visual area, corresponds very closely in location to the medial area in the owl monkey. Our interpretation of Martinez-Millan and Hollander's results is that there may exist a projection from the peripheral parts of the first visual area to the medial area and that this projection may be related to the relatively large representation of the more peripheral portions of the visual field in the medial area (*10*). In addition, there exist other probable projections to the medial area from the middle temporal area and the dorsomedial area. Spatz and Tigges (*11*) found in marmosets that the middle temporal area projects to a zone on the medial wall of occipital-parietal cortex (their focus 6), which corresponds very closely in location to the medial area, and Wagor *et al.* (*11*) found in the owl monkey that the dorsomedial area projects to the medial area.

Adjoining the anterior border of the second visual area are four visual areas: the dorsolateral crescent, the dorsointermediate area, the dorsomedial area, and the medial area. Collectively these areas comprise a *third tier* of cortical visual areas with the primary visual area (V I) constituting the first tier and V II the second tier. In the third tier, the relative proportion of each area devoted to the central versus the more peripheral portions of the visual field differs greatly from area to area. In the dorsolateral crescent, approximately 75 percent of the area is devoted to the portion of the visual field within 10° of the center, while only about 4 percent of the medial area is devoted to the same portion of the visual field within 10° of the center. These differences in visuotopic organization in the *third tier* suggest that in the dorsolateral crescent, which emphasizes central vision, functions in which central vision is important, such as form perception, may predominate, while in the medial area, where the more peripheral parts of the visual field are much better represented, functions in which peripheral vision is important, such as motion perception or orientation in space, may predominate.

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10. It is unlikely that these projections from the first visual area were to the peripheral parts of a single representation corresponding to area 19 with a visuotopic organization the mirror image of area 18 (second visual area). Martinez-Millan and Hollander (*8*) found that an injection in the first visual area deep in the calcarine sulcus resulted in a projection focus in area 18 on the *lower* bank of the calcarine sulcus, but the additional projection focus, which resulted only from peripheral first visual area injections, was on the medial wall *above* the *upper* bank of the calcarine sulcus. If area 19 were organized as the mirror image of area 18, such as it is in the cat [D. H. Hubel and T. N. Wiesel, *J. Neurophysiol.* **28**, 229 (1965); R. Tusa, *Anat. Rec.* **181**, 497 (1975)], then it would be expected that both projection foci would be located on the *lower* bank of the calcarine sulcus [see Martinez-Millan and Hollander's figures 6 and 19 in (*8*)].
11. W. B. Spatz and J. Tigges, *J. Comp. Neurol.* **146**, 451 (1972); E. Wagor, C. S. Lin, J. H. Kaas, *ibid.* **163**, 227 (1975). If only the peripheral parts of the first visual area project to the medial area, then the small representation of the central visual field in the medial area must receive its input from another source, such as the dorsomedial area or the middle temporal area.
12. The experiments reported in this study were conducted at the Department of Neurophysiology, University of Wisconsin. We thank Dr. Leon Schmidt, Southern Research Institute, Birmingham, Alabama, for providing the owl monkeys. Dr. R. H. Lane and Mr. F. M. Miezin assisted in some of the data collection. Histological materials were prepared by Mrs. I. Lucey and Mrs. J. Eckleberry. Figures were drawn by Ms. D. Urban. This work was supported by NIH grants NS-05236, NS-06225, and NS-12131; NSF grant GB-36779; and an Alfred P. Sloan fellowship to J.M.A. A brief abstract of this work was published in *Anat. Rec.* **178**, 297 (1974).

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Amphibious Behavior of *Alligator mississippiensis*: Roles of a Circadian Rhythm and Light

Abstract. *Juvenile American alligators in outdoor pens moved out of and into the water at sunrise and sunset, respectively. When the natural light cycle was extended with artificial illumination, these movements gradually shifted into phase with the altered light cycles; therefore, the amphibious behavior was modulated by a circadian rhythm cued by light. Movement between land and water was characterized by a decrease in body temperature, which suggests that it was not simply a proximate heat-seeking response. After the movements had been in phase with the altered light cycles for a time, they spontaneously shifted back into phase with the natural light cycle. A changing response to light is viewed as an adaptation to seasonal changes in heat availability.*

Crocodilians utilize both aquatic and terrestrial habitats during a 24-hour cycle. Typically, they spend much of the day on land and are in the water at night. In nature, Nile crocodiles (*Crocodylus niloticus*) move with regularity out of the water at sunrise and into the water at sunset (*1, 2*). Searching for the basis of this behavior, Cloudsley-Thompson noted a daily rhythm of activity in two captive Nile crocodiles (*3*). Although he referred to this rhythm of activity as circadian, as yet no evidence has been presented to substantiate the endogenous nature of the response or to identify a periodic environmental factor that might serve as a time cue, or zeitgeber.

