Chapter 2

Effects of Artificial Night Lighting on Terrestrial Mammals

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All 986 species of bats, badgers and most smaller carnivores, most rodents (with the notable exception of squirrels), 20% of primates, and 80% of marsupials are nocturnal, and many more are active both night and day (Walls 1942). Thus it would be surprising if night lighting did not have significant effects on mammals. Compared with investigations on birds, lepidopterans, other insects, and turtles, however, few studies, or even anecdotal reports, document the effects of artificial night lighting on mammals in the wild. Because of the dearth of empirical evidence, this chapter begins with a review of the biology of mammalian vision, including the extensive literature on how moonlight affects nocturnal behavior of mammals and how light influences mammalian biological clocks. I then discuss several classes of likely effects of artificial night lighting on mammals, namely disruption of foraging patterns, increases in predation risk, disruption of biological clocks, increases in mortality on roads, and disruption of dispersal movements through artificially lighted landscapes. I include recommendations for experiments or observations that could advance our understanding of the most likely and significant effects.

Light and the Ecology and Physiology of Mammals

Insight into the potential consequences of artificial night lighting on mammals can be gained from an understanding of the activity patterns, visual ability, and physiological cycles of species under normal patterns of light and dark. Artificial light at night may disrupt the various daily, monthly, and annual cycles described in this section.

Mammals vary in their activity periods, with corresponding adaptations in their visual systems (Walls 1942). Activity patterns can be classified into five types (Halle and Stenseth 2000). Mammals with a nocturnal pattern obviously are most likely to be affected by artificial night lighting. I will treat the crepuscular pattern, defined as nocturnal with activity peaks at dawn and dusk, as a variant on the nocturnal theme; this group includes most lagomorphs. Diurnal mammals include all squirrels except the flying squirrels and most primates, including humans. Indeed, if human vision were not so anatomically diurnal, artificial lighting would not be necessary. Mammals with the 24-hour pattern include ungulates and larger carnivores, plus some smaller carnivores. These species have excellent night vision and usually are most active at night but have regular daytime activity periods as well. I ignore the ultradian pattern—periodicity less than 24 hours, typically 3- to 5-hour cycles—because it has been documented only in voles and is light-independent (Gerkema et al. 1990).

Anatomy and Physiology of Vision in Mammals

How various mammals respond to light depends, among other things, on the architecture of the eye, including its pupil, type of lens, and especially whether the photosensitive cells in the retina are dominated by rods or cones. Nocturnal mammals have large pupils to admit more light, huge lenses to minimize spherical aberration, and rod-rich retinas (Walls 1942). The rod system has high sensitivity but low acuity; that is, it can be stimulated by a few photons, but ability to see detail is poor because many rod cells connect to a single neuron. This means that small stimuli from several rods can act in concert to stimulate a neuron and thus deliver a signal to the brain. Because the brain is unable to determine exactly which rods were stimulated, however, it cannot discern the exact size and shape of the perceived object. In contrast, there is little summation among neurons where cones and neurons approach a 1:1 ratio in parts of some mammalian retinas.

Most nocturnal mammals have few cones; bats and armadillos have nearly cone-free retinas (Walls 1942). Nocturnal mammals with few cones are temporarily blinded by bright light because the rods become unresponsive (i.e., saturated) above 120 cd/m^2, approximately the light level at twilight. Narrowing the pupil is the primary short-term defense of cone-poor mammals against rod saturation in bright light but is only marginally effective at reducing the blinding effect of light (Perlman and Normann 1998).

Because they lack high-resolution cones, few nocturnal mammals eat seeds, small fruits, or small mobile insects unless such foods are clumped into large, visually detectable aggregations such as inflorescences or anthills or are detectable by other means such as echolocation or scent. Nocturnal animals can partially overcome the poor resolving power of the rod-dominated retina by having large eyes that permit large retinal images. Because the size of rods does not decrease with body size, what matters here is the absolute, not relative, size of the retinal image (Walls 1942). Thus the limited skull size of small nocturnal mammals limits their evolutionary ability to improve visual resolution.

The retina of diurnal mammals is rich in cones, which provide clear images at close range or in good light. A large number of photons is needed to stimulate a cone, however, which makes cones useless in dim light. Most, perhaps all, diurnal squirrels are similar to diurnal birds in having retinas so poor in rods that they are nearly blind at night. Although most diurnal mammals, including humans, have fewer cones than rods, most of these mammals are large, and their large retinal image ensures high visual acuity in daylight. The lenses of diurnal mammals resemble those of 24-hour mammals.

Like some nocturnal and crepuscular mammals, most mammals capable of 24-hour activity have a retina composed mostly of rods, but they have enough cones for a second image-forming system useful in bright light (Perlman and Normann 1998). Changes in pupil size are less important than photon saturation of the rods in switching between systems (Perlman and Normann 1998). When a mammal with a 24-hour eye comes from darkness into light, the rods saturate, thereby becoming incapable of stimulation, and the shift to the cone system occurs within about 2 seconds. The shift from bright to low light takes much longer (Lythgoe 1979) and involves more complex chemical reactions for the rods to fully resensitize (Perlman and Normann 1998). Although the rod system may gain a 100-fold increase in sensitivity within 10 minutes after the transition to darkness, another 10-fold gain in sensitivity can occur between 10 and 40 minutes (Lythgoe 1979). The presence of a bright light in an otherwise dark environment may suppress the rod system in part or all of the retina, leaving the animal not fully adjusted to the dark.

Many 24-hour mammals, and some nocturnal and crepuscular mammals, have a highly reflective layer behind the photoreceptive cells, the tapetum lucidum, that amplifies the light reaching those cells. The tapetum is found in most carnivores and ungulates but rarely in rodents, lagomorphs, or higher primates.

In mammals with both rod and cone systems, the shift between systems is accompanied by a change in spectral sensitivity called the Purkinje shift. Cone cells have a variety of photoreactive pigments, and this variety creates a capacity for color vision in the cone system. Because rods rely on only one photoreactive pigment, rhodopsin, with maximum absorption around 496 nm, the color-blind rod system discriminates only on the basis of brightness.

Influence of Moonlight on Behavior of Nocturnal Mammals

Most nocturnal mammals react to increasing moonlight by reducing their use of open areas, restricting foraging activity and movements, reducing total duration of activity, or concentrating foraging and longer movements during the darkest periods of night. Such behaviors have been recorded in studies of desert rodents (Lockard and Owings 1974, Price et al. 1984, Bowers 1988, Alkon and Saltz 1988), temperate zone rodents (Kaufman and Kaufman 1982, Travers et al. 1988, Vickery and Bider 1981, Wolfe and Summerlin 1989, Topping et al. 1999), desert lagomorphs (Butynski 1984, Rogowitz 1997), Arctic lagomorphs (Gilbert and Boutin 1991), fruit bats (Morrison 1978, Law 1997, Elangovan and Marimuthu 2001), a predatory bat (Subbaraj and Balasingh 1996), some primates (Wright 1981), male woolly opossums (Julien-Laferrière 1997), and European badgers (Cresswell and Harris 1988).

