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Photoperiodic Hatching Rhythms Suggest Circadian Entrainment of *Anolis sagrei* Eggs

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Abstract.—**Synchronous hatching occurs in many reptiles that lay multi-egg clutches, but this phenomenon and its potential environmental cues are poorly documented for species that lay their eggs singly, such as *Anolis* lizards. We tested for a circadian hatching rhythm in 196 Brown Anole (*Anolis sagrei*) eggs maintained in social isolation under a 12 : 12 L : D photoperiod with constant temperature and humidity. Hatching occurred exclusively in the morning and was approximately normally distributed around the transition from dark to light, with most (94%) eggs hatching ±1 hour from the onset of light. Hatching times differed significantly between sexes, such that most males hatched after the onset of light (71%), whereas only half of all females hatched after the onset of light (52%). That a substantial proportion of eggs (38% across sexes) hatched in the dark suggests circadian entrainment to photoperiod, rather than a direct behavioral response to light. Whether this reflects a natural circadian rhythm of hatching or an artifact of increased light exposure in our artificial incubation environment is presently unknown. If this circadian rhythm of hatching is a natural phenomenon, then its potential fitness benefits (e.g., optimal timing for predator avoidance, prey detection, water balance, or thermoregulation) warrant further attention.**

Synchronization of hatching in response to light or photoperiod occurs in diverse taxa, including insects (Minis and Pittendrigh, 1968; Lazzari, 1991; Sakamoto and Shimizu, 1994; Itoh and Sumi, 2000), crustaceans (Branford, 1978; Forward and Lohmann, 1983; Forward et al., 1986; Forward, 1987), and monogenean parasites (Gannicott and Tinsley, 1997). This can arise from circadian entrainment of an endogenous biological clock to exogenous light cues (Minis and Pittendrigh, 1968; Lazzari, 1991; Sakamoto and Shimizu, 1994; Itoh and Sumi, 2000) or from a direct response to exogenous light cues without establishment of an endogenous rhythm (Gannicott and Tinsley, 1997). Hatching is often synchronized at or near the light-phase transition, although this can occur at the transition into either light or dark, depending upon the ecology of the species (Gannicott and Tinsley, 1997; Itoh and Sumi, 2000). Despite its prevalence in other taxa, photoperiodic regulation of hatching has received relatively little attention in reptiles, presumably because the eggs of many species are buried at depths that shelter them from light.

Among oviparous reptiles, environmental cues influence hatching in turtles, crocodilians, lizards, snakes, and tuatara (Doody, 2011); however, evidence for precise temporal synchronization of hatching is restricted primarily to turtles and crocodilians (Doody, 2011). Because most turtles bury their clutches at considerable depths, hatching and emergence tend to be synchronized by temperature, hypoxia, and cues from other eggs and hatchlings, rather than light cues (Spencer et al., 2001; Colbert et al., 2010; Doody et al., 2012; Spencer, 2012). Likewise, crocodilians synchronize hatching via vocal cues from nestmates, which also signal the mother to excavate the nest (Lee, 1968; Vergne and Mathevon, 2008).

In contrast to turtles and crocodilians, *Anolis* lizards often bury their eggs at shallow depths or in sites potentially exposed to light cues, such as the undersides of decaying bark and logs, in leaf litter, under small rocks, in tree holes and rock crevices, or in bromeliads and other vegetation (Rand, 1967; Andrews, 1982; Losos, 2009). All anoles lay one or two eggs at a time, although some species deposit their eggs in communal nesting sites, and emergence from these communal nests may be synchronous (Rand, 1967; Andrews and Rand, 1974; Losos, 2009). Collectively, these observations suggest that light cues often may be perceptible to *Anolis* eggs, whereas cues from other eggs or hatchlings are typically reduced or absent, at least in species that do not nest communally. Also, anoles have a photosensitive pineal complex (pineal gland and parietal eye) that produces a circadian rhythm of melatonin secretion (Underwood and Menaker, 1976; Menaker and Wisner, 1983; Underwood, 1983, 1985; Tosini et al., 2001). The pineal complex develops early in lizard development and, at least in other oviparous vertebrates, is capable of regulating circadian rhythms in melatonin secretion well before hatching (Akasaka et al., 1995; Faluhelyi et al., 2004). Therefore, light cues could potentially regulate the timing of hatching in *Anolis* eggs through circadian entrainment of embryos.