Here I present evidence that the amphibious behavior of juvenile alligators is regulated by an internal circadian rhythm, that light is an important zeitgeber, and that an alligator's response to light is adaptable. Although alligators are poikilothermic reptiles, their daily cycle of behavior may be governed proximally by a light-cued circadian rhythm rather than by temperature.

I studied recently captured alligators (*Alligator mississippiensis*) under seminatural conditions. Juvenile alligators were caught in Lake Okeechobee and Lake Hicpochee near Moore Haven, Florida, in July 1972 ($N = 30$), and October 1973 ($N = 30$). They weighed 0.8 to 3.8 kg, measured 68 to 114 cm in length, and were probably 2 to 4 years old (*4*). The alligators were marked individually and maintained in two identical outdoor pens (*5*) at the Archbold Biological Station, Lake Placid, Florida (50 km northwest of the capture site). Air and water temperatures were monitored continuously in one pen. Body temperatures (T_b) were taken at varying times of the day (*6*).

The alligators were observed in the natural light-dark (LD) cycle during July and August 1972, and under natural and experimentally altered LD cycles during October and November 1973. Hourly observations were made between 0400 and 1000 (E.S.T.) and 1700 and 2400 to determine whether individual animals were on land or in the water (*7*).

In the natural photoperiod, alligators

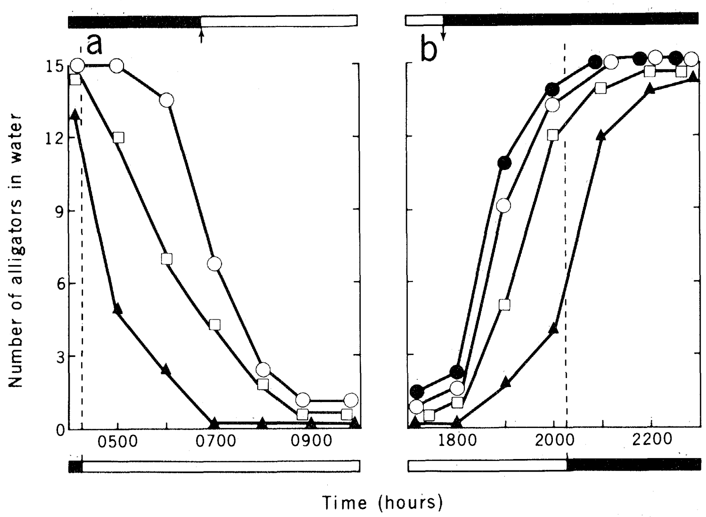
moved out of the water at sunrise and into the water at sunset. These daily movements were observed in recently caught alligators, in those held for 2 months in outdoor pens, and in newly hatched young. The pattern in October (LD 11 : 13, synchronized with the natural sunrise and sunset) was typical. In the morning, alligators began moving out of the water between 0500 and 0600; by 0900, all were on land. Movement out of the water was most apparent between 0600 and 0700, the hour of sunrise (Fig. 1a). In the evening, alligators began moving into the water between 1700 and 1800; by 2100, all were in the water. Movement into the water was greatest between 1800 and 1900, during the hour after sunset (Fig. 1b). In July and August (LD 13.5 : 10.5), the alligators behaved similarly with respect to sunrise and sunset, and in consequence, more time was spent on land.

