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Impact of Nest Temperature Fluctuations on the Growth and Survival of Bird and Reptile Embryos

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Abstract: *Nests of reptiles and birds that lay eggs show significant temperature variability at various geographical and temporal scales. Temperature affects embryonic growth rates and trajectories, favoring embryo adaptability. Thermal fluctuation may be large inside a nest, between nearby nests, across populations in various climates, and between species with distinct climates and nest characteristics. Temporal thermal regime variation affects nests within a population, between populations, and across species. This temporal and regional temperature variation is increased by human activity. Research on embryos' temporal and spatial nest temperature adaptation is examined. Our study shows multiple cases where natural selection seems to have modified embryogenesis to local heat regimes, despite just a few species having been fully explored and the proximate mechanisms remaining unclear. Developmental rates vary across populations from cooler or warmer regions, between early and late-season eggs, and between the highest and lowest eggs in a nest. We identify early life cycle thermal adaption knowledge gaps and suggest possible research directions.*

Keywords: Adaptive Responses, Bird Embryos, Reptile Embryos, Nest Temperature

I. INTRODUCTION

Because mortality before hatching and the influence of developmental circumstances on offspring phenotypes produce considerable within-population variance among individuals in lifetime reproductive success, the embryo is a crucial stage of life for many species. The eggs of oviparous animals are exposed to ambient circumstances that fluctuate in both abiotic and biotic elements, in contrast to viviparous species where the mother may buffer the influence of external conditions on her offspring. One of the most crucial environmental factors affecting embryonic survival is temperature, which may also significantly alter the phenotypes of the progeny. Despite the buffering effect of maternal nest-site selection, embryos in natural nests encounter ambient temperatures that fluctuate both geographically and temporally. For instance, the mean ambient temperature is greater in the summer than in the spring and tends to decrease with increasing latitude. We anticipate that embryos growing under various thermal settings would display modifications that fine-tune developmental biology to suit local circumstances, given the sensitivity of embryogenesis to external temperature.

We must investigate the developmental correlates of various temperature environments via inter- and intra-specific comparisons at a variety of temporal and geographical dimensions in order to elucidate the adaptive responses of embryos to thermal variation. Such intraspecific and interspecific comparisons across temporal and geographical dimensions have drawn extensive study in post-embryonic phases. However, due to practical considerations and more significantly the fact that embryos have historically been thought of as a passive stage incapable of reacting to environmental changes, the patterns and underlying mechanisms of embryonic responses to environmental variation have received little attention. Nonetheless, a growing body of research indicates that embryos have adaptation mechanisms that allow them to survive and produce viable phenotypes in a variety of environmental settings.

Scope of this Review

Because local meteorological and physical variables are stochastic, the thermal regimes that eggs encounter fluctuate across short temporal and geographical ranges. Because they favor the emergence of developmentally flexible

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responses that alter developmental trajectories in response to short-term temperature stimuli, such stochastic fluctuations may have significant effects on embryonic development. However, over longer periods, temperature changes linked to geographical or temporal shifts or shifts in time remain comparatively constant. We anticipate that in these situations, canalized variance in the mother's choice of nest location and/or embryonic norms of behavior will show evolutionary responses to longer-term local factors.

The present study focuses on these later reactions, which are embryos' adaptations to steady and hence predictable variations in temperature regimes across time and place. In order to encourage further study in the developing subject of temperature adaptation in reptile and avian embryos, we would like to provide an overview of current discoveries in this area. We have selected papers that reflect the taxonomic and geographic diversity of embryonic adaptation examples, rather than trying to thoroughly examine every article on the subject. In order to facilitate discussion, we employ a conceptual framework that acknowledges embryonic adaptations to two scales of temporal variation and three scales of spatial variation in incubation temperatures.

Thermal variation within a nest

The quantity of eggs in a nest may be sufficiently great in species where a female lays a very large clutch to permit a considerable variance in the temperature regimes that each egg experiences. For instance, eggs set deeper in a nest will develop at less variable temperatures than eggs deposited shallower in a nest because diel fluctuation in temperature predictably diminishes with depth below the sun-heated ground surface. Additionally, mean incubation temperatures may change. For instance, in sea turtles and freshwater turtles, eggs in the top and middle parts of the nest were consistently warmer than those at the base and side of the nest. As a result of thermal change at different depths under the soil surface, for instance, temperature clines inside a nest are dependent on a variety of characteristics of the substrate and the nest cavity. In certain freshwater turtles' very tiny and shallow nests, the thermal differences between the highest and lowest eggs are larger than in sea turtles' deeper nests.