To our knowledge, the only data addressing this possibility come from a study of hatching and neonatal behavior in the Green Anole, *Anolis carolinensis* (Greenberg and Hake, 1990). In that study, 97% of hatchlings emerged between 1000 and 1200 h when eggs were unburied and exposed to light under a 14 : 10 L : D photoperiod and constant 30°C temperature. Timing of the transition from dark to light was not reported for that experiment, but a similar daily rhythm in hatching was observed even when eggs were incubated under constant dim light (Greenberg and Hake, 1990). Although the eggs in that study were not in physical contact with one another, they were housed communally in a single vivarium, raising the possibility that social cues may have contributed to the observed daily rhythm of hatching. In this study, we tested for photoperiodic hatching rhythms by incubating eggs from a congener (*Anolis sagrei*, Brown Anole) in social isolation and under a constant 12 : 12 L : D photoperiod at a constant temperature of 28°C.

Materials and Methods

The Brown Anole, *Anolis* (*Norops*) *sagrei* Duméril and Bibron (1837), is a small dactyloid lizard native to Cuba, the Bahamas, and surrounding islands. In January 2012, we collected approximately 100 adult females and 50 adult males from each of two islands in the Commonwealth of the Bahamas: near Georgetown on Great Exuma (23°29′N, 75°45′W), and near the Island School on Eleuthera (25°06′N, 76°08′W). We imported these adults to our breeding facility at the University of Virginia and housed them individually in small terraria (Lee's Kritter

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Keepers, Pet Mountain, Inc., San Diego, CA) containing a potted plant, a carpet substrate, a section of PVC pipe (30 × 2.5 cm), and a strip of fiberglass porch screen suspended across the top of the cage as a perch. We placed each cage beneath two ReptiSun 10.0 UVB bulbs (ZooMed, San Luis Obispo, CA) and maintained constant temperature (29°C), relative humidity (65%), and photoperiod (13 : 11 L : D from March through October, transition to light at 0800 h; 12 : 12 L : D from November through February, transition to light at 0900 h) via programmed vivarium settings. Three times per week, we offered males 5–7 large (1/2 inch) crickets and females 3–5 medium (3/8 inch) crickets (*Gryllus assimilis* and *Gryllodes sigillatus*; Ghann's Cricket Farm, Augusta, GA), dusted weekly with Fluker's Reptile Vitamin and Calcium supplements (Fluker's Cricket Farms, Port Allen, LA). We manually and daily sprayed cage walls and potted plants with deionized water.

In April 2012 and again in August 2012 and April 2013, we mated each female to a single male from the same population and then allowed her to oviposit repeatedly in her potted plant over an ensuing five-month period. In captivity, females from these populations lay one or two eggs at a time at an overall mean interval of about 11 days between successive eggs (Cox et al., 2009). In the wild, *A. sagrei* females may bury their eggs or place them on the soil surface beneath small cover objects (Delaney et al., 2013). In captivity, females typically bury their eggs in potted plants within several centimeters of the soil surface; occasionally, eggs are visible in the clustered stems or roots of potted plants. Each week, we searched the pot in each cage, removed any new eggs, and transferred the eggs to individual plastic cups containing vermiculite and deionized water (mixed 1 : 1 by weight). We placed each egg in a small indentation in the surface of the vermiculite, such that the upper half of the egg was exposed to light. We did not note the orientation of the egg prior to transfer, and we did not disturb eggs after placing them in vermiculite. Each cup was fitted with a transparent lid with pinholes for ventilation. Cups were nested in plastic bins that were placed on racks within two synchronized incubators (Percival Intellus 136VL) set to maintain 12 : 12 L : D photoperiod (transition to light at 0900 h), 28°C temperature, and 80% relative humidity. Mean (± SD) incubation time was 34.6 ± 2.5 days from placement in the incubators (which occurred 0–7 days after oviposition) to hatching.

