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LIGHT MEDIATION OF CIRCADIAN PREDATORY BEHAVIOR IN THE YOUNG ALLIGATOR

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ABSTRACT: Minnow predation by 10 young American alligators (*Alligator mississippiensis*) was systematically measured during four daily time periods under four different conditions of lighting in order to investigate a circadian rhythm of predatory behavior. The four daily time periods were night (1:00 a.m.-7:00 a.m.), morning (7:00 a.m.-1:00 p.m.), afternoon (1:00 p.m.-7:00 p.m.), and evening (7:00 p.m.-1:00 a.m.). Each of the following lighting conditions had a duration of 4 weeks: continuous complete darkness (DD); continuous artificial illumination (LL); naturally varying light-dark conditions (natural LD); and reversed light-dark conditions with artificial lights on at sunset and off at sunrise (reversed LD). Predatory behavior (i.e., the number of prey fish consumed wholly or partially during each test session) varied significantly as a function of the interaction between time period and lighting condition. Under natural LD, the mean number of prey killed during night sessions was significantly higher than either morning or afternoon sessions. Under reversed LD, the pattern of predation reversed from that exhibited under normal lighting, with both morning and afternoon predation significantly higher than either evening or night. Under conditions of continuous illumination (LL and DD) the natural LD circadian pattern persisted for over 1 week with significantly higher predation rates during the night periods as compared to the morning and afternoon periods. The gradual transition of predation pattern in response to manipulations of the light-dark cycle suggests that the circadian rhythm of alligator predation is dependent upon light-dark variation for entrainment.

INTRODUCTION

The adult American alligator (*Alligator mississippiensis*) has been described as an opportunistic scavenger as well as an active predator

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(McIlhenny, 1976; Pooley, 1989; Weldon, Swenson, Olson, & Brinkmeier, 1990). Hatchling alligators eat insects, small crustaceans, and small fish (Coulson & Hernandez, 1983), whereas adult alligators prey upon frogs, snakes, birds, muskrats, nutria, and larger mammals (McIlhenny, 1976; Pooley, 1989; Ross & Magnusson, 1989; Scott & Weldon, 1990). The alligator is generally considered a nocturnal species with most of its feeding behavior and general activity taking place during the night (Lang, 1976; McIlhenny, 1976; Murphy, 1981; Pooley, 1989). Alligator predatory behavior appears to follow a circadian rhythm, but this has not been systematically investigated and reported.

In almost all vertebrates, endogenous circadian rhythms regulate temporally certain types of behavior (e.g., sleep) and bodily functions (e.g., hormone secretions, Aschoff, 1989). The rhythm itself is often entrained or synchronized by environmental cues such as daily cycles of light-dark and temperature change (Aschoff, 1989; Griffiths, 1986). These environmental cues that set the timing of circadian behavior are referred to as *zeitgebers* (Aschoff, 1989). Aschoff reports that the most powerful of all *zeitgebers* is a light-dark cycle. In the absence of *zeitgebers* (e.g., an environment of continuous darkness), circadian rhythms are free-running and self-sustaining. The free-running rhythm may cycle every 24 hours, be slightly longer, or slightly shorter.

In lower vertebrates, light mediates circadian rhythm via the photosensitive pineal gland. Although alligators lack pineal glands, studies have indicated that some circadian rhythms in alligators are controlled or mediated by light cycles. Circadian rhythm of young alligator motor activity was documented by Kavaliers and Ralph (1980). Lang (1976) found that movement between land and water in juvenile alligators varied as a function of circadian rhythm cued by light-dark cycles. A study by Murphy (1981) indicated the existence of an endogenous clock synchronized by the circadian light-dark cycle which enabled young alligators to use solar compass orientation. Kavaliers (1980) demonstrated that extraretinal responses to light pulses varied according to circadian phase. Moreover, photoperiod manipulation indicated exogenous entrainment of the extraretinal responses by light-dark cycles. In light of the alligators' lack of a pineal gland, Kavaliers and Ralph (1981) argued that overall organization of circadian rhythm and period length depends on a complex interaction of retinal inputs, extraretinal inputs, and other neural areas.

