Roadrunners: Activity of Captive Individuals

Abstract. *Two roadrunners,* Geococcyx californianus, *readily accepted an activity wheel as an outlet for locomotor activity. The birds were strictly diurnal and tended to be most active per unit of time in the predusk hours. There was less activity on partly overcast days than on clear days. Dim light and darkness were strongly inhibitory, even during daytime hours; bright light was stimulatory, even during nighttime hours. These findings appear to open the way for quantitative comparative studies of the influences of environmental factors on the activity of cursorial birds.*

Locomotion in activity wheels is a valuable laboratory technique for quantitative comparative studies of the activity of small mammals. In effect, a wheel provides an endless straight path along which animals can tread unhindered at their chosen gaits. This technique has proved to be a sensitive indicator of influences of light on activity, including such factors as rhythmicity, phasing, and active time (*1–4*). In addition to the possible ecological significance, results of such studies may have implications for the evolution and state of adaptation of the visual system (*1*, *3*). Accordingly, the technique has been extended to cat- and dog-sized animals (*3*, *4*). We report here its first use with a bird, the roadrunner or chaparral cock, *Geococcyx californianus.*

The roadrunner inhabits deserts, chaparral, and arid grasslands in southwestern North America. It is active during the day, preying on lizards, rodents, snakes, spiders, and insects; various fruits and seeds also are eaten. It can run at up to 8 m/sec (18 mile/hour) for short distances. Little is known of the pattern of distribution of its activity, but reduced activity during the hot midday hours has been noted in the Mojave (*5*) and Sonoran (*6*) deserts.

Two hand-raised birds, weighing roughly 340 g each, were studied outdoors for 3 to 4 weeks during June and July 1969. An activity wheel 91 cm (3 feet) in diameter and an adjoining cage were housed in a wire-mesh enclosure to which artificial plants were fastened in a fairly dense arrangement on the sides and top, thus giving cover and a seminatural setting. The enclosure was located on the roof of the Life Sciences Building at UCLA. Temperature, relative humidity, light intensity, and time of raining were monitored continuously. With this arrangement it was possible to establish the roadrunners' responses to fairly natural light and to weather conditions.

During the following July to September the birds were studied indoors for 3 to 4 weeks in a similar 122-cm (4-foot) wheel at relatively constant temperature (19° to 23°C) and relative humidity (40 to 60 percent), and with 1-hour artificial twilights [range 0.015 to 39 lux (1 lux = 1 lumen per square meter)] (*1*, *7*). The light cycle consisted of 12 hours of bright light (150 to 3000 lux in various experiments, as described below), 10 hours of dim light (0.002 lux), and 1 hour each of dawn and dusk (*8*). The indoor beginning of dawn and end of dusk occurred within 15 to 40 minutes of outdoor sunrise and sunset (*9*). Providing food once daily at irregular times during the daylight hours did not interfere with "normal" activity. The diet consisted of mealworms and small pieces of raw chicken neck. Experimental procedures, recording, programming, and other details were the same as those used for mammals (*1*, *7*, *10*).