Most authors attributed these changes to increased predation risk in open habitats under bright moonlight. Although no field study conclusively confirms or refutes this explanation, circumstantial evidence supports it. Increased coyote howling during the new moon is consistent with the unprofitability of hunting rodents under these conditions (Bender et al. 1996). In laboratory studies (Clarke 1983, Dice 1945), owls were better able to catch deer mice in brighter light. However, as Clarke (1983) explained, these laboratory results may not reveal much about the effect on predation rate under natural conditions. On bright nights, most prey remain in secure places, but the few that are in bright conditions may be readily killed. On dark nights, owl efficiency per prey may be reduced, but with many active prey available, the total prey consumption and the prey's mortality rate from the owl may be unchanged (Daly et al. 1992). Similarly, ocelot behavior is consistent with the hypothesis that fewer but more successful prey encounters occur under bright light (Emmons et al. 1989).

Some nocturnal species neither decrease activity nor seek habitats with canopy cover during bright moonlight. Many insectivorous bats do not decrease activity during bright moonlight (Negraeff and Brigham 1995, Hecker and Brigham 1999), although some species do, at least in captivity (Erkert 2000). Some insectivorous bats prefer to forage in upper canopy under bright moonlight (Hecker and Brigham 1999) or under artificial night lighting (Rydell and Baagøe 1996), in both cases because insect prey are more abundant in the brighter areas (for further discussion of bats see Chapter 3, this volume). Moonlight is associated with increased activity in woodland rodents such as *Peromyscus leucopus* (Barry and Francq 1982), the nocturnal monkey *Aotus trivirgatus* (Wright 1981), and the galagos (Galagonidae; Nash 1986). In most instances, these studies provided adaptive reasons for increased activity in moonlight. For example, the galagos, although nocturnal, visually detect their insect prey, and they avoid predation not by concealment but by visual detection, mobbing, and flight. Moonlight does not change the activity pattern of ocelots (Emmons et al. 1989) or white-tailed deer (Beier and McCullough 1990; but see Kie 1996).

The Circadian Clock in Mammals

The freerunning period of activity, the activity cycle for an animal under constant light or darkness, ranges from 23 to 25 hours for most vertebrates, with extremes of 21 to 27 hours (Foster and Provencio 1999). Because the freerunning clock is not exactly 24 hours, the internal circadian system must be synchronized to local time by a cue in the animal's environment. This process is called entrainment, and the cue used to synchronize the internal clock is called a zeitgeber. For all vertebrates, the primary zeitgeber is change in the quantity, and perhaps the spectral quality, of light at dawn and dusk (Foster and Provencio 1999). In vertebrates, the two image-forming visual systems (i.e., the rod and cone systems) do not entrain the biological clock, which is governed by a special photoreceptor system separate from them. In mammals, this photoreceptor system lies in the retina and communicates to a different part of the brain, the suprachiasmatic nuclei (SCN), via a different neural system, comprising less than 0.01% of retinal ganglion cells (Foster and Provencio 1999). Loss of the eyes or SCN blocks entrainment of the circadian clock in all mammals studied. Shifting circadian rhythm requires more light than that needed to form a visual image, and the stimulus must be of longer duration, 30 seconds to 100 minutes (Figure 2.1; Foster and Provencio 1999).

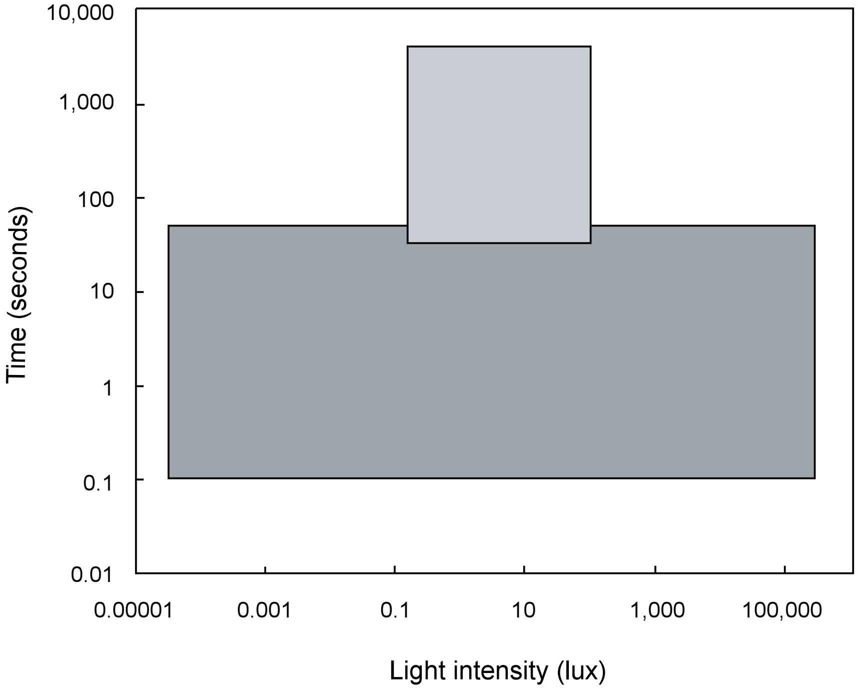

Figure 2.1. The response range of the visual imaging system (large box) has minimal overlap with the response range of the circadian system in vertebrates (small box). Influencing the biological clock requires both more light (*x*-axis) and longer duration (*y*-axis) than forming a visual image. This protects the circadian system from many photic stimuli that do not provide reliable time cues. The upper threshold in light intensity makes the circadian clock more sensitive to twilight intensities than to full sunlight. Artificial lights within the range of duration and intensity described by the small box disrupt the mammalian biological clock. Figure adapted from Foster and Provencio (1999: Figure 3), with the *x*-axis converted from photons per unit area. Although there is no exact conversion to lux, this approximation allows the reader to compare these light intensities with those illustrated in Figure 2.2.