This study sought to determine if alligator predation was subject

to circadian rhythmicity. Minnow predation (i.e., number of minnows wholly or partially consumed) by young alligators was systematically measured during four daily time periods under different conditions of lighting. It was hypothesized that predation rates would peak during the dark periods of 24-hour natural and reversed light-dark cycles, and that an endogenous circadian rhythm would persist under continuous illumination. It was predicated that the circadian fluctuation could be altered by manipulating the light-dark cycle, thus supporting dependence upon light-dark alternation as a zeitgeber. A gradual transition of predation pattern in response to light-dark cycle manipulations would indicate entrainment by a light-dark zeitgeber.

TABLE 1
Subject Size After the Study Compared with Number of Prey Captured During 6-Hr Sessions

Subject	Subject Size		Number of Prey Captured		
	Length	Weight	Range	Mean	SD
1	46.0	304.0	0-9	1.89	2.28
2	46.5	285.5	0-10	2.77	2.94
3	42.5	215.0	0-10	2.57	2.97
4	42.5	203.5	0-10	2.36	2.78
5	41.9	208.5	0-10	2.28	2.84
6	38.5	176.5	0-9	2.16	2.37
7	39.0	164.0	0-6	1.59	1.84
8	44.0	228.5	0-10	2.71	2.94
9	37.0	148.5	0-5	1.65	1.73
10	38.0	151.5	0-10	2.08	2.48

METHOD

Subjects

Ten 1990 hatchling alligators (*Alligator mississippiensis*), 27 to 29 cm in length and weighing 56 to 80 gm, were obtained from the Rockefeller Wildlife Refuge, Grand Chenier, Louisiana when they

were approximately 1 month of age. (Age is approximate because exact date of hatching is not known). Testing began when subjects were approximately 6 months old and continued until subjects were approximately 14 months old. At the completion of testing, subjects ranged from 37 to 46 cm in length and 148.5 to 304 gm in weight (Table 1). Individual subjects were identified by removing a specific tail scute.

Maintenance

When not being tested, all 10 alligators were maintained in a home pool measuring 45.72 cm deep and 2.44 m in diameter. Ten cm of water covered the bottom, and a 60.96 cm diameter gravel-surfaced concrete "island" was situated near the center of the pool. The pool was retained in a heated enclosed garage with windows facing north and east. Air temperature ranged from 21 to 28°C with an average of 25°C. Water temperature ranged from 20 to 27°C with an average of 24°C. The pool was drained and filled with fresh water as necessary (usually once each week).

Food included two species of live minnows (*Notropis cornutus* and *Cyprinus idus idus*) and Burris Alligator Feed. Alligators were permitted to obtain live prey (minnows) beginning when they were 2 months old. Once testing began, live prey was available only in the testing arenas during test sessions. Burris Alligator Feed was provided ad libitum in the home pool.

Live minnows were obtained as needed (about every 2 weeks) from local bait shops and fish supply outlets. They were maintained in a plastic barrel, 55.88 cm in diameter and 71.12 cm high, filled with water. Aeration was furnished by an electric Second Nature Whisper 400 aquarium pump. Water and air temperature were the same as that for the alligators. The minnows were fed an adequate amount of Wardley Tropical Flakes fish food every evening.

Apparatus

Each test arena consisted of a plexiglass tray 45.72 cm x 25.4 cm x 12.7 cm high with a grill-type metal lid that allowed air circulation but prevented escape. Each arena was filled with 7.62 cm of water. The test arenas were located in the same room as the alligator home pool. Water temperature was the same as that in the home pool.

Procedure

All subjects were tested under all conditions. A two-factor (4 x 4) within-subjects experimental design was used, with one factor (daily time period) nested within the other factor (lighting condition).