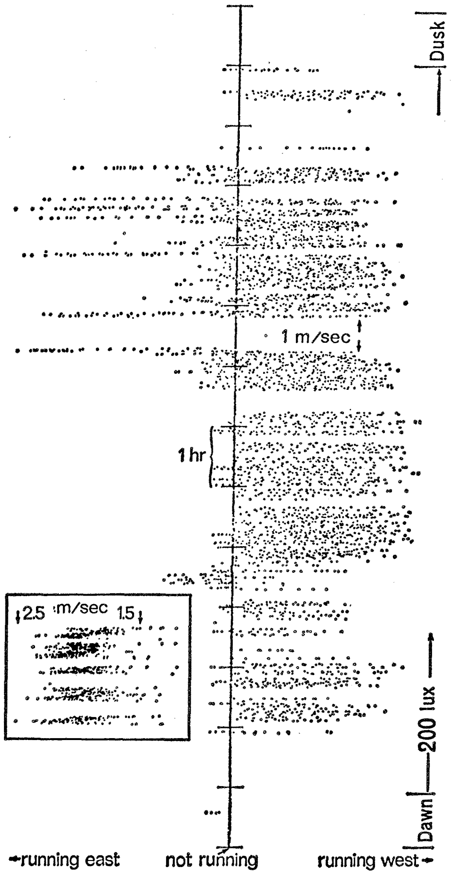

Fig. 1. Analog record for a day of indoor running by bird No. 1. Each dot gives the instantaneous direction of rotation and speed at the periphery of the wheel, as recorded every 4 seconds. Center dots and the vertical center line indicate a stationary wheel. Speed is proportional to the displacement to the right and left (1 meter-per-second value is indicated). Short horizontal lines crossing the center line mark off 1-hour intervals, with time advancing from the bottom to the top. The inset (lower left) shows the peripheral part of a record of routine-3 activity to the same scale.

Both activity wheels were 29 cm wide. They were constructed of 0.6-cm-thick plywood disks joined along their circumferences by 1-cm wooden dowels at 3.8-cm spacings. A strip of hardware cloth was attached outside the dowel treading surface. The plywood disks of the outdoor wheel were honeycombed and faced with hardware cloth to allow the animals to see in all directions. The amount of sunlight reaching the birds through the artificial plant cover and other obstructions, which depended upon the birds' position and the position of the sun, varied from 20 to 90 percent. Maximum outdoor, unshielded sunlight attained about 120,000 lux.

The birds (referred to as No. 1 and No. 2) took readily to running in the wheels (Fig. 1) and were well adapted to this activity after only a few days. They developed several activity routines. Routine 1 consisted of more or less continuous treading in the wheel at a slow to fast walk with occasional running. In routine 2 (Fig. 1, running westward) the animals left the treading surface of the wheel frequently; they alternated between jumping onto the surface and walking or running for a few seconds to a few minutes, and returning to the cage or perching on the axle for a like period. Routine 3 was used only by bird No. 1 indoors; bona fide treading of the wheel played only a partial role in it. The wheel was propelled mostly by the bird's jumping on and off the axle repeatedly, in such a way as to increase the speed of rotation gradually with each jump from the axle. After having attained maximum speed (about 2.5 m/sec at the periphery), the animal continued this routine for 5 to 15 minutes; the result was a series of sustained patterns (Fig. 1, inset).

The birds were strictly diurnal (Figs. 1 and 2). Outdoors, their active time tended to peak at around noon; indoors, activity increased gradually during the early morning hours but remained fairly constant from 9 a.m. to 3 p.m. Except for a small amount of late dawn and early dusk activity by bird No. 1, the birds were inactive during indoor twilights (Fig. 2). However, both animals evidenced a tendency to be very active before dusk. Thus, the indoor active time of bird No. 1 peaked markedly about 1.5 hours before dusk began, whereas its average speed and session lengths (periods of continuous unidirectional rotation of the wheel) peaked just before the beginning of dusk. The indoor active time and session lengths of bird No. 2 also were greatest just before dusk began. Although bird No. 1 showed no increased predusk activity outdoors, the measured activity parameters of bird No. 2 peaked markedly just before sunset (Fig. 2). There were no dawn or postdawn peaks under any conditions.

Most of the activity was of the routine-2 type, but more sustained routine-1 activity occurred from time to time. For a period of about 2 weeks indoors (not included in Fig. 2), bird No. 1 often used routine 3 from midmorning to midafternoon and routine 2 in late afternoon. As a result, its average speed, session lengths, and amount of activity were two to three times greater at the former time than at the latter.

Like most of the mammals studied (*1–4*), both birds sometimes ran in one direction for long periods. This occurred only to a minor extent outdoors (*11*). Indoors, bird No. 2 was more than 95 percent unidirectional on 12 of the 14 days for which data are shown in Fig. 2; bird No. 1 usually faced west during its routine-2 activity (Fig. 1) but east during its routine-3 activity (Fig. 1, inset).