During 2012, we checked each egg container twice daily for hatchlings, once between 0800 and 1200 h and once between 1600 and 2000 h. We anecdotally noted that, when the morning census occurred early in the 0800–1200 h time frame, relatively few hatchlings were found in the morning and more were found in the afternoon. Conversely, when the morning census occurred later in the 0800–1200 h timeframe, relatively more hatchlings were found in the morning and few, if any, were found in the afternoon. Therefore, we hypothesized that hatching is concentrated in the early morning, potentially at or near the transition from dark to light at 0900 h. In 2013, we tested this hypothesis by recording hatch times in 30-min intervals spanning 0800–1200 h and bracketing the onset of light at 0900 h. We obtained data on hatching times of 196 individual eggs that were laid between April and June 2013 and hatched between May and July 2013. We defined "hatching" as the complete emergence of hatchlings from eggs (Greenberg and Hake, 1990). We predicted: 1) if hatching is synchronized in the early morning, then hatch times should be nonrandomly distributed between 0800 and 1200 h with a peak near the onset of light at 0900 h; 2) if hatching is regulated by a direct response to light cues, then few (if any) eggs should hatch in the dark; whereas 3) if hatching is regulated by circadian entrainment to photoperiod, then the distribution of hatching times should be approximately normal and could extend into the dark phase of the light cycle.

We tested for nonrandom distributions of hatching time using χ^2-tests against null hypotheses that hatchings were equally distributed across sampling intervals or between light and dark phases. We tested for deviations of hatching time from normal distributions using Kolmogorov–Smirnov and Shapiro–Wilk normality tests. We tested for sex and population differences in hatching times by binning hatching times and then using ordinal logistic (30-min bins) or logistic (light and dark bins) regressions.

Results

Hatching times were not randomly distributed across 30-min measurement intervals, even when omitting the final two intervals between 1100 and 1200 h, in which no hatching occurred ($\chi^2 = 191.27$; df = 6; $P < 0.0001$; Fig. 1A). Instead, hatching peaked in the 30-min interval following the onset of light (45% of hatchings). The distribution of observations around this peak did not differ significantly from Gaussian (KS = 0.28; $P > 0.10$; W = 0.83; $P = 0.081$). Nearly all hatching (94%) occurred within ±1 h of the onset of light. Significantly more eggs hatched in light (62%) than in dark (38%) ($\chi^2 = 10.80$; df = 1; $P = 0.001$; Fig. 1B). Hatching time did not differ as a function of source population (Exuma or Eleuthera) when comparing the overall distribution across 30-min bins ($\chi^2 = 1.99$; $P = 0.16$) or when dichotomizing hatching as occurring in either dark or light ($\chi^2 = 2.94$; $P = 0.086$).

The sex ratio of hatchlings was approximately 1 : 1, with 97 eggs hatching as females and 98 as males (1 hatchling was not sexed). The distribution of hatching times differed significantly between sexes ($\chi^2 = 9.68$; $P = 0.002$), with the distribution of males strongly centered on the first 30-min interval after the transition to light and that of females shifted toward slightly earlier hatch times (Fig. 1C). Although relatively few (29%) males hatched in the dark, nearly half (48%) of the females hatched in the dark (Fig. 1D), a highly significant difference ($\chi^2 = 8.00$; $P = 0.005$). Within each sex, males were significantly more likely to hatch after the onset of light ($\chi^2 = 18.00$; df = 2; $P < 0.001$), but females exhibited no bias with respect to light or dark ($\chi^2 = 0.09$; df = 2; $P > 0.75$).