For instance, sea turtles Chelonia mydas and Caretta caretta's nests only have a maximum temperature difference of 1.4°C, but the nests of the freshwater turtle Emydura macquarii may have a maximum temperature divergence of 6°C. However, in the latter nests, the large volume of rapidly developing embryonic tissue produces metabolic heat during the second half of the incubation period, contributing to higher temperatures for eggs in the center of the nest compared to those at the periphery and a 1.5–6°C increase in nest temperatures above substrate temperatures. The majority of birds have clutch sizes small enough to reduce temperature variation within the nest, but central eggs may be kept warmer than peripheral eggs due to their closer proximity to parental brood patches that provide heat; this difference can be mitigated if the brooding female moves the eggs around the nest cup. Furthermore, during incubation in a nest, the temperature of the eggs of avian brood parasites, such as cuckoos, is greater than that of the host eggs.

Geographical variation in nest temperatures

(i) Variations among nest-sites within a single region

Even on extremely tiny spatial scales within a single location, many natural habitats are made up of a complex mosaic of temperature conditions. As a result, females' choice of nest location may expose their embryos to varying temperatures. For instance, females of the water python Liasis fuscus and grass snakes Natrix natrix deposit their eggs in two different kinds of nests. The morphological characteristics of the hatchling snakes change in both situations because the two kinds of nest locations provide distinct temperature conditions for growing embryos. The eggs of gregarious weavers have more consistent temperatures, and the older females build their nests in the middle of the communal nesting space. Within an area, nest temperatures might also differ amongst subpopulations. A single island-breeding population of the green turtle Chelonia mydas, for instance, has nest temperatures that differ significantly between two beaches that are only a few kilometers apart because the sand has different physical properties. The snapping turtle Chelydra serpentina nests in natural sites are warmer than those at disturbed sites with a larger proportion of overstory plant cover, and nests in sandy patches are warmer than those in grassy patches.

(ii) Variations among nest-sites due to latitude and elevation

Geographically isolated populations of oviparous animals may exhibit significant differences in embryonic developmental temperatures, which are indicative of local abiotic circumstances. According to field data, nests are generally predicted to be warmer and less varied at lower latitudes. However, such regional variations in nest temperatures may be somewhat offset by variations in maternal behaviors. As shown by certain freshwater turtle populations in high latitudes, where females choose more open nesting locations than do females in low latitudes, such behavioral changes may actually reverse latitudinal tendencies in nest temperature. Similar to the effects of latitude, elevation has an influence on lizards; their montane nests tend to be colder and more variable in temperature than their low-elevation counterparts. Once again, however, nests could be shallower at high altitudes than at low ones, resulting in thermally changeable circumstances that are contrary to the mean air temperature overall. Although parental nest construction and brooding behavior partially mitigate the effects of ambient temperature, nest temperatures generally exhibit similar latitudinal and elevational patterns in birds. For instance, seven species of birds that nest in the Arctic had median incubation temperatures between 33°C and 35°C, which was lower than the nest temperature f the majority of birds from other locations.

Temporal variations in egg temperature

(a) Seasonal variation in nest temperatures

The developmental temperature of embryos is determined by the time of reproduction; nest temperatures exhibit a significant seasonal variation. Reptiles that live in temperate regions have seasonal change in nest temperatures during the reproductive season, in contrast to many reptiles from tropical regions that have high and generally constant ambient temperatures. First, springtime nest temperatures are often colder than summertime ones. Second, during incubation, the temperature of the eggs deposited by early-breeding females in the spring rises, whereas the temperature of the eggs placed by late-breeding females in the summer falls. In contrast, parental incubation behavior buffers the seasonal fluctuation in nest temperatures of facultatively endothermic reptiles and birds. For instance, blue tits on females As the ambient temperature rises, Cyanites caeruleus need less material for the cup lining. Additionally, reptiles may deposit their eggs on the slopes of active volcanoes or within or next to active termite mounds to attain reasonably high incubation temperatures throughout the year.

(b) Nest warming in the context of global change

Many oviparous mammals will nest warmer owing to global warming. The three-lined skink Basina dupery adjusted nest depth and seasonal oviposition to climatic changes, although nest temperatures rose between 1997 and 2006. Climate change will raise tropical sea turtle nest temperatures and lower hatching success. Temperate populations may improve. Rising evidence suggests global warming favors female sea turtles. Man has changed many animal species' environments, including embryo temperature. Urban heat islands may boost mean and severe nest temperatures relative to neighboring natural habitats. Warm snapping turtle eggs in anthropogenically altered habitats with pale soil and little vegetation.