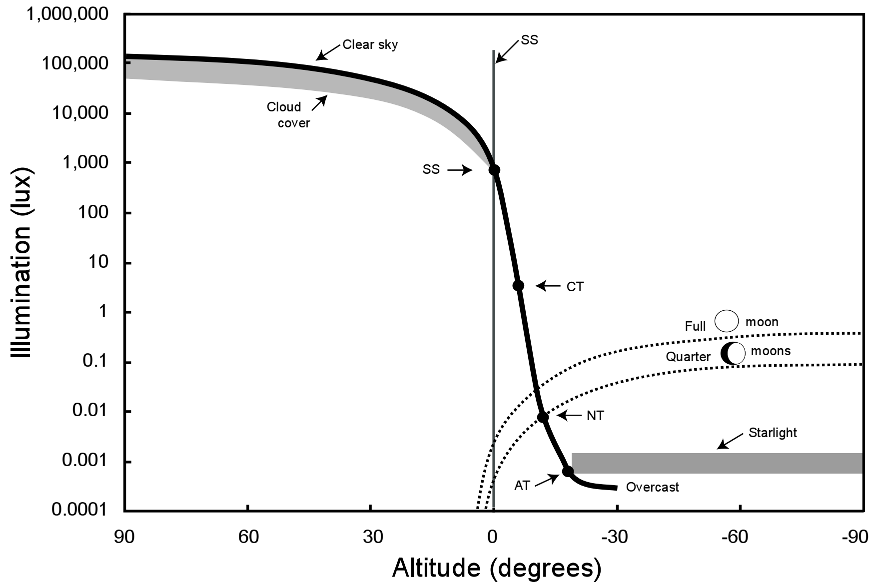

Figure 2.2. Illumination at Earth's surface varies with solar and lunar altitude above the horizon. For comparative purposes, the Illuminating Engineering Society recommends 3–16 lux illumination for U.S. highways or as a maximum for off-site spill from recreational sports facilities. In practice, these recommendations often are exceeded by an order of magnitude. Note log scale on *y*-axis. The altitude of the moon above the horizon is deliberately displayed on the negative (below horizon) half of the *x*-axis so that the *x*-axis can be interpreted as time relative to sunset. AT, astronomical twilight with sun 18° below horizon; CT, civil twilight with sun 6° below horizon; NT, nautical twilight with sun 12° below horizon; SS, sunset. Figure adapted from McFarland et al. (1999: Figure 1).

Light level at twilight falls at the lower end of this range (Figure 2.2; McFarland et al. 1999). These thresholds—as well as the upper limits—are useful in preventing photic noise from resetting the circadian clock. For instance, lightning, which can be fifty times brighter than direct sunlight, would confuse circadian rhythm if it were of sufficient duration. It has long been thought that the irradiance of starlight and the full moon both fall below the threshold for entrainment and cannot reset the circadian clock, although entrainment of circadian rhythm recently has been recorded at illuminances as low as 10^{-5} lux in bats (Erkert 2004). Low-intensity stimuli of sufficient duration can suppress melatonin production in rats (Dauchy et al. 1997) and humans (Brainard et al. 1997), suggesting that such stimuli also affect the circadian clock, at least in humans (Shanahan et al. 1997) in addition to bats.

The light regime and the circadian clock also influence production of some hormones, notably melatonin, which mediates not only the activity patterns discussed earlier but also almost every physiological or behavioral rhythm in mammals (Bartness and Goldman 1989). In all species, melatonin production is high at night and suppressed during daytime, although reaction to melatonin often differs between diurnal and nocturnal species. Among its many roles, melatonin suppresses tumor growth by regulating production and tumor use of linoleic acid. In a laboratory experiment, Dauchy et al. (1997) determined that minimal light contamination of 0.2 lux, simulating a light leak around a laboratory door during an otherwise normal dark phase, disrupted normal circadian production of melatonin and promoted tumor growth in rats. Compared with rats experiencing a cycle of 12 hours light and 12 hours total darkness per day, rats experiencing light contamination produced 87% less melatonin, similar to the 94% decline observed in rats held in full light 24 hours per day. There were corresponding dramatic increases in tumor growth. Remarkably, low-intensity light exposure during the subjective dark phase had virtually the same effect as constant light in blocking melatonin production and stimulating tumor growth.

The Circannual Clock and Lunar Clock in Mammals

Mammals also have an endogenous rhythm with a freerunning period of about 1 year. The circannual clock influences annual changes in body mass, hormones, reproductive status, hibernation, and the circadian activity pattern over the course of the year. By controlling breeding season, delayed fertilization of the ovum, and delayed implantation of the blastocyst, the circannual clock causes parturition of most species of mammals to occur in a highly compressed period. This reduces the neonatal mortality rate by predator swamping and synchronizes parturition with favorable foraging conditions (Vaughan 1978, Gwinner 1986).

Because experiments on the circannual clock take years to complete, our understanding of it remains poor, and only three mammal species have been studied in any detail, namely the golden hamster (*Mesocricetus auratus*; Bronson 1989), domestic sheep (Bronson 1989), and golden-mantled ground squirrel (*Spermophilus lateralis*; Dark et al. 1990, Zucker et al. 1983, Pengelley and Fisher 1963, Lee et al. 1986). Light appears to be the most important—perhaps the only—zeitgeber for the circannual clock of hamster and sheep (Bronson 1989). Both of these species are highly domesticated, however, and all laboratory stocks of the hamster are highly inbred, having descended from a single mother and her litter captured in 1930. These factors may limit the extent to which we can extrapolate to wild mammals.

Light may be of equal or lesser importance than temperature in setting the circannual clock of the golden-mantled ground squirrel and especially in governing the hibernation cycle of the species. Zucker et al. (1983) demonstrated that light was involved in entraining the circannual clock in golden-mantled ground squirrels. However, loss of the SCN disrupted the annual reproductive cycle and the annual cycle of body mass in only eight of nineteen squirrels, indicating existence of a circannual oscillator that is anatomically separate from the SCN. Although the neural structure that functions as the circannual oscillator has not been identified, it is influenced by the retinal system that terminates in the SCN (Dark et al. 1990). Although Hock (1955) reported a strong role for light in initiating hibernation of the Arctic ground squirrel (*Spermophilus undulatus*), Pengelley and Fisher (1963) reported that although an artificially reversed thermal regime caused golden-mantled ground squirrels to hibernate in summer, it was impossible to produce a similar reversal in the phase of the hibernation cycle by changing light conditions. Emergence from hibernation in spring cannot possibly be influenced by photoperiod because these squirrels hibernate in dark burrows.

In summary, studies of circannual cycles of a few mammalian species suggest that light is an important zeitgeber but perhaps not the only one. The importance of light as a circannual regulator is also a logical necessity, given the crucial role of light in production of melatonin and the well-documented importance of melatonin in governing reproductive activity (Bartness and Goldman 1989). Bronson (1989) and Gwinner (1986) provide excellent overviews of this complex topic.

Lunar cycles also may play an important role in timing of mammalian reproductive behaviors. Murray (1982) and Skinner and van Jaarsveld (1987) suggested that moonlight may synchronize estrus in some ungulates. Both of these were observational studies, and there appears to be no experimental work on how lunar cycles affect mammalian reproduction or whether the mammalian brain has a neural circalunar oscillator that is entrained by moonlight. The absence of such evidence is a result of a lack of effort and cannot be construed as refuting the existence or importance of a circalunar clock.

Plausible Effects of Artificial Night Lighting on Mammals

In the rest of this chapter I make inferences about plausible effects of artificial night lighting by considering the foregoing information in relation to the properties of artificial night light and evaluating the handful of studies on how artificial lighting influences mammal behavior in the wild. Potential influences of artificial lights at night on mammals include disruption of foraging behavior, increased risk of predation, disruption of biological clocks, increased deaths in collisions on roads, and disruption of dispersal movements and corridor use.