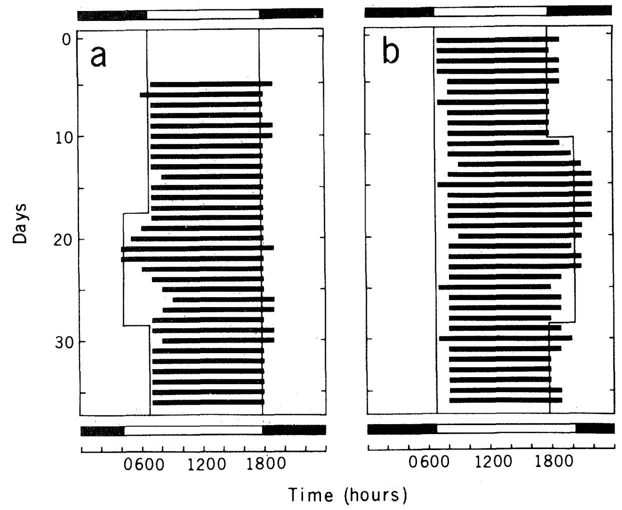
Artificial illumination was provided by four 150-watt incandescent bulbs, positioned 3 m above the floor, and evenly spaced across the top of each pen. The intensity of illumination was 200 lux at 0.5 m (approximating the natural intensity at sunrise and sunset). The lights did not affect ambient temperatures measurably. In one pen, the lights were timed to go on 2.5 hours before sunrise and to remain on until 3 hours after sunrise; in this way, sunrise was advanced by 2.5 hours. In the other pen, sunset was delayed for 2.5 hours. Thus, the October-November photoperiod was extended with artificial illumination in either the morning or evening to LD 13.5 : 10.5, equivalent in LD ratio to that of the July-August photoperiod.

Alligators responded to an extension of the natural LD cycle by moving out of the water earlier in the morning or by moving into the water later in the evening (Figs. 1 and 2). The land-water movements shifted into phase with the altered light cycles gradually, that is, transients occurred (Figs. 1 and 2). Transients were evident in all individuals for about 5 days following the initial photoperiod alteration. Gradual phase-shifting in response to the altered LD cycle indicates that these movements are coupled to an endogenous circadian rhythm, rather than being direct responses to changes in illumination or responses due to masking (*8*).

The alligators were held in outdoor pens where they were exposed to natural cycles of light, temperature, and other periodic environmental factors. These factors are all potential zeitgebers for a circadian rhythm. The fact that the alligators responded to changes in illumination despite the persistence of the natural cycles is evidence that the light cycle plays a major role in the timing of the rhythm.

It is significant that the alligators responded to the extended photoperiod by increasing the time spent on land. The morning light manipulation had no obvious effect on evening behavior; similarly, evening light manipulation had no effect on morning behavior (Fig. 2). Movements remained in phase with the onset or termination of the natural portion of the cycle, that is, sunset in the light-advanced (morning) group and sunrise in the dark-delayed (evening) group. This result implies a time