The four lighting conditions were continuous complete darkness (DD), continuous artificial illumination (LL), naturally varying light-dark (natural LD), and reversed light-dark with artificial light on at sunset and off at sunrise (reversed LD). Each lighting condition was maintained for 4 weeks, and each followed a 2-week period of natural lighting to control for carryover effects. (Kavaliers and Ralph [1980] demonstrated that, following light manipulation, 10 days of natural light were sufficient to restore normal circadian rhythmicity of alligator motor activity).

Artificial illumination was provided by a Power-Glo 40-watt full spectrum fluorescent lamp. When necessary to shut out natural light, the windows were covered with black shades taped tightly against the walls so that no light could enter.

A total of 640 predation test sessions of 6-hour duration were conducted (160 test sessions per lighting condition). Predation test sessions were alternated randomly among four time periods: night (1:00 a.m.-7:00 a.m.), morning (7:00 a.m.-1:00 p.m.), afternoon (1:00 p.m.-7:00 p.m.), and evening (7:00 p.m.-1:00 a.m.). No time period was repeated until the other three had been used. All four time periods were tested each week.

Because movement between land and water has been demonstrated to follow a circadian pattern itself (Lang, 1976), alligators and prey animals were placed in test arenas to control for this possible confound. Each test session was conducted as follows: ten minnows, five specimens each of *Notropis cornutus* and *Cyprinus idus idus*, were moved with a net by the investigator from their home barrel to a test arena at the beginning of the designated 6-hr time period. An alligator was then carried by the investigator by hand from its home pool to the test arena. A grill-type metal lid was then placed on the test arena. During the 6-hr test session, the animals were not disturbed. At the end of the session, the number of prey killed (i.e., number of minnows missing or partially consumed) was recorded. The alligator and remaining minnows (if any) were then returned to their respective homes. The water in the test arena was emptied and replaced with fresh water after each test session.

RESULTS

The dependent variable, number of minnows consumed wholly or partially, was analyzed with a repeated measures analysis of variance (ANOVA), in which time period and lighting condition were independent variables (both repeating) with time periods nested within lighting conditions. Predatory behavior varied significantly as a function of the interaction between time period and lighting condition, $F(9,270) = 15.79$, $p < .001$. Mean prey killed for each time period within each lighting condition are reported in Table 2.

TABLE 2
Means and Standard Deviations of Prey Killed During Time
Periods Under Different Lighting Conditions

Lighting Conditions	Time Periods			
	Night	Morning	Afternoon	Evening
Continuous Dark				
Mean	0.393	0.260	0.065	0.203
SD	(0.507)	(0.404)	(0.227)	(0.377)
Continuous Light				
Mean	2.775	2.975	2.800	2.350
SD	(2.769)	(3.109)	(2.757)	(2.107)
Natural Light				
Mean	2.700	1.300	1.250	2.075
SD	(2.221)	(1.488)	(1.256)	(1.542)
Light Reversal				
Mean	2.600	4.500	4.600	1.750
SD	(1.646)	(2.491)	(3.177)	(1.932)

Figure 1 compares the predation patterns that occurred under natural LD and reversed LD cycles. Tukey HSD multiple comparisons showed that under natural LD the mean number of prey killed at night was significantly higher than either morning ($p < .01$) or afternoon ($p < .01$). Although mean number of prey killed was higher during evening than either morning or afternoon, the differences were

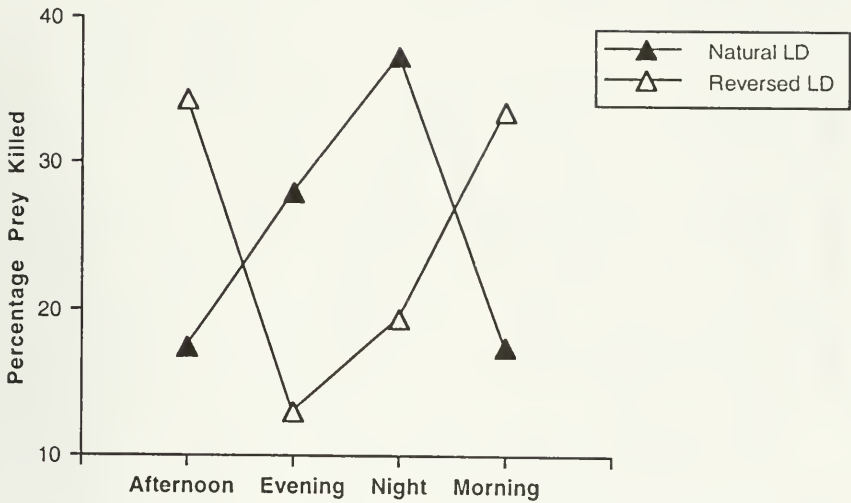


Figure 1. Circadian predatory behavior patterns under lighting conditions natural and reversed LD.