Disruption of Foraging Behavior and Increased Risk of Predation

Many studies cited in this chapter have shown that bats, nocturnal rodents, and other nocturnal mammals respond to moonlight by shifting their activity periods, reducing their activity, traveling shorter distances, and consuming less food. Artificial light of similar intensity to moonlight caused rodents in experimental arenas to reduce their activity, movement, and food consumption (Vasquez 1994, Kramer and Birney 2001, Brillhart and Kaufman 1991, Clarke 1983, Falkenberg and Clarke 1998). These experiments used both fluorescent and incandescent lights to simulate moonlight, with rodents responding to stimuli equivalent to that of a half moon (0.1 lux) as well as a full moon (0.3 lux). Thus, artificial night lighting of similar intensity to moonlight reduces activity and movement of many nocturnal animals, particularly those that rely on concealment to reduce predation risk during nocturnal foraging. Because roadway lighting in the United States is designed to illuminate the road surface at a minimum of 3 lux (the lowest acceptable value midway between light standards) and an average of 4–17 lux, depending on type of pavement and roadway, with maximum values two or three times the average directly under lampposts (IESNA 2000), all artificial night lighting can be expected to have such effects along road edges.

Although small mammals can respond to bright moonlight by shifting foraging and ranging activities to darker conditions, this option is not available to animals experiencing artificially increased illumination throughout the night. Under these circumstances, unless they abandon the lighted area, nocturnal animals have only two unfortunate choices. One is to accept the risk of predation by foraging under bright light, as Alkon and Saltz (1988) observed when food shortages forced crested porcupines (*Hystrix indica*) to abandon their light-phobic behaviors. The other option is to continue to minimize predation risk even at the cost of loss of body mass, as observed in an experiment on the cricetid rodent *Phyllotis darwini* (Vasquez 1994). The rodents responded to simulated moonlight by carrying 40% of their food to the refuge site in the arena and consuming it there, compared with less than 4% of food consumption under dark conditions. On bright nights, the rodents consumed 15% less food and lost 4.4 g, compared with a 1.1-g weight loss on dark nights. Despite difficulties in translating these experimental results to field conditions, artificial night lighting undoubtedly reduces food consumption and probably increases predation risk for nocturnal rodents in the wild.

Few studies have investigated the effects of artificial light on feeding behavior of mammals in natural populations. In one study Kotler (1984) strongly confirmed that artificial night lighting affects nocturnal rodents. During the new moon, Kotler observed that seed harvest by the desert rodent community (four species of *Dipodomys*, *Peromyscus maniculatus*, and possibly *Perognathus longimembris* and *Microdipodops pallidus*) decreased an average of 21% in response to a single fluorescent or gasoline camping lantern placed to cast light equivalent to 160% (8 m [26 ft] from lantern) to 25% (35 m [115 ft] from lantern) of the light of a full moon. He also reported that, within trials, harvesting rate was lower at feeding sites that were most brightly illuminated, but he did not quantitatively describe that relationship. To help planners estimate the magnitude of this effect, future research should determine the functional relationship between food harvest (or other variables related to fitness) and illumination and determine whether there is a threshold illumination below which no effect occurs. Although lighting at sport stadiums, gas stations, and some commercial operations is brighter than highway lighting, the latter probably is the brightest lighting that affects large areas of wildlands. Thus, research focusing on the intensities and heights of lighting that are prescribed or implemented along highways, and their effects in a landscape context, would be most helpful.

Bird et al. (2004) also investigated the effects of artificial lighting on rodent foraging. In coastal Florida, they measured foraging of Santa Rosa beach mouse (*Peromyscus polionotus leucocephalus*) as a proxy for another threatened and endangered subspecies of *Peromyscus polionotus*. Resource patches of food were placed along transects with arrays of low pressure sodium lights, "bug" lights, and no lights. The percentage of resource patches foraged by mice was significantly higher in dark arrays than light arrays and higher at arrays with bug lights than low pressure sodium lights. Effects of actual beachfront lighting were presumed to be greater those observed in the experiment because taller and more intense light sources are commonly used in coastal development.

De Molenaar et al. (2003) studied mammal response to streetlamps experimentally installed on small earthen dams that crossed flooded drainage ditches in the Netherlands. Aquatic mammals such as muskrats (*Ondatra zibethicus*) had to cross these dams to move along the ditch, and other mammals used the dams to pass between patches of upland habitat without swimming. The four predators—polecat (*Mustela putorius*), stoat (*Mustela erminea*), weasel (*Mustela nivalis*), and fox (*Vulpes vulpes*)—were more likely to walk on or near illuminated dams than unlit ones, and the brown rat (*Rattus norvegicus*) seemed to avoid lighted dams. The four other species studied (muskrat, hedgehog [*Erinaceus europaeus*], hare [*Lepus europaeus*], and roe deer [*Capreolus capreolus*]) showed no marked response.

With their cone-rich retinas, most sciurids probably are nearly blind at night, even under moonlight or artificial night lighting. To conceal themselves from visual predators, most tree squirrels spend the night in nests in trees, and ground squirrels sleep underground. To the extent that artificial night lighting assists visual predators at night, it could decrease squirrel survival rates.

Does artificial night lighting benefit owls, bats, or other predators? If desert rodents are more vulnerable to owls and other nocturnal predators under moonlight or its equivalent, it is tempting to think of artificial night lighting as enhancing habitat for these predators. Many species of insectivorous bats aggregate at streetlamps to exploit aggregations of moths and other insects that are attracted to the light (Blake et al. 1994, Rydell and Baagøe 1996). Some reports have implied that this is good for bats, but this makes sense only under the nonecological valuation that more is better. Certainly such aggregations are not natural, nor are they beneficial to insect prey of the bats. Such lighting should not be justified in terms of benefits to bats unless the feeding stations are explicitly intended to compensate for human-caused loss of other food sources or human-caused excess of the insect populations attracted to the lights.

Disruption of Biological Clocks

Assuming that the circadian clock evolved to maximize foraging efficiency, to reduce risk of predation, to enhance parental care, or for similarly important reasons, artificial night lighting can adversely affect animals by disrupting that clock. These individuals also would be out of phase with their neighbors living in a natural light–dark cycle; in more social mammals this could affect mating success, group-mediated antipredator vigilance, and other processes.

Almost all studies of how light pulses can shift the biological clock used artificial light, either fluorescent or incandescent, as the stimulus. All of these studies demonstrate that brief (10- to 15-minute duration) and moderately bright (about 1,000 lux, equivalent to bright twilight) stimuli can shift the circadian clock by 1–2 hours (Halle and Stenseth 2000). This finding suggests that artificial night lighting can disrupt circadian patterns in the wild. These experiments were conducted only on captive animals held in 24-hour darkness except for the experimental stimuli, however. One experiment on the nocturnal flying squirrel *Glaucomys volans* came much closer to natural conditions in that the experimental animals had free access to a completely dark nest box and could choose when to emerge to a larger chamber where they might encounter artificial light (DeCoursey 1986). If the squirrel encountered light at arousal time, when it expected to enter a dark world, it would return to its nest box to sleep, delaying its circadian clock by 40 minutes. Because most nocturnal animals spend the day in burrows or cavities with unmeasured but presumably very low light levels, these experimental results probably are ecologically relevant to all nocturnal mammals.