Discussion

Eggs of *A. sagrei* displayed a pronounced daily rhythm of hatching when incubated under a 12 : 12 L : D photoperiod (Fig. 1). Hatching was concentrated at the morning transition from dark to light (0900 h) and frequently occurred both before and after this transition. This rhythm was observed even when eggs were incubated in isolation and at a constant temperature and humidity. Collectively, these results strongly imply that social cues are not required for hatching synchrony and that light cues can stimulate hatching, either directly and/or indirectly, through endogenous circadian entrainment. We note, however, that a previous study of a congener, *A. carolinensis*, reported a similar daily rhythm of hatching times under both 14 : 10 L : D photoperiod and constant dim light (Greenberg and Hake, 1990). This raises the possibility that a regular photoperiod is

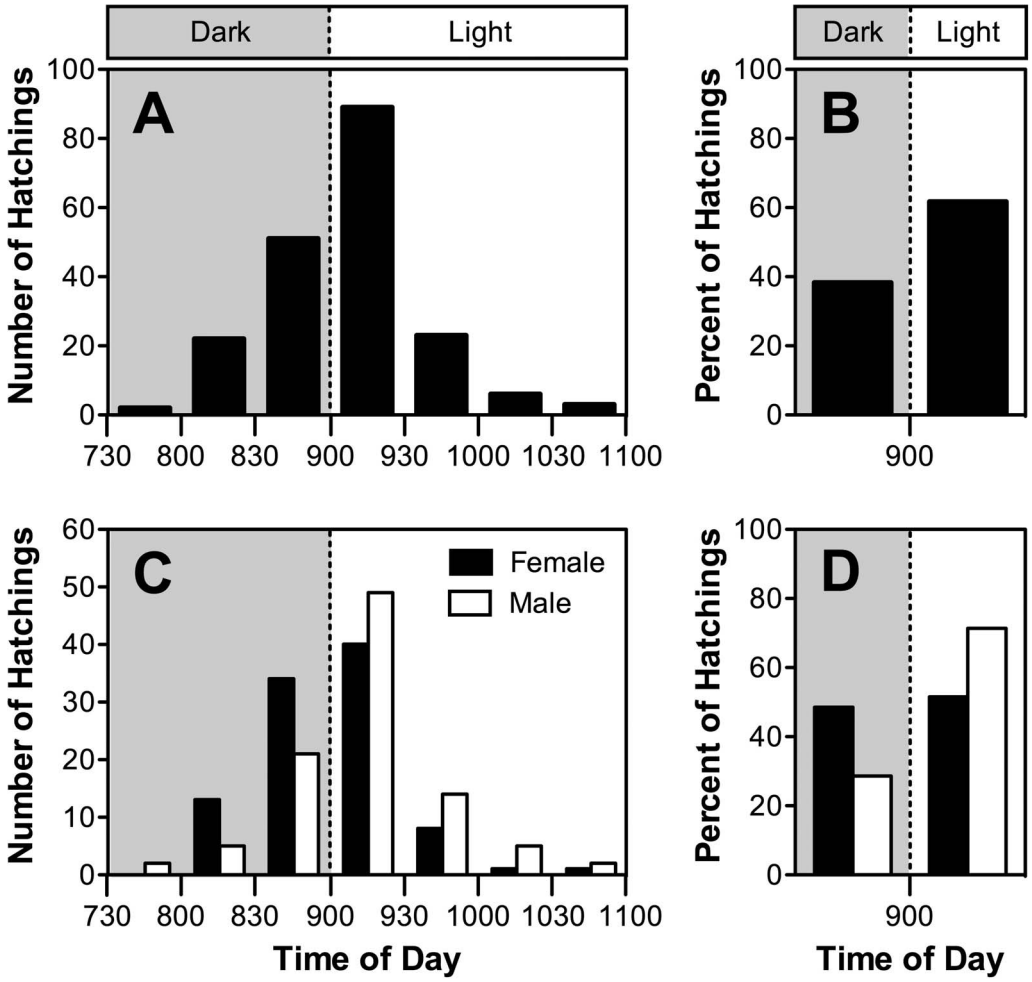

FIG. 1. Distribution of hatching times in *Anolis sagrei* eggs incubated under 12 : 12 L : D photoperiod. (A) Number of hatchlings observed in each of seven 30-min intervals bracketing the transition from dark to light at 0900 h, with two final intervals from 1100–1200 omitted because no hatchlings were observed at those times. (B) Percent of hatchlings observed before and after the transition from light to dark. (C–D) Panels analogous to A and B, with hatching times reported separately for males and females, illustrating sex differences in hatching times.

neither involved in nor required for circadian hatching rhythms. Nonetheless, the tight clustering of hatching times around the transition from dark to light in our experiment (Fig. 1) strongly implicates light cues.