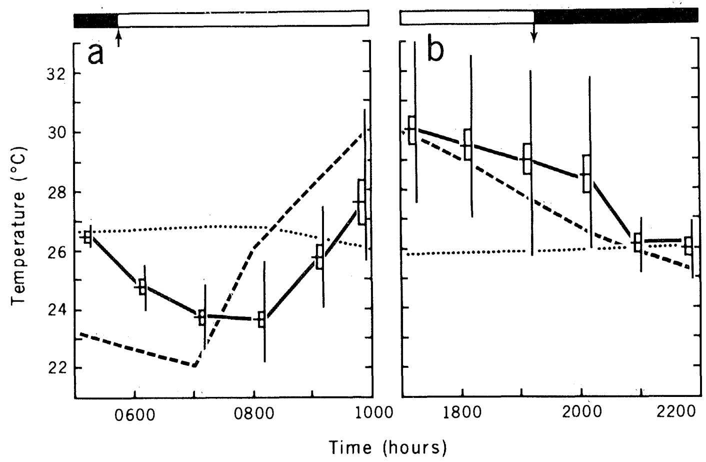


Fig. 1 (top left). Number of alligators in the water in the morning (a) and evening (b). ○, Number during the natural photoperiod (LD 11 : 13) 5 days prior to the onset of the altered light cycle; □, the second day of the altered light cycle; ▲, the fifth day; ●, controls in the pen exposed to the natural photoperiod on the fifth day after onset of the altered light cycle in the evening. Horizontal bars above and below the graphs indicate the natural (top) and altered (bottom) light cycles (upward arrow, sunrise; downward arrow, sunset). Fig. 2 (top right). Time spent on land (dark horizontal bar) each day (abscissa) for 36 days (ordinate). The alligators were initially exposed to natural light and subsequently to altered light in the morning for one alligator (a) and evening for another (b). Vertical lines represent the time of sunrise and sunset in natural light and the time and duration of the altered light cycle in the morning [(a) days 18 through 28] or evening [(b) days 11 through 28]. Horizontal bars above and below each record indicate the natural (top) and altered (bottom) light cycles for the period 18 October (day 1) to 22 November 1973. Fig. 3 (bottom left). Mean body temperatures (solid line) of alligators at hourly intervals (N = 105 at each data point) in the morning (a) and evening (b) for 28 days in summer 1972 (20 July through 16 August) (*6*). Horizontal lines indicate means, vertical lines indicate ranges, and bars equal ± 2 standard errors. Mean hourly temperatures of shaded air (dashed line) and water (dotted line) are shown for the same period. Most alligators moved onto land between 0500 and 0600 and into the water between 2000 and 2100; a thermal lag resulted in body temperatures below and above air temperatures in the morning and evening, respectively. Horizontal bars above the figure indicate the natural photoperiod (LD 13.5 : 10.5) in the morning and evening (upward arrow, sunrise; downward arrow, sunset).

system capable of independent control of emergence at sunrise and submergence at sunset, and is compatible with a two-oscillator model of circadian organization (*9*).

At the onset of the altered light cycle, the timing of movements gradually came into phase with the new light cycles. After 5 to 8 days, and despite the continuance of the altered light cycles, there was a gradual shift in the timing of movements back into phase with the natural light cycle. These spontaneous, reverse shifts were more abrupt in the light-advanced animals (about 1.0 to 1.5 hours per day) than in the dark-delayed animals (about 0.5 to 1.0 hour per day) (Fig. 2). The asymmetry of these reversals may reflect the typically asymmetrical phase response curves that characterize circadian systems (*10*), or it may indicate the influence of the natural temperature cycle (*11*). The temperature difference between air and water was more pronounced in the morning than in the evening; this difference may have accelerated the shift of morning movements back into phase with the natural cycles of light and temperature.

In both groups, the phase relationships with the nautral light cycle were reestablished before the termination of the altered light cycles, and were maintained once the altered light cycles had been terminated (Fig. 2). Two explanations seem plausible. The reversals may represent a recoupling of morning and evening movements that were temporarily uncoupled in response to the altered light cycles (*9*). Alternately, the land-water movements may have been synchronized with a new cue (perhaps associated with natural light or temperature) that provided more useful time information than that provided by the altered light cycle. Thus, an alligator may distinguish between the light cues (differing in quality, intensity, or duration) available to it (*12*). Or it may respond not to light, but to temperature (*11*) or an interaction of light and temperature cycles (*13, 14*). In these ways, the animal comes to respond adaptively to a complex and changing environment (*15*).

In responding to natural LD cycles, the alligators moved from a warm environment to a cooler environment both in the morning (into cool air) and in the evening (into cool water). This behavior resulted in a marked drop in body temperature at sunrise and sunset. During the summer, the mean decrease in T_b was 3.0°C in the morning and 3.4°C in the evening (Fig. 3). In the fall, even greater decreases accompanied land-water transitions; mean T_b dropped 4.3°C in the morning and 7.6°C in the evening.

Similarly, Nile crocodiles in nature move out of the water in the morning before air temperature rises above that of the water and before solar radiation is appreciable. In the evening, crocodiles frequently move from land before the air temperature drops to that of the water (*1*). Yet, the land-water movements of crocodilians are usually interpreted as thermoregulatory responses that function to elevate or maintain body temperatures at desired levels (*1, 2*). While the ultimate effect of moving into the water in the evening or onto land during the day may be to maximize T_b, my studies of alligators indicate that these movements are not simply movements toward warmer temperatures in the environment. Instead, they typically result in a decrease in T_b, at least temporarily. In a proximate sense, heat-seeking behavior is probably "relaxed" during these transitions (*16*).