Only two studies compared artificial light with daylight in terms of their effects on the circadian clock. In one study, wild-caught nocturnal mice were subjected to pulses of daylight, incandescent light, and fluorescent light, each 1,000 lux and 15 minutes in duration, at various points in the circadian cycle (Sharma et al. 1997). The phase shift response was strongest 2–3 hours after the transition from subjective day to subjective night, at which time the daylight stimulus produced a greater delay in activity (about 2.5 hours) than the two types of artificial light (each about 1.5 hours). The other study (Joshi and Chandrashekaran 1985) applied the same experimental protocol on a bat and found that incandescent lights produced large phase shifts in the opposite direction as the shifts elicited by daylight and fluorescent light. Artificial night lighting is about as effective as natural light in setting or disrupting the circadian clock.

The effect of the circadian clock on melatonin production may have serious ecological consequences. Dauchy et al. (1997) documented that modest levels of nocturnal light suppressed melatonin production with dramatic effects on tumor growth in rats. Although these results cannot be directly translated to wild mammals, this study suggests that disruption of biological clocks by artificial night lighting could have profound effects on individual animals. If a significant fraction of individuals in a population are affected, population and ecosystem effects are also possible. In the golden hamster, the visual system that regulates the circadian clock is responsive to stimuli between 300 and 500 nm but insensitive to wavelengths of 640 nm or longer and 290 nm or shorter (Brainard et al. 1994). Further research on the spectral sensitivity of additional mammals may provide guidance that would allow the selection of outdoor lighting to avoid or minimize this potential effect, perhaps in the red–yellow spectrum.

Despite ample evidence that artificial lighting can disrupt circadian and circannual clocks in the laboratory setting—where all existing research has been conducted—there is no confirmation of these effects in wild populations. In part this is an intractable problem because phase shifts have been defined in a way (Gwinner 1986) that can be measured only in a laboratory. However, melatonin levels in wild populations subject to artificial night lighting could be compared with levels in undisturbed populations, controlling for time of day, to yield a biologically meaningful estimate of the magnitude of this problem in nature. In addition, population-level studies can demonstrate the overall effect of artificial night lighting on mammal populations, although it may be difficult or impossible to disentangle the effects of disrupted biological clocks from those of other mechanisms, such as reduced foraging or increased predation risk.

Effect of Street Lighting on Roadkill of Mammals

Intensity and type of street lighting may influence the probability of wildlife mortality in collisions with vehicles. It seems logical that most types of lighting will make animals more visible to drivers and thus reduce risk of mortality by giving the driver more time to react. There is no research supporting this idea, however, and Reed (1995), Reed et al. (1979), and Reed and Woodward (1981) concluded that increased highway illumination was not effective at reducing deer–vehicle accidents in the United States.

Some artificial night lighting makes it difficult for nocturnal mammals to avoid collisions with vehicles if the animal experiences a rapid shift in illumination. Many nocturnal species are using only the rod system, and bright lighting saturates their retinas. Although many nocturnal mammals have a rudimentary cone system and can switch over to it within a couple seconds, during those seconds they are blinded. Once they switch to the cone system, areas illuminated to lower levels become black, and the animal may become disoriented, unable to see the dark area across the road and unwilling to flee into the unseeable shadows whence it came. This is not solely a problem for a rod-dominated visual system because even a cone-dominated system is ineffective when a small part of the visual field is many orders of magnitude brighter than the remaining field. This glare phenomenon is familiar to any backcountry camper who has been temporarily blinded by a companion's flashlight. Finally, if the animal is in the lighted area long enough to saturate its rod system, it will be at a distinct disadvantage for 10–40 minutes after returning to darkness.

The lowest possible lighting level consistent with human safety is the best for mammals crossing roads. There is no advantage to using lighting that is closer to the sunlight spectrum for these cone-poor animals. Indeed, low pressure sodium lights, with emission at 589 nm, provide reasonably effective vision for human drivers, who have mixed cone and rod vision, while interfering least, of the available lamp types, with the dominant rod-based vision of nocturnal mammals. Because the rod system has peak sensitivity near 496 nm, low pressure sodium lights should appear about one-tenth as bright to a rod-dominated retina as to a human retina.

Little ecological research, and a modest amount of human and engineering research, is needed on the issue of designing highway lighting to minimize roadkill mortality. Our knowledge of mammalian vision is sufficient to conclude that, from the animal's perspective, less is better. Research should focus on the straightforward issue of determining the lowest level of illumination that increases the ability of human drivers to see a large animal, thus allowing the driver to avoid collision, without disabling the rod-dominated retina of mammals, thus allowing them to escape into the darkness. Other technical questions, relevant not only to roadkill but also to biological clocks, predation risk, and foraging behavior, include developing cost-effective designs to confine lighting to the roadway and balancing them with a lamp height and beam pattern that reduces effects on the sensitive central part of the driver's retina.

Disruption of Dispersal Movements and Corridor Use

With increasing emphasis on providing biotic connectivity at the landscape scale, there is an increased need for information on how various factors influence the utility of a connective area. It follows from the preceding that street lighting negatively affects a mammal's ability and willingness to cross a road or to move through any area with artificial night lighting. Although planners and conservationists have focused on the issue of how wide a corridor should be, it is obvious that the answer depends on how bright it is.

Only two studies attempted to address how a mammal, moving at night through unfamiliar terrain, might react to natural or artificial light or otherwise use visual information to find suitable habitat. A study of dispersing puma (*Puma concolor*) in urban southern California noted several exploratory movements that did not follow favored topography or vegetation patterns (Beier 1995). Beier speculated that the pumas were moving away from the urban glow and navigating toward the darkest horizon. Beier also noted instances in which an animal, exploring new habitat for the first time, stopped during the night at a lighted highway crossing its direction of travel with unlit terrain beyond. In several instances, the animal would bed down until dawn, selecting a location where it could see the terrain beyond the highway after sunrise. The next evening, the puma would attempt to cross the road if wildland lay beyond or would turn back if industrial land lay beyond.

Another study revealed that white-footed mice (*Peromyscus leucopus*) are capable of a similar "look now and move later" strategy (Zollner and Lima 1999). Zollner and Lima experimentally released woodland mice in bare agricultural fields at night under dark or moonlit conditions and at various distances from a single woodland patch, which was suitable habitat for the mouse, in the area. Under dark conditions, the mice were incapable of perceiving and orienting to the woodland patch at distances of 30 m (98 ft) or more. Full moonlight extended the perceptual range to 60 m (197 ft), and mice given a twilight look at the landscape before sunset were able to orient from 90 m (295 ft) away. Thus, if mice were not deterred by psychology, activity pattern, and predation risk, interpatch dispersal by mice would be more successful under daylight illumination. The study demonstrates that mice are able to assess the landscape under full light and use that information to move successfully in the dark, however.

Zollner and Lima (1999) also open a new realm of research, namely empirically determining the perceptual range of an animal, or the distance at which habitat patches can be perceived. Goodwin et al. (1999) provide helpful suggestions for sound statistical analyses and alternative approaches. Such research, using species for which corridors are designed, may provide a scientific basis for designing corridors and determining how animals use vision to explore new terrain.