In an effort to test the influences of light intensity during the active phase, a series of experiments were carried out with bird No. 1 in which the brightness of the daytime light was alternated abruptly between two levels every half hour. During 3 days of tests at 200 versus 3000 lux, the activity parameters consistently were higher at the higher light level—speed, session lengths, and amount of active time averaging 8.2, 17, and 56 percent greater, respectively (*12*). There were no differences at 150 versus 200 lux. During days of tests at 150 lux versus darkness, the bird was inactive during the dark half hours. With 10 lux versus darkness, there was essentially no activity at any time. There were no half-hour alternation tests with bird No. 2, for which the daytime light level was 3000 lux (Fig. 2).

The low level of activity or complete inactivity in darkness and dim light made the birds particularly interesting subjects for tests with long sequences of alternating twilights. In these tests, a 1-hour dawn was followed by 30 minutes of light at 200 lux, a 1-hour dusk, and 30 minutes of light at 0.002 lux; then the light cycle would be repeated, so that the birds experienced essentially a 3-hour "day." Both birds responded in the same clear-cut fashion; the responses of bird No. 1 are illustrative.

In its tests, the alternating twilights occurred during the normal daytime periods on the first 3 days (4:30 a.m. to 6:30 p.m.) and continuously (around-the-clock) for the next 84 hours. The animal showed some activity during all but two of the total of 43 3-hour-"day" cycles. The two cycles "missed" came on the first occurrences of bright light during the normal night period. Activity was confined exclusively to the last quarter of dawn (16 percent), daylight (57 percent), and the first half of dusk (27 percent). The lowest light level at which activity began during dawn was about 15 lux, and the lowest level at which activity ceased during dusk was about 2 lux. Speed and session lengths averaged 30 percent lower during dawn than during daytime and dusk (*13*). This may be indicative of a "warming-up" period, since many mammals warm up to top speed and session length at the beginning of an active period (*1–4*).

Although a wide diversity of weather conditions was not encompassed, a few weather effects were noted. Active time was less and tended to peak later in the afternoon on days with overcast mornings than on clear days. On a day with thundershowers, activity stopped abruptly at the onset of the first of three successive showers. No running occurred in the rain but some did occur between two of the showers.

Several factors other than light can influence activity phasing in the wild, for example, prey availability, predator pressure, and temperature (*1*, *3*). The study of animals in the laboratory has the crucial advantage over field studies that these other factors can be kept constant. As a result, the light regime probably is the chief external factor influencing the captive animal's activity phasing. Kavanau (*1*, *3*) has postulated that this phasing gives a more reliable indication of the genetically determined state of adaptation of the visual system (the eye and all central nerve connections) than the phasing observed in the field. Since the laboratory and field findings agree for roadrunners, their visual system probably is well adapted for a diurnal existence.

Calder (*6*) has suggested that the reduction of field activity in the heat of midday reduces demands for heat dissipation and the consequent water loss