Although we cannot unambiguously demonstrate that daily rhythm of hatching in *A. sagrei* results from an endogenous circadian rhythm, two lines of evidence indirectly support this interpretation. First, although significantly more eggs hatched after the onset of light, a substantial proportion (38%) hatched in the dark. We might expect this pattern because of variance in the intrinsic circadian period or in the precision of circadian entrainment, but it is inconsistent with the hypothesis that light cues directly stimulate hatching. Second, we classified hatching as the time at which the entire lizard emerged from the egg. In *A. carolinensis*, complete emergence is typically preceded by 30 min or more of activity that includes initial rupture of the eggshell, movement within the egg, emergence of the head, and scanning of the environment (Greenberg and Hake, 1990). If these behaviors and their timelines are comparable in *A. sagrei*, this would suggest that actual initiation of activity within the egg may occur well prior to the onset of light (i.e., the onset of activity associated with hatching may be shifted approximately one interval to the left of the distributions of emergence times in Fig. 1A,C). We rarely noted rupture of an eggshell or exposure of a head prior to the interval in which emergence occurred and hatching was scored, however, suggesting that hatching may typically occur more quickly in *A. sagrei*.

One caveat to each of the above arguments is that we may have introduced some sensory and/or low-intensity light cues (dim ambient room lights) when sliding each bin of egg containers out of the incubator and briefly scanning for hatchlings prior to the onset of the actual light phase within the incubator. This could have led us to overestimate the extent to which hatching would otherwise occur in the dark; however, this caveat cannot account for our initial observations in 2012, in which containers were not repeatedly disturbed, that also supported a rhythmic pattern of hatching in the early morning. Moreover, in these initial observations and our subsequent, detailed descriptions of hatch times, we repeatedly observed emergence in darkness prior to any disturbance by light or sensory cues. Nonetheless, the daily hatching rhythms we document are largely descriptive, and further experiments are required to conclusively determine whether hatching rhythmicity in *A. sagrei* is primarily attributable to circadian entrainment, direct response to light cues, or other confounding factors.

Although hatching was tightly clustered around the transition from dark to light in both sexes, females tended to hatch slightly earlier than did males (Fig. 1C). Whereas males hatched

predominantly after the transition to light, females exhibited no bias with respect to light phase (Fig. 1D). We did not have any a priori expectation that hatching times would differ between the sexes, but the differences we observed were highly significant. Nonetheless, it is difficult to imagine that a relatively minor offset in timing of hatching between males and females (Fig. 1C) has pronounced fitness consequences. Sex differences in circadian rhythms of various biological functions have been documented in other species, and data from mammals generally indicate a shorter free-running circadian period and earlier daily initiation of entrained activity in females, relative to males (Davis et al., 1983; Schull et al., 1989; Duffy et al., 2011). This is broadly consistent with our observation that *A. sagrei* females hatched earlier than males.