Although perceptual range of mice increased in moonlight, there are two reasons that artificial night lighting may not similarly increase perceptual range and help animals find new patches. First, by saturating an animal's rod system, artificial night lighting plunges most of the landscape into darkness. Second, because a dispersing animal can anticipate this effect, it may orient away from the lights.

Movement in connective areas can be affected by adjacent lights of recreational fields, industrial parks, service stations, and housing. In southern California, where the South Coast Missing Linkages effort is attempting to maintain and restore landscape linkages between fifteen pairs of large wildlands, three riparian corridors are lined with homes sitting atop a low manufactured slope, and all fifteen linkages are crossed by lighted freeways (Beier et al. in press). Efforts to maintain and restore these landscape linkages should incorporate the general rule that less light is better for animal movement.

Research Issues

The literature on the effects of light on foraging behavior, predation risk, and biological clocks consists of two distinct approaches with little overlap. One approach is to study effects of moonlight on behavior of individual wild mammals; the other is to study the effects of artificial light on animals in laboratories. The discussion in this chapter underscores the need for studies using artificial lights on natural populations. Substantial expertise already exists, and productive collaborations between ecologists and laboratory physiologists could result in rapid progress.

Population-Level Research

A simple fusion of the two approaches will fall short of the mark unless at least some research efforts focus above the level of the response of individual animals. For instance, if research were to confirm that artificial night lighting increased numbers of tumors in wild mice by 25% or increased predation risk by 15%, this finding still would not address the issue of effects on the wild population. Conceivably, the induced tumors could shorten the lifespan of affected mice by only a few weeks or days, or predation mortality could act in a compensatory fashion with other types of mortality to reduce greatly the net effect on survival rates of animals living in the light-polluted zone. This effect could be further diluted if the light-polluted zone were part of a larger habitat, most of which was not directly affected by light, in which case the polluted zone may be a small population sink. Conversely, interactions between individuals from the polluted zone with neighbors in dark zones, such as dissolution of the synchrony of estrus and parturition, could amplify the effect. Only careful, whole-population studies can address these more important questions.

A critical element in study design is to include both treatment populations and control populations. Ideally, studies will include both replication with more than one treatment and control population and observations in both treatment and control populations before light pollution (Stewart-Oaten et al. 1986). This paired before–after–control–impact study design also is appropriate for situations in which replication is not possible. Although this design lacks random allocation of treatments to experimental units, it can provide meaningful answers to important applied questions (Beier and Noss 1998). It is far better to have an approximate answer to the right question than a precise answer to the wrong question.

Equivalence Testing

In the study of individuals or populations, the statistical analysis of the effects of artificial night lighting should use equivalence testing (Patel and Gupta 1984, McBride et al. 1993), in which the null hypothesis is "artificial night lighting has biologically meaningful negative effects on mammals," rather than the traditional null hypothesis of "no effect." Failure to reject the traditional null hypothesis typically leads to complacency, even if the failure to reject resulted from undersampling or other design flaws. The burden of proof falls, inappropriately, on the most plausible point of view. In contrast, in an equivalence test, failure to reject the null hypothesis lends continued support to the most plausible state of nature, namely that there is an effect, and shifts the burden of proof to proponents of the idea that there is no biologically significant effect. Equivalence testing therefore is appropriate in all situations in which related studies and known cause–effect relationships suggest an environmental impact. Because the procedure requires the analyst to specify the direction and magnitude of a biologically meaningful effect, rejection of the null hypothesis is by definition a biologically, as well as statistically, significant outcome. This is in marked contrast to tests of traditional null hypotheses, in which the "insignificance of significance testing" (Johnson 1999) is an intractable issue.

Conclusion

For small, nocturnal, herbivorous mammals, artificial night lighting increases risk of being killed by a predator and decreases food consumption. Such lighting probably also disrupts circadian rhythms and melatonin production of mammals. Most research has documented the response of individual wild animals to moonlight or of laboratory animals to artificial light, however. Research on how artificial lights affect wild mammals at the population level is lacking. Significant progress relevant to management decisions will entail collaboration between ecologists and laboratory physiologists and assessment of population-level responses (e.g., rates of survival and reproduction) as well as individual behavioral and physiological responses (e.g., food consumption, avoidance of lighted areas, and melatonin levels). I recommend an experimental design that includes observation on paired control (dark) and treatment (lighted) landscapes both before and after installation of artificial night lighting. Given the preponderance of evidence from previous studies and known cause–effect relationships, statistical procedures should test the null hypothesis that artificial night lighting has a biologically significant negative effect on survival and reproduction, appropriately placing the burden of proof on proponents of the idea that such lighting is benign.

Night lighting also may increase roadkill of animals and can disrupt mammalian dispersal movements and corridor use. Research on these issues is a straightforward matter of determining an intensity, spectral output, and physical arrangement of lighting fixtures that enhances human safety while minimally affecting the rod-dominated visual system of nocturnal mammals. In addition, experiments to determine the perceptual range of mammals (i.e., the distance at which habitat patches can be discerned by an animal exploring new terrain) may enhance significantly a land manager's ability to locate artificial night lighting adjacent to wildlife linkages such that it minimizes interference with perception of habitat patches by species to be served by the linkage.

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Literature Cited

Alkon, P. U., and D. Saltz. 1988. Influence of season and moonlight on temporal activity patterns of Indian crested porcupines (*Hystrix indica*). *Journal of Mammalogy* 69:71–80.

Barry, R. E. Jr., and E. N. Francq. 1982. Illumination preference and visual orientation of wild-reared mice, *Peromyscus leucopus*. *Animal Behaviour* 30:339–344.

Bartness, T. J., and B. D. Goldman. 1989. Mammalian pineal melatonin: a clock for all seasons. *Experientia* 45:939–945.

Beier, P. 1995. Dispersal of juvenile cougars in fragmented habitat. *Journal of Wildlife Management* 59:228–237.

Beier, P., and D. R. McCullough. 1990. Factors influencing white-tailed deer activity patterns and habitat use. *Wildlife Monographs* 109:1–51.

Beier, P., and R. F. Noss. 1998. Do habitat corridors provide connectivity? *Conservation Biology* 12:1241–1252.

Beier, P., K. L. Penrod, C. Luke, W. D. Spencer, and C. Cabañero. In press. South coast missing linkages: restoring connectivity to wildlands in the largest metropolitan area in the United States. In K. R. Crooks and M. A. Sanjayan (eds.), *Connectivity and conservation*. Cambridge University Press, Cambridge, UK.

Bender, D. J., E. M. Bayne, and R. M. Brigham. 1996. Lunar condition influences coyote (*Canis latrans*) howling. *American Midland Naturalist* 136:413–417.

Bird, B. L., L. C. Branch, and D. L. Miller. 2004. Effects of coastal lighting on foraging behavior of beach mice. *Conservation Biology* 18:1435–1439.