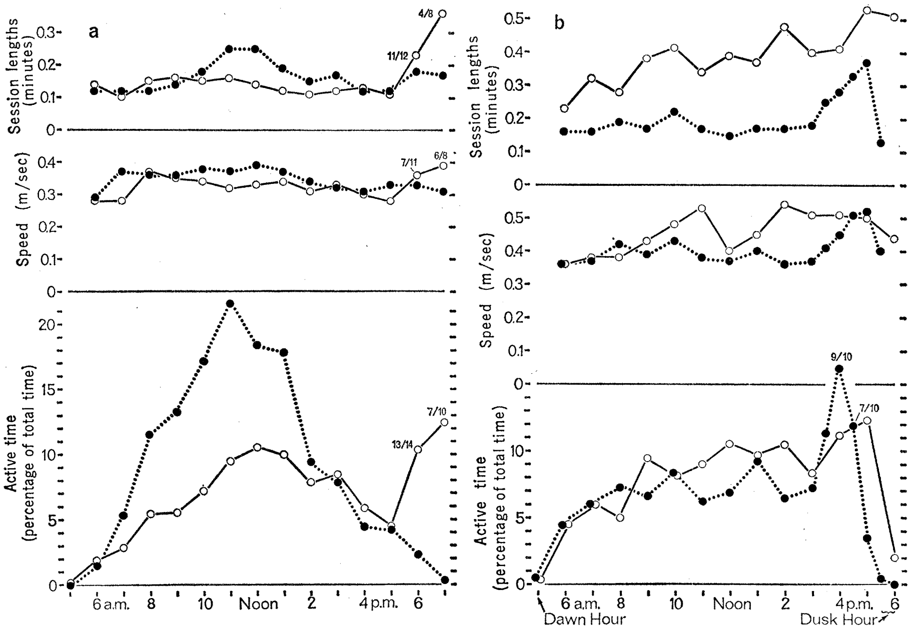

Fig. 2. Plots of (a) outdoor and (b) indoor activity parameters. (Filled circles) Bird No. 1; (open circles) bird No. 2. Two weeks of activity are represented for all cases except bird No. 1 indoors, for which the period is 10 days. Each hourly point includes data for the preceding and following half hours (*16*). For the outdoor studies, sunrise occurred at 4:43 to 4:49 a.m. and sunset at 7:52 to 7:53 p.m. for bird No. 2, and at 4:50 to 4:58 and 7:43 to 7:52 for bird No. 1 (*9*). In the plots for bird No. 2 indoors, the parameters for the last 3 hours are plotted half-hourly to show the structure of the peaks in detail. The consistency of the peaking in predusk hours can be assessed from the fractions associated with the plotted points. These give the fractional number of days (9/10 = 9 days out of 10) that the given point was higher (or lower) than the immediately preceding point, for days for which valid comparisons can be made.

in evaporative cooling. His observations were made in June and July, when maximum air temperature in the shade reached 41°C. In our study at the same time of the year, the maximum outdoor air temperature was 31° to 32°C. Since our birds were very active during the midday hours, the activity reduction in the field may be a specific response to high temperatures, rather than an invariable feature of the activity pattern (that also prevails in cool weather). The tendency of the activity parameters to peak before sunset may be indicative of enhanced late afternoon activity in the field, possibly related to heavy predation on insects. The low level of early morning activity correlates with the known propensity of roadrunners to sunbathe at this time (*14*).

The inactivity of our birds during outdoor twilights and during indoor early dawn, late dusk, dim light, and darkness suggests that the visual system of the roadrunner is unsuited to dim-light vision. The fact that the birds almost always ran during the bright-light periods and always retired during the dim periods of a continuous cycle of 3-hour "days" suggests, at the least, that light conditions are highly restrictive for roadrunners and that sleeping birds are "aware" of marked changes in the ambient light level. Two findings suggest that roadrunner activity tends to increase with increasing light level: (i) greater activity on clear than on overcast days; and (ii) 56 percent greater activity of bird No. 1 at 3000 lux than at 200 lux in half-hour alternation tests.

Since roadrunners will accept an activity wheel as an outlet for locomotion, the way may be open for quantitative comparative studies of the influences of environmental factors on bird activity (*15*), at least for other running birds. The roadrunner may be an extreme diurnal case with pure-cone vision and little or no summation in the retina. Nocturnal birds and diurnal birds with some rods in their retinas may, like many mammals, show a greater range of responses to changes in ambient light intensities.