The alligators that I observed reversed their response to light a few days after the light cycles were changed experimentally. In nature, seasonal changes in the timing of movements between land and water have been noted in alligators (*17*) and crocodiles (*1*). Alligators move onto land early in the morning, often before sunrise during the warm summer months. During the cool winter months, they move onto land at midday on warm sunny days. Flexibility in responding to natural light cycles may facilitate adaptation to seasonal changes in heat availability. In the summer when ambient temperatures are high, light cycles are probably good predictors of heat availability; movements between land and water that are coupled to a circadian rhythm cued by light would be reliable. During the winter, alligators become increasingly dependent on solar radiation rather than on air or water temperatures as a source of heat. Under these conditions, assessing heat availability directly is probably a better strategy than relying on the photoperiod. Attempts to explain crocodilian behavior solely on the basis of immediate environmental factors, particularly temperature, should be viewed with caution.

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5. Each pen (6 by 12 by 4.5 m) of sandy soil contained a concrete aquatic pool (5.5 by 5.5 by 1 m) with sloping sides. The pens were screened but open to direct sunlight as well as ambient temperature and light fluctuations; shaded areas were available throughout the day. Fifteen alligators were held in each pen.
6. A quick-reading mercury thermometer was used to measure cloacal temperatures to the nearest 0.1°C. Readings were taken at 4-hour intervals from 0500 to 2400 for 28 days in the summer of 1972. Each day the initial sampling time was advanced 1 hour for 3 days, and then the original schedule was resumed. In this way, hourly measurements were collected with minimal disturbance to the animals. In the fall of 1973, measurements were taken in an identical manner between 0500 and 0900 and between 1700 and 2100 for 12 days under natural LD after the termination of the lighting experiments.
7. More frequent initial observations had indicated that this schedule was adequate. Observations at night (2400 to 0400) and during the day (1000 to 1700) indicated that the alligators were rarely on land at night or in the water during the day. There was no midday movement into water as has been observed in large (>2 m) alligators (J. W. Lang, in preparation) and in large crocodiles (*1, 2*).
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11. Weak daily temperature cycles (<1°C) entrained locomotor activity in a lacertid lizard [K. Hoffman, *Verh. Dtsch. Zool. Ges.* **62**, 265 (1968); *Z. Vgl. Physiol.* **58**, 225 (1968)].
12. When given a choice, juvenile alligators prefer red to either green or blue illumination [A. M. Reese, *J. Comp. Physiol. Psychol.* **5**, 69 (1925)]. Thus, it is likely that alligators are able to discriminate between light sources that differ in spectral composition.
13. In the lizard *Klauberina riversianna*, heat-seeking activity was clearly entrained only by a complex cycle of light and heat availability (*14*).
14. P. J. Regal, thesis, University of California at Los Angeles (1968).
15. For example, if the availability of thermal reinforcement is manipulated in an operant conditioning situation, a lizard normally active during the day can be made into one active at night (*14*). In many animals, responses to environmental stimuli change seasonally. In a few species of invertebrates, birds, and mammals, an internal calendar or circannual rhythm is known to mediate seasonal changes in certain physiological parameters [E. T. Pengelley, Ed., *Circannual Clocks* (Academic Press, New York, 1974)].
16. (i) In nature, the amphibious behavior of alligators is variable and influenced by numerous factors. Thermoregulatory behavior is dependent on the animal's size. Large (>2 m) alligators rely heavily on solar radiation as a source of heat, in contrast to smaller ones, which are more dependent on environmental temperatures. Consequently, in large individuals, fluctuations in sunshine frequently result in land-water movements. During the warm summer months, large alligators retreat into the water at midday, apparently to reduce further heat gain and stabilize T_b (J. W. Lang, in preparation). Most social interactions among adult alligators occur in the water; they may enter or remain in the water to engage in social activities [L. D. Garrick, *Anim. Kingdom* **78**, 2 (1975); J. W. Lang and L. D. Garrick, in preparation]. Small alligators may move onto land during the day to escape aquatic predators active during the day, such as herons, while movement into the water at night may afford protection from nocturnal predators, such as raccoons, that hunt along shorelines. Alligators of all sizes presumably forage at night and may move into the water to feed. (ii) Data on reptiles that in nature actively select thermal conditions that result in lowered body temperatures are scarce. Marine iguanas enter the water to feed after basking [F. N. White, cited as a personal communication in Regal (*14*)]. The semiaquatic snake *Natrix taxispilota* submerges in the evening independently of temperature [D. E. Goodman, thesis, University of Florida (1971)].
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