Blake, D., A. M. Hutson, P. A. Racey, J. Rydell, and J. R. Speakman. 1994. Use of lamplit roads by foraging bats in southern England. *Journal of Zoology, London* 234:453–462.

Bowers, M. A. 1988. Seed removal experiments on desert rodents: the microhabitat by moonlight effect. *Journal of Mammalogy* 69:201–204.

Brainard, G. C., F. M. Barker, R. J. Hoffman, M. H. Stetson, J. P. Hanifin, P. L. Podolin, and M. D. Rollag. 1994. Ultraviolet regulation of neuroendocrine and circadian physiology in rodents. *Vision Research* 34:1521–1533.

Brainard, G. C., M. D. Rollag, and J. P. Hanifin. 1997. Photic regulation of melatonin in humans: ocular and neural signal transduction. *Journal of Biological Rhythms* 12:537–546.

Brillhart, D. B., and D. W. Kaufman. 1991. Influence of illumination and surface structure on space use by prairie deer mice (*Peromyscus maniculatus bairdii*). *Journal of Mammalogy* 72:764–768.

Bronson, F. H. 1989. *Mammalian reproductive biology*. University of Chicago Press, Chicago.

Butynski, T. M. 1984. Nocturnal ecology of the springhare, *Pedetes capensis*, in Botswana. *African Journal of Ecology* 22:7–22.

Clarke, J. A. 1983. Moonlight's influence on predator/prey interactions between short-eared owls (*Asio flammeus*) and deermice (*Peromyscus maniculatus*). *Behavioral Ecology and Sociobiology* 13:205–209.

Cresswell, W. J., and S. Harris. 1988. The effects of weather conditions on the movements and activity of badgers (*Meles meles*) in a suburban environment. *Journal of Zoology, London* 216:187–194.

Daly, M., P. R. Behrends, M. I. Wilson, and L. F. Jacobs. 1992. Behavioural modulation of predation risk: moonlight avoidance and crepuscular compensation in a nocturnal desert rodent, *Dipodomys merriami*. *Animal Behaviour* 44:1–9.

Dark, J., T. S. Kilduff, H. C. Heller, P. Licht, and I. Zucker. 1990. Suprachiasmatic nuclei influence hibernation rhythms of golden-mantled ground squirrels. *Brain Research* 509:111–118.

Dauchy, R. T., L. A. Sauer, D. E. Blask, and G. M. Vaughan. 1997. Light contamination during the dark phase in "photoperiodically controlled" animal rooms: effect on tumor growth and metabolism in rats. *Laboratory Animal Science* 47:511–518.

DeCoursey, P. J. 1986. Light-sampling behavior in photoentrainment of a rodent circadian rhythm. *Journal of Comparative Physiology* 159:161–169.

Dice, L. R. 1945. Minimum intensities of illumination under which owls can find dead prey by sight. *American Naturalist* 79:385–416.

Elangovan, V., and G. Marimuthu. 2001. Effect of moonlight on the foraging behaviour of a megachiropteran bat *Cynopterus sphinx*. *Journal of Zoology, London* 253:347–350.

Emmons, L. H., P. Sherman, D. Bolster, A. Goldizen, and J. Terborgh. 1989. Ocelot behavior in moonlight. Pages 233–242 in K. H. Redford and J. F. Eisenberg (eds.), *Advances in neotropical mammalogy*. Sandhill Crane Press, Gainesville, Florida.

Erkert, H. G. 2000. Bats: flying nocturnal mammals. Pages 252–272 in S. Halle and N. C. Stenseth (eds.), *Activity patterns in small mammals: an ecological approach* (Ecological Studies, 141). Springer, Berlin.

Erkert, H. G. 2004. Extremely low threshold for photic entrainment of circadian activity rhythms in molossid bats (*Molossus molossus*; Chiroptera–Molossidae). *Mammalian Biology* 69:361–374.

Falkenberg, J. C., and J. A. Clarke. 1998. Microhabitat use of deer mice: effects of interspecific interaction risks. *Journal of Mammalogy* 79:558–565.

Foster, R. G., and I. Provencio. 1999. The regulation of vertebrate biological clocks by light. Pages 223–243 in S. N. Archer, M. B. A. Djamgoz, E. R. Loew, J. C. Partridge, and S. Vallerga (eds.), *Adaptive mechanisms in the ecology of vision*. Kluwer Academic Publishers, Dordrecht, The Netherlands.

Gerkema, M. P., G. A. Groos, and S. Daan. 1990. Differential elimination of circadian and ultradian rhythmicity by hypothalamic lesions in the common vole *Microtus arvalis*. *Journal of Biological Rhythms* 5:81–95.

Gilbert, B. S., and S. Boutin. 1991. Effect of moonlight on winter activity of snowshoe hares. *Arctic and Alpine Research* 23:61–65.

Goodwin, B. J., D. J. Bender, T. A. Contreras, L. Fahrig, and J. F. Wegner. 1999. Testing for habitat detection distances using orientation data. *Oikos* 84:160–163.

Gwinner, E. 1986. *Circannual rhythms: endogenous annual clocks in the organization of seasonal processes*. Springer-Verlag, Berlin.

Halle, S., and N. C. Stenseth (eds.). 2000. *Activity patterns in small mammals: an ecological approach* (Ecological Studies, 141). Springer, Berlin.

Hecker, K. R., and R. M. Brigham. 1999. Does moonlight change vertical stratification of activity by forest-dwelling insectivorous bats? *Journal of Mammalogy* 80:1196–1201.

Hock, R. J. 1955. Photoperiod as a stimulus for onset of hibernation. *Federation Proceedings* 14:73–74.

IESNA (Illuminating Engineering Society of North America). 2000. *American national standard practice for roadway lighting*. ANSI/IESNA RP-8-00. IESNA, New York.

Johnson, D. H. 1999. The insignificance of statistical significance testing. *Journal of Wildlife Management* 63:673–772.

Joshi, D., and M. K. Chandrashekaran. 1985. Spectral sensitivity of the photoreceptors responsible for phase shifting the circadian rhythm of activity in the bat, *Hipposideros speoris*. *Journal of Comparative Physiology A* 156:189–198.

Julien-Laferrière, D. 1997. The influence of moonlight on activity of woolly opossums (*Caluromys philander*). *Journal of Mammalogy* 78:251–255.

Kaufman, D. W., and G. A. Kaufman. 1982. Effect of moonlight on activity and microhabitat use by Ord's kangaroo rat (*Dipodomys ordii*). *Journal of Mammalogy* 63:309–312.

Kie, J. G. 1996. The effects of cattle grazing on optimal foraging in mule deer (*Odocoileus hemionus*). *Forest Ecology and Management* 88:131–138.

Kotler, B. P. 1984. Effects of illumination on the rate of resource harvesting in a community of desert rodents. *American Midland Naturalist* 111:383–389.

Kramer, K. M., and E. C. Birney. 2001. Effect of light intensity on activity patterns of Patagonian leaf-eared mice, *Phyllotis xanthopygus*. *Journal of Mammalogy* 82:535–544.