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References and Notes

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8. The light intensities were measured at the bottom of the wheel, 125 cm from the incandescent lights and 185 cm from the nearest fluorescent lights. The 200-lux value (Spectra Candela X-100 lightmeter) is for a 100-watt incandescent bulb supplemented by 480 watts of ceiling fluorescent lamps. In some experiments one or two 150-watt General Electric cool-beam (PAR38/2FL) or regular (PAR/FL) flood lamps were used (about 1500 lux per lamp). The night light was a General Electric No. 44 incandescent bulb energized at 1.5 volts.
9. The sunrise and sunset times referred to are the arbitrarily defined (although exactly definable) and biologically unimportant almanac times (unobstructed horizons and zero elevation above the earth's surface). The use of astronomical sunrise and sunset as reference times would be more pertinent, since these are the times of beginning and ending of the sun's contribution to the light level, that is, the ending and beginning of the night. The astronomical times in Los Angeles during June and July occur roughly 43 to 49 minutes earlier for sunrise and 49 to 51 minutes later for sunset.
10. J. L. Kavanau, *Ecology* **44**, 95 (1963).
11. Bird No. 2 exceeded 90 percent unidirectionality on only 1 day; bird No. 1 exceeded 80 percent on only 4 days.
12. When a 150-watt cool beam was alternated with a regular flood lamp (1500 lux each), the magnitudes of the three measured activity parameters were slightly greater in the cool beam, possibly in part because the animal tended to spend more time perching on the axle in the sunning posture in the warmer light of the regular flood lamp.
13. Although the bird followed the 3-hour "day" closely with regard to times of activity and inactivity, its main activity was concentrated in a period of 10 to 14 hours that tended to begin later each day and was 9 hours out of phase with the previous rhythm after 84 hours of continuous cycles. This suggests that the animal began to shift to a 26- to 27-hour endogenous rhythm once the 24-hour exogenous light cycle ceased.
14. A. C. Bent, *Life Histories of North American Cuckoos, Goatsuckers, Hummingbirds, and Their Allies* (Dover, New York, 1964).
15. In the past, quantitative studies of bird activity in the laboratory have depended heavily on recording from spring-mounted perches and other substrata, which register all kinds of minor movements.
16. The percent active time for the last point for bird No. 2 outdoors is corrected to allow for the time when activity ceased, rather than being computed for the full hour.
17. Supported by NSF grant GB 7750 and by a NASA training grant to J.R.

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Temporal Summation and Refractoriness in Hypothalamic Reward Neurons as Measured by Self-Stimulation Behavior

Abstract. *A neurophysiological technique of double-pulse stimulation has been applied to freely moving rats with chronic indwelling electrodes in the hypothalamic reward area. Self-stimulation thresholds, measured as a function of the interpulse interval, generated curves with time constants characteristic of refractory periods and temporal synaptic summation. The results indicate a way of studying central neuronal processes for which the overt behavior of the animal is the dependent variable.*

It is generally true of the overt behavior of an organism that the strength of a response varies as some function of the rate and pattern of the stimulus eliciting it. Similarly, it has been shown that a complex relationship, termed the neural poststimulation excitability cycle, exists between (i) the rate and pattern in which neurons and synapses are stimulated and (ii) their ability to transmit this information. Since overt behavior is mediated by way of neural pathways, it seems plausible that the response strength–stimulus rate functions for a given type of overt behavior and for the behavior of the neurons and synapses in these pathways might be the same in shape. Kestenbaum, Deutsch, and Coons (*1*) have, indeed, obtained evidence that such is the case at least in the pain system. The purpose of this study was to ascertain whether the isomorphism between strength-rate functions for overt and for neuronal behavior holds for a reward system as well.

The general plan involved implanting electrodes in the medial forebrain bundle of the hypothalamus, a structure which rats find rewarding to stimulate (*2*). Through these electrodes various patterns and rates of brief electrical pulses could be administered as samples of what the rat could then administer to himself by pressing a lever. With any fixed number of reinforced presses per minute defined as the overt behavior criterion of reward, the intensity of current required to elicit this criterion at each given rate or pattern of stimulation became the response-strength measure for generating the strength-rate function holding for self-stimulation behavior. Since the expectations regarding the shape of such a function were that it should resemble the shape of the excitability cycle already established for individual neurons and synapses, certain predictions were possible against which to test the validity of these expectations. For example, the more rapidly a neuron is stimulated, the more likely it is that the postsynaptic neuron will fire, because the neurotransmitter