Although the artificial conditions in our study likely exposed eggs to a much higher intensity of light than would be typical in a natural environment, that many anoles bury their eggs at shallow depths, in vegetation or tree hollows, and under small cover objects and leaf litter suggests some photic cues may be perceptible to *Anolis* eggs in nature. If photoperiodic hatching rhythms also occur under natural conditions, this would raise the question of whether this phenomenon is adaptive in *A. sagrei*. In reptiles that bury their multi-egg clutches at considerable depth, synchrony of hatching or emergence may facilitate successful escape from the nest (Andrews, 2004). This benefit is unlikely to apply to *A. sagrei*, which typically lays its single eggs at or near the soil surface. In turtles, synchrony in hatching and emergence, which often occurs nocturnally, is an ancestral trait thought to have evolved to reduce predation, although it may have secondarily acquired other adaptive functions (Colbert et al., 2010). Although synchronized emergence may aid some lizards in avoiding or confusing predators (Burghardt, 1977), benefits of "predator satiation" through sheer numbers of emerging hatchlings are unlikely to accrue to most lizards (Andrews, 2004). Given that hatching Brown Anoles are presumably dispersed in space because of their iterative, single-egg clutches, predator satiation seems unlikely as an explanation for restricting hatching to a particular time of day. Also, predation could favor diurnal hatching for other reasons (e.g., by facilitating visual detection of predators or allowing hatchlings to attain body temperatures that maximize their ability to evade predators; Christian and Tracy, 1981). More generally, emergence in the early morning could facilitate a suite of outcomes conducive to offspring survival by providing a favorable thermoregulatory environment, minimizing water loss during the hottest and driest parts of the day, and permitting immediate foraging, for which anoles rely primarily on visual cues. Alternatively, photoperiodic hatching rhythms could be an indirect consequence of circadian rhythms that are subsequently adaptive for regulating the daily activity period of free-living juveniles and adults but adaptively neutral with respect to hatching time per se. If photoperiodic rhythms and circadian entrainment of hatching are natural phenomena in *Anolis* and other reptiles, we suggest their potential fitness benefits warrant further attention.

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Literature Cited

Akasaka, K., T. Nasu, T. Katayama, and N. Murakami. 1995. Development of regulation of melatonin release in pineal cells in chick embryo. Brain Research 692:283–286.

Andrews, R. M. 1982. Spatial variation in egg mortality of the lizard *Anolis limifrons*. Herpetologica 38:165–171.

———. 2004. Patterns of embryonic development. Pp. 75–102 in D. C. Deeming (ed.), Reptilian Incubation: Environment, Evolution and Behaviour. Nottingham University Press, UK.

Andrews, R. M., and A. S. Rand. 1974. Reproductive effort in anoline lizards. Ecology 55:1317–1327.

Branford, J. R. 1978. The influence of daylength, temperature and season on the hatching rhythm of *Homarus gammarus*. Journal of the Marine Biological Association of the United Kingdom 58:639–658.

Burghardt, G. M. 1977. Of iguanas and dinosaurs: social behavior and communication in neonate reptiles. American Zoologist 17:177–190.

Christian, K., and C. R. Tracy. 1981. The effect of the thermal environment on the ability of hatchling Galapagos land iguanas to avoid predation during dispersal. Oecologia 49:218–223.

Colbert, P. L., R.-J. Spencer, and F. J. Janzen. 2010. Mechanism and cost of synchronous hatching. Functional Ecology 24:112–121.

Cox, R. M., D. S. Stenquist, and R. Calsbeek. 2009. Testosterone, growth, and the evolution of sexual size dimorphism. Journal of Evolutionary Biology 22:1586–1598.

Davis, F. C., J. M. Darrow, and M. Menaker. 1983. Sex differences in the circadian control of hamster wheel-running activity. American Journal of Physiology–Regulatory, Integrative and Comparative Physiology 244:R93vR105.

Delaney, D. M., A. M. Reedy, T. S. Mitchell, A. M. Durso, K. P. Durso, A. J. Morrison, and D. A. Warner. 2013. *Anolis sagrei* (brown anole). Nest-site choice. Herpetological Review 44:314.

Doody, J. S. 2011. Environmentally cued hatching in reptiles. Integrative and Comparative Biology 51:49–61.

Doody, J. S., B. Stewart, C. Camacho, and K. Christian. 2012. Good vibrations? Sibling embryos expedite hatching in a turtle. Animal Behaviour 83:645–651.

Duffy, J. F., S. W. Cain, A.-M. Chang, A. J. K. Phillips, M. Y. Münch, C. Gronfier, J. K. Wyatt, D.-J. Dijk, K. P. Wright, and C. A. Czeisler. 2011. Sex difference in the near–24-hour intrinsic period of the human circadian timing system. Proceedings of the National Academy of Sciences 108:15602–15608.

Duméril, A. M. C., and G. Bibron. 1837. Erpétologie Générale ou Histoire Naturelle Complete des Reptiles. Roret, France.