not significant. Kill rates for evening and night sessions did not differ significantly from each other. Morning and afternoon kill rates also did not differ significantly from each other.

Under reversed LD conditions, the pattern of predation reversed from that exhibited under natural LD. Tukey HSD multiple comparisons revealed that morning predation was significantly higher than either night ($p < .001$) or evening predation ($p < .001$). Afternoon predation was also significantly higher than either night ($p < .001$) or evening predation ($p < .001$). The reversed LD condition produced no significant differences between morning and afternoon predation. However, night predation was significantly higher than evening predation ($p < .05$).

Under DD, night predation was significantly higher than afternoon predation ($p < .01$). Under LL, no significant differences were found among the time periods.

The data for the initial week under each of the two constant conditions, LL and DD, were examined to see to what degree the natural LD pattern persisted. Figure 2 illustrates that the natural LD pattern did persist during the first week of LL and DD with predation rates peaking during night periods. Tukey HSD multiple comparisons determined the following significant differences. Under DD, night predation was significantly higher than after noon ($p < .05$)

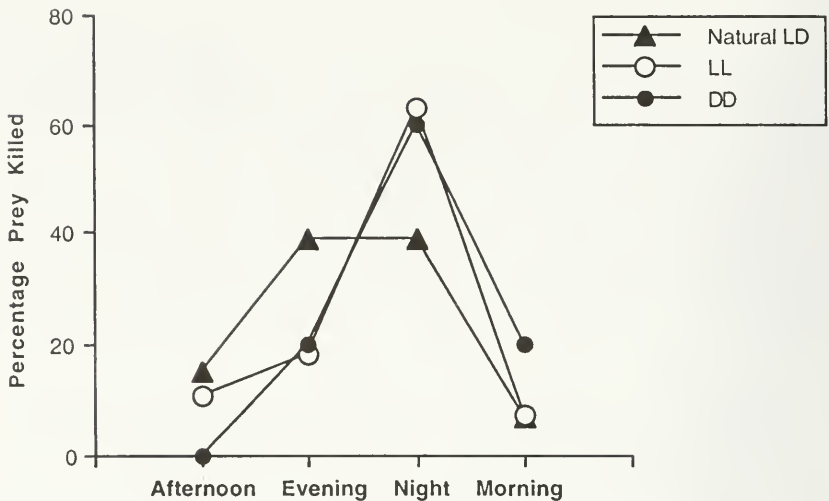


Figure 2. Circadian rhythm of predation during the first week of LL, DD, and natural LD conditions.

predation. Under LL, night predation was significantly higher than morning ($p < .01$), afternoon ($p < .01$), and evening ($p < .05$) predation.

Table 1 displays the mean number of prey killed by each subject. Predation rates of the 10 subjects were analyzed with a one-way ANOVA to determine if predation differed among subjects. No significant differences were found.

DISCUSSION

Alligators as young as 2 months of age are capable of capturing very active prey. The evidence accrued in this study suggests that predatory behavior in the young alligator varies as a function of light-mediated circadian rhythm. Light plays a critical role, as predation during dark periods was significantly higher than during light periods, whether lighting conditions were natural or reversed. Predation rates during natural and reversed LD climaxed during the second contiguous time period of darkness (i.e., night period of natural LD and afternoon period of reversed LD). This suggests that, in the wild, predatory behavior of the young alligator reaches a peak during the hours before dawn, declines sharply after daybreak, remains low throughout the day, and then rises steadily after nightfall. Such an

activity cycle is similar to the circadian rhythms of alligator motor activity found in other research (Kavaliers, 1980; Kavaliers & Ralph, 1980, 1981; Lang, 1976).