Law, B. S. 1997. The lunar cycle influences time of roost departure in the common blossom bat, *Syconycteris australis*. *Australian Mammalogy* 20:21–24.

Lee, T. M., M. S. Carmichael, and I. Zucker. 1986. Circannual variations in circadian rhythms of ground squirrels. *American Journal of Physiology* 250:R831–R836.

Lockard, R. B., and D. H. Owings. 1974. Moon-related surface activity of bannertail (*Dipodomys spectabilis*) and Fresno (*D. nitratoides*) kangaroo rats. *Animal Behaviour* 22:262–273.

Lythgoe, J. N. 1979. *The ecology of vision*. Clarendon Press, Oxford.

McBride, G. B., J. C. Loftis, and N. C. Adkins. 1993. What do significance tests really tell us about the environment? *Environmental Management* 17:423–432.

McFarland, W., T. S. C. Wahl, and F. McAlary. 1999. The behaviour of animals around twilight with emphasis on coral reef communities. Pages 583–628 in S. N. Archer, M. B. A. Djamgoz, E. R. Loew, J. C. Partridge, and S. Vallerga (eds.), *Adaptive Mechanisms in the Ecology of Vision*. Kluwer Academic Publishers, Dordrecht, The Netherlands.

Molenaar, J. G. de, R. J. H. G. Henkens, C. ter Braak, C. van Duyne, G. Hoefsloot, and D. A. Jonkers. 2003. *Road illumination and nature, IV. Effects of road* *lights on the spatial behaviour of mammals*. Alterra, Green World Research, Wageningen, The Netherlands.

Morrison, D. W. 1978. Lunar phobia in a neotropical fruit bat, *Artibeus jamaicensis* (Chiroptera: Phyllostomidae). *Animal Behaviour* 26:852–855.

Murray, M. G. 1982. The rut of impala: aspects of seasonal mating under tropical conditions. *Zeitschrift für Tierpsychologie* 59:319–337.

Nash, L. T. 1986. Influence of moonlight level on travelling and calling patterns in two sympatric species of galago in Kenya. Pages 357–367 in D. M Taub and F. A. King (eds.), *Current perspectives in primate social dynamics*. Van Nostrand Reinhold, New York.

Negraeff, O. E., and R. M. Brigham. 1995. The influence of moonlight on the activity of little brown bats (*Myotis lucifugus*). *Zeitschrift für Saeugetierkunde* 60:330–336.

Patel, H. I., and G. D. Gupta. 1984. A problem of equivalence in clinical trials. *Biometrical Journal* 26:471–474.

Pengelley, E. T., and K. C. Fisher. 1963. The effect of temperature and photoperiod on the yearly hibernating behavior of captive golden-mantled ground squirrels (*Citellus laterallis tescorum*). *Canadian Journal of Zoology* 41:1103–1120.

Perlman, I., and R. A. Normann. 1998. Light adaptation and sensitivity controlling mechanisms in vertebrate photoreceptors. *Progress in Retinal and Eye Research* 17:523–563.

Price, M. V., N. M. Waser, and T. A. Bass. 1984. Effects of moonlight on microhabitat use by desert rodents. *Journal of Mammalogy* 65:353–356.

Reed, D. F. 1995. *Efficacy of methods advocated to reduce cervid–vehicle accidents: research and rationale in North America*. Colloque International "Route et Faune Sauvage," Strasbourg, Conseil de l'Europe, June 5–7, and Sapporo, Japan, January 27.

Reed, D. F., and T. N. Woodward. 1981. Effectiveness of highway lighting in reducing deer–vehicle accidents. *Journal of Wildlife Management* 45:721–726.

Reed, D. F., T. N. Woodward, and T. D. I. Beck. 1979. *Regional deer–vehicle accident research*. U.S. Department of Transportation Federal Highway Administration Report No. FHWA-RD-79-11. National Technical Information Service, Springfield, Virginia.

Rogowitz, G. L. 1997. Locomotor and foraging activity of the white-tailed jackrabbit (*Lepus townsendii*). *Journal of Mammalogy* 78:1172–1181.

Rydell, J., and H. J. Baagøe. 1996. Bats & streetlamps. *Bats* 14:10–13.

Shanahan, T. L., J. M. Zeitzer, C. A. Czeisler. 1997. Resetting the melatonin rhythm with light in humans. *Journal of Biological Rhythms* 12:556–567.

Sharma, V. K., M. K. Chandrashekaran, and P. Nongkynrih. 1997. Daylight and artificial light phase response curves for the circadian rhythm in locomotor activity of the field mouse *Mus booduga*. *Biological Rhythm Research* 28(Supplement):39–49.

Skinner, J. D., and A. S. van Jaarsveld. 1987. Adaptive significance of restricted breeding in southern African ruminants. *South African Journal of Science* 83: 657–663.

Stewart-Oaten, A., W. W. Murdoch, and K. R. Parker. 1986. Environmental impact assessment: "pseudoreplication" in time? *Ecology* 67:929–940.

Subbaraj, R., and J. Balasingh. 1996. Night roosting and "lunar phobia" in Indian false vampire bat *Megaderma lyra*. *Journal of the Bombay Natural History Society* 93:1–7.

Topping, M. G., J. S. Millar, and J. A. Goddard. 1999. The effects of moonlight on nocturnal activity in bushy-tailed wood rats (*Neotoma cinerea*). *Canadian Journal of Zoology* 77:480–485.

Travers, S. E., D. W. Kaufman, and G. A. Kaufman. 1988. Differential use of experimental habitat patches by foraging *Peromyscus maniculatus* on dark and bright nights. *Journal of Mammalogy* 69:869–872.

Vasquez, R. A. 1994. Assessment of predation risk via illumination level: facultative central place foraging in the cricetid rodent *Phyllotis darwini*. *Behavioral Ecology and Sociobiology* 34:375–381.

Vaughan, T. A. 1978. *Mammalogy*. Saunders, Philadelphia.

Vickery, W. L., and J. R. Bider. 1981. The influence of weather on rodent activity. *Journal of Mammalogy* 62:140–145.

Walls, G. L. 1942. *The vertebrate eye and its adaptive radiation*. Cranbrook Institute of Science Bulletin No. 19, Bloomfield Hills, Michigan.

Wolfe, J. L., and C. T. Summerlin. 1989. The influence of lunar light on nocturnal activity of the old-field mouse. *Animal Behaviour* 37:410–414.

Wright, P. C. 1981. The night monkeys, genus *Aotus*. Pages 211–240 in A. F. Coimbra-Filho and R. A. Mittermeier (eds.), *Ecology and behavior of neotropical primates*, Volume 1. Academia Brasileira de Ciencias, Rio de Janeiro.

Zollner, P. A., and S. L. Lima. 1999. Illumination and the perception of remote habitat patches by white-footed mice. *Animal Behaviour* 58:489–500.

Zucker, I., M. Boshes, and J. Dark. 1983. Suprachiasmatic nuclei influence circannual and circadian rhythms of ground squirrels. *American Journal of Physiology* 244:R472–R480.