Early female reptile eggs will likely end up in the nest's bottom, where they'll be cooler and more stable. Nest temperature adaptability in embryos. Despite little evidence, this prediction suggests that females may respond to an egg's oviduct location embryonically. Top-layer eggs develop better in hot or fluctuating conditions than bottom-layer eggs. Different temperatures promoted upper-level freshwater turtle Medora Macquarie embryo development, but constant temperatures accelerated lower-level embryo growth. Because the embryos in the top and bottom eggs utilize physiological mechanisms to modify development and reduce incubation, some turtles hatch simultaneously despite nest heat fluctuations.

Within-nest embryos respond differentially to thermal development. Due to enhanced metabolic rates, numerous bird species develop embryos from late-season eggs in a clutch faster, but the methods are unclear. Because the embryo may increase its heart rate in the last weeks, high and low nest eggs may match temperature regimes. Reptile embryonic heat sensitivity variations within-clutch origin unknown. Another concern is whether pre-laying processes like the mother spreading steroids or embryos' developmentally flexible post-oviposition responses generate within-clutch variability. First- and last-laid eggs in a clutch might be compared instead of waiting until the eggs were at different levels. This would indicate if eggs responded facultatively to heat following oviposition.

Regional local variance adjustment Regional phenotypic heterogeneity affects organismal performance at optimum levels. Under the conditions, a population's members may have fitness traits that support lifelong reproduction.

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Location impacts bird and reptile embryo thermal physiology. Regional response to ambient temperature changes likely explains most variation.

Nest temperature differences Substrate type, depth, and shading affect adjacent nest temperatures. Are mothers helping embryos adapt to their nests' abiotic features? A female nesting under shade may produce embryos that survive this temperature. Diamond-backed terrapins To limit seasonal hatching variance, manacles terrapins lay giant eggs in hotter nests and small eggs in cooler nests. Incubation time rises with egg size at typical temperatures. A field experiment that reciprocally transferred eggs across natural nests found no evidence that female Bassiana duperreyi relate nest-site temperature to embryo incubation optima. varied populations may have varied embryo thermal physiologies. Island-nesting green turtles nest on dark-sand beaches, therefore "hot beach" embryos can endure higher temperatures than "cool beach" embryos. Differences are genetic. Geographically varied animals may have nest temperature-embryonic developmental biology. Latitude changes Reactivity standards change to local incubation settings because ambient thermal regimes and embryonic thermal tolerances or optimal development temperatures correlate. Ectotherms' well-studied heat tolerance may determine species distributions and climate change susceptibility. Here, we compare embryos' latitudinal heat tolerance across species and groups. Reduced latitude raises reptile embryonic development lower temperature limits. Different embryonic heat tolerance-latitude connections exist throughout lineages.

Chinese Eumenes skinks' maximum embryonic development temperature reduces at lower latitudes, whereas North American Sceloporus lizards' does not. Every egg stage length feature is selected strongly because incubation periods affect embryo vulnerability to predation and abiotic extremes. High-latitude eggs incubate faster at controlled temperatures in several reptile species because low temperatures impede embryonic development. Faster embryonic growth, thermal adaptation and adjustment at low temperatures, advanced embryogenesis before oviposition, or early hatching but less-developed offspring may shorten incubation durations in high-latitude reptiles. Counter gradient change in incubation period accelerates fence lizard Sceloporus undulatus and Mongolian racerunner Enemies argus, although Gaydoms welter embryonic development is sooner. Different S. undulatus populations have faster or larger hearts, accelerating development. High-latitude embryos cannot heat adapt or hatch early, resulting in slimmer offspring. The incubation period may reverse temperature gradients, complicating matters. High-latitude Asian yellow pond turtles incubated slower in cold temperatures.

Adjusting to seasonal changes Seasonal ecotypes perform better due to changing environmental circumstances. Despite not understanding how embryos respond to seasonal incubation temperature changes, nest temperature fluctuations are predictable signals they may adapt to. Early-breeding females in numerous bird and reptile species produce better-performing and longer-lasting eggs. Early breeding may create a healthier embryonic environment. Seasonal temperature fluctuations may matter. Falling temperatures may cause more lizard infant malformations and impaired mobility than rising nest temperatures. Early- and late-breeding female embryos react differently to seasonal variation. At nest regimes with dropping temperatures, late-breeding females of the toad-headed agamid Pyrocephalus prelawsuit and brown anole Anolis sager grow and survive better. Turtles with environmental sex determination may shift their young's sex ratio by producing yolk estradiol (E2) year-round.

