avian incubation: behaviour, environment, and evolution. New York: Oxford University Press. p. 299–313.

Tzschentke B, Halle I. 2009. Influence of temperature stimulation during the last 4 days of incubation on secondary sex ratio and later performance in male and female broiler chicks. Br Poult Sci 50:634–40.

Uller T, Nakagawa S, English S. 2013. Weak evidence for anticipatory parental effects in plants and animals. J Evol Biol 26:2161–70.

U.S. Environmental Protection Agency. 2015. *Climate CHANGE in the United States: BENEFITS of global action*. United States Environmental Protection Agency, Office of Atmospheric Programs, EPA 430-R-15-001.

U.S. Environmental Protection Agency. 2016. *Climate change indicators in the United States, 2016*. 4th ed. EPA 430-R-16-004.

Vincze O, Kosztolányi A, Barta Z, Küpper C, Alrashidi M, Amat JA, Argüelles Ticó A, Burns F, Cavitt J, Conway WC, et al. 2017. Parental cooperation in a changing climate: fluctuating environments predict shifts in care division. Glob Ecol Biogeogr 26:347–58.

Vincze O, Székely T, Küpper C, AlRashidi M, Amat JA, Ticó AA, Burgas D, Burke T, Cavitt J, Figuerola J, et al. 2013. Local environment but not genetic differentiation influences biparental care in ten plover populations. PLoS One 8.

Wada H, Kriengwatana B, Allen N, Schmidt KL, Soma KK, MacDougall-Shackleton SA. 2015. Transient and permanent effects of suboptimal incubation temperatures on growth, metabolic rate, immune function and adrenocortical responses in zebra finches. J Exp Biol 218:2847–2855.

Wada H, Kriengwatana BP, Steury TD, MacDougall-Shackleton SA. 2018. Incubation temperature influences sex ratio and offspring's body composition in Zebra Finches (*Taeniopygia guttata*). Can J Zool 96:1010–15.

Walsberg GE, Voss-Roberts KA. 1983. Incubation in desert-nesting doves: mechanisms for egg cooling. Physiol Biol Zool 56:88–93.

Webb DR. 1987. Thermal tolerance of avian embryos: a review. Condor 89:874–98.

Willemsen H, Kamers B, Dahlke F, Han H, Song Z, Pirsaraei ZA, Tona K, Decuypere E, Everaert N. 2010. High and low-temperature manipulation during late incubation: effects on embryonic development, the hatching process, and metabolism in broilers. Poult Sci 89:2678–90.

Willemsen H, Li Y, Willems E, Franssens L, Wang Y, Decuypere E, Everaert N. 2011. Intermittent thermal manipulations of broiler embryos during late incubation and their immediate effect on the embryonic development and hatching process. Poult Sci 90:1302–12.

Yilmaz A, Tepeli C, Garip M, Caglayan T. 2011. The effects of incubation temperature on the sex of Japanese quail chicks. Poult Sci 90:2402–6.

Zicus MC, Hennes SK, Riggs MR. 1995. Common goldeneye nest attendance patterns. Condor 97:461–72.