Faluhelyi, N., D. Reglödi, I. Lengvári, and V. Csernus. 2004. Development of the circadian melatonin rhythm and the effect of PACAP on melatonin release in the embryonic chicken pineal gland. An in vitro study. Regulatory Peptides 123:23–28.

Forward, R. B., Jr. 1987. Larval release rhythms of decapod crustaceans: an overview. Bulletin of Marine Science 41:165–176.

Forward, R. B., Jr., and K. J. Lohmann. 1983. Control of egg hatching in the crab *Rhithropanopeus harrisii* (Gould). Biological Bulletin 165:154–166.

Forward, R. B., Jr., J. K. Douglass, and B. E. Kenney. 1986. Entrainment of the larval release rhythm of the crab *Rhithropanopeus harrisii* (Brachyura: Xanthidae) by cycles in salinity change. Marine Biology 90:537–544.

Gannicott, A. M., and R. C. Tinsley. 1997. Egg hatching in the monogenean gill parasite *Discocotyle sagittata* from the rainbow trout (*Oncorhynchus mykiss*). Parasitology 114:569–579.

Greenberg, N., and L. Hake. 1990. Hatching and neonatal behavior of the lizard, *Anolis carolinensis*. Journal of Herpetology 24:402–405.

Itoh, M. T., and Y. Sumi. 2000. Circadian clock controlling egg hatching in the cricket (*Gryllus bimaculatus*). Journal of Biological Rhythms 15: 241–245.

LAZZARI, C. R. 1991. Circadian rhythm of egg hatching in *Triatoma infestans* (Hemiptera: Reduviidae). Journal of Medical Entomology 28:740–741.

LEE, D. S. 1968. Possible communication between eggs of the American alligator. Herpetologica 24:88.

LOSOS, J. B. 2009. Lizards in an Evolutionary Tree: Ecology and Adaptive Radiation of Anoles. University of California Press, USA.

MENAKER, M., AND S. WISNER. 1983. Temperature-compensated circadian clock in the pineal of *Anolis*. Proceedings of the National Academy of Sciences 80:6119–6121.

MINIS, D. H., AND C. S. PITTENDRIGH. 1968. Circadian oscillation controlling hatching: its ontogeny during embryogenesis of a moth. Science 159:534–536.

RAND, A. S. 1967. Communal egg laying in anoline lizards. Herpetologica 227–230.

SAKAMOTO, K., AND I. SHIMIZU. 1994. Photosensitivity in the circadian hatching rhythm of the carotenoid-depleted silkworm, *Bombyx mori*. Journal of Biological Rhythms 9:61–70.

SCHULL, J., J. WALKER, K. FITZGERALD, L. HIILIVIRTA, J. RUCKDESCHEL, D. SCHUMACHER, D. STANGER, AND D. L. MCEACHRON. 1989. Effects of sex, thyro-parathyroidectomy, and light regime on levels and circadian rhythms of wheel-running in rats. Physiology and Behavior 46:341–346.

SPENCER, R. J. 2012. Embryonic heart rate and hatching behavior of a solitary nesting turtle. Journal of Zoology 287:169–174.

SPENCER, R.-J., M. B. THOMPSON, AND P. B. BANKS. 2001. Hatch or wait? A dilemma in reptilian incubation. Oikos 93:401–406.

TOSINI, G., C. BERTOLUCCI, AND A. FOÀ. 2001. The circadian system of reptiles: a multioscillatory and multiphotoreceptive system. Physiology and Behavior 72:461–471.

UNDERWOOD, H. 1983. Circadian organization in the lizard *Anolis carolinensis*: a multioscillator system. Journal of Comparative Physiology 152:265–274.

———. 1985. Pineal melatonin rhythms in the lizard *Anolis carolinensis*: effects of light and temperature cycles. Journal of Comparative Physiology A 157:57–65.

UNDERWOOD, H., AND M. MENAKER. 1976. Extraretinal photoreception in lizards. Photochemistry and Photobiology 23:227–243.

VERGNE, A. L., AND N. MATHEVON. 2008. Crocodile egg sounds signal hatching time. Current Biology 18:R513–R514.

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