Aschoff (1989) describes circadian rhythms as "self-sustaining oscillations", and the test for such persistence is a recording of the activity under continuous non-varying illumination. Under DD, a predation pattern similar to natural LD persisted (i.e., night predation was significantly higher than afternoon), although predation was relatively suppressed during all time periods (see Table 2). Examination of predation rates of the first week under conditions of LL and DD showed that a general pattern of circadian rhythm, similar to the natural LD pattern, persisted. During the second week of LL, the pattern became arrhythmic. This is in accord with Kavaliers and Ralph's (1980) study where the free-running circadian rhythm of alligator motor activity became arrhythmic after 10-15 days of LL.

The suppression of predation during DD may have been due to melatonin, a hormone that increases during periods of darkness (Galluscio, 1990) and appears to regulate cycles of sleep and activity in many animals (Wurtman & Lieberman, 1987). Melatonin is present in the blood of alligators (Gern, Owens, Ralph, & Roth, 1978), but its exact role is not known. In birds, the increase in melatonin appears to cause a decrease in activity and in body temperature (Binkley, 1979). Although alligators are poikilotherms, an increase in melatonin due to continuous darkness may suppress predatory behavior.

Figure 3 provides further evidence of an endogenous circadian rhythm of predatory behavior. If the temporal occurrence of the young alligator's predatory behavior was solely under light stimulus control with no endogenous circadian rhythm, then an abrupt change in predatory behavior should occur immediately following light reversal. However, Figure 3 demonstrates a gradual transition of predation pattern in response to reversed LD, more indicative of a circadian rhythm being reprogrammed by the zeitgeber than behavior cued directly by light. Alligator predation follows a circadian rhythm and appears to be dependent upon light-dark variation for entrainment.

As an ancient species that has evolved in latitudes subject to seasonal shifts in photoperiod, the alligator is an excellent subject for the study of endogenous circadian clocks that are fine tuned by environmental cues (eg., light-dark, temperature variations). Whether there is one circadian clock or a number of subordinate circadian clocks each kept in synchronization with the others by natural

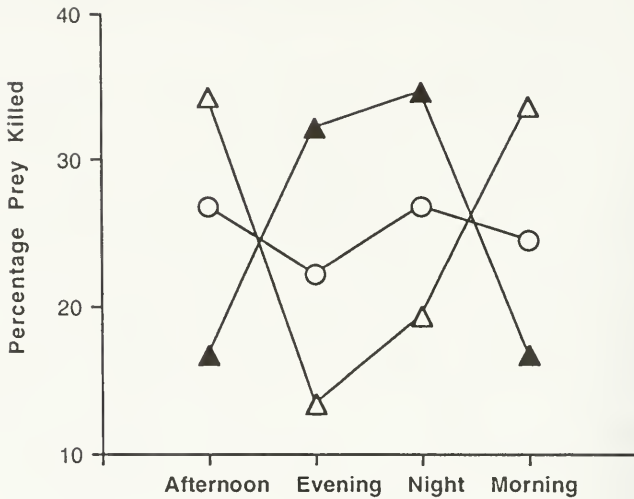


Figure 3. Transition of circadian predatory pattern from natural LD (solid triangles) to the first week (open circles) and fourth week (open triangles) of reversed LD.

zeitgebers can only be determined by extensive research. Amphibious behavior, solar compass time compensation, photoreceptor sensitivity, motor activity, and predatory behavior all may be controlled by one "master" circadian clock, or each behavior may have its own independent circadian clock. Conversely, all of the above behaviors may reflect variations symptomatic of the animals' activity cycles. To resolve these issues, it would be necessary to measure continuously and concurrently all of these behaviors under controlled laboratory conditions. By manipulating light and temperature cues, it may be possible to produce desynchronization of the behaviors from each other thereby demonstrating subordinate circadian clocks for some or all of these behaviors.

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