Human-caused nest warming embryonic responses Evolutionary adaptation and phenotypic plasticity may help embryos adapt to human-caused temperature changes. City temperatures boost development compared to woodland nests, however a temporary thermal increase reduces Puerto Rican crested anole lizard embryonic survival. In a western US study of sympatric bird species on an urban-to-rural gradient, modest hatching temperature changes increased nest survival, suggesting mild springtime warming may be beneficial. Global warming may hinder ground-nesting bird reproduction because they leave their eggs unattended for days or weeks before incubation. The logistical limitations of conducting a long-term experiment to explore embryonic thermal physiology alterations due to climate change make embryos' adaptive responses to anthropogenically caused nest warming unusual.

Future perspectives

Out of the heat Although many uncertainties remain, our research gives an overview of how avian and reptile embryos adjust to nest temperature across temporal and geographical dimensions. We know little about how avian and reptile embryos respond to geographically modest nest temperature variations among individuals within a population. Since nesting behavior in female turtles and possibly other reptiles is highly heritable, finding embryonic adaptations to

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thermal environments of nests chosen by their mothers can help us understand between-individual and between-population thermal adaptation variations and their ecological consequences. There is little long-term data on nest temperature and embryo development in any species or group. Few long-term studies have examined the embryonic response to nest temperatures in birds and reptiles such the painted turtle Chryses's pacta and the three-lined skink Basina dupery.

Such data may address embryonic adaptability and ecological and evolutionary biology questions. What are embryos' phenotypic and genetic responses to climate change? How do genetic adaptability and developmental plasticity affect species distribution? In addition to temperature, oxygen, moisture, and predation may affect embryonic fitness and drive adaptive changes in developmental norms of responding. Few studies have examined how embryos respond to environmental factors other than temperature. Variable interactions may be important due of nature's complexity. Hypoxia reduces reptile embryos' heat tolerance. Interactions between biotic and abiotic components enable further study on embryos' nest environmental adaptations.

Environmental influences of embryonic thermal adaptation It is important to know that vertebrate embryos have established several nest temperature responses, but this is only the start. These adaptive responses' ecological ramifications have not been thoroughly described since embryonic responses to environmental changes are hard to test for fitness. We require well-planned, long-term manipulative field studies to determine offspring fitness under ecologically appropriate conditions, yet these are notoriously difficult. However, these adaptive reactions' fitness effects are seldom examined. Long-term fieldwork requires factorial experimental designs that monitor individuals to maturity and quantify fitness.

Biochemical and genetic bases underlying embryonic adaptation

Embryos' molecular, biochemical, and physiological pathways for adapting to environmental changes are yet unknown. Recent advances in physiological and molecular technology provide several techniques to studying embryonic adaptability's proximal mechanisms. Hormones regulate physiological processes in response to environmental stress throughout embryonic and post-embryonic development, therefore understanding their control is essential to defining proximal mechanisms. Changes in thyroid hormone levels may influence mitochondrial density and function and embryo development. Multi-omics profiling may also identify heat variance's genetic response. Through de novo transcriptome profiling, ecologists have found several genes connected to heat tolerance or embryo harm in embryonic sea turtles subjected to physiologically relevant thermal pressures. As NGS techniques grow cheaper, evolutionary biologists studying non-model species will have greater access to these methodologies. Finding the genes behind heat adaptation is crucial to understanding its molecular mechanisms. Gene function in model species has been widely examined utilizing transgenic technology, but non-model animals are problematic. Other approaches to modulate gene expression include vector-mediated gene transfer and RNA interference. The proximal pathways that underlie embryonic plasticity are exciting for future research.

II. CONCLUSION

Oviparous embryos are immediately exposed to the nest, thus they experience temperature fluctuations across time and distance. Some nest temperature changes are predictable and may induce embryo adaptation. Large-scale and small-scale nest temperature changes are predictable. Nest temperatures grow with global warming, decline from summer to autumn, and climb from spring to summer. Latitude, height, and nest depth lower nest temperature. Early or late eggs implanted in the season; chilly or warm-climate eggs may affect embryos' physiology, such as development pace and heat tolerance. Finding embryos' adaptive physiological responses to complex temporal and spatial nest temperature fluctuations remains difficult. With the fast advancement of molecular technologies like multi-omics and gene editing, the proximal stages of embryonic adaption provide many exciting research opportunities. Understanding this topic can assist plan conservation and management by identifying high-priority species and populations and anticipating their sensitivity to global change. It will also illuminate how abiotic forces choose biological traits in an understudied life-history stage.

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