STUDYING THE ECOLOGICAL IMPACTS OF LIGHT POLLUTION ON WILDLIFE: AMPHIBIANS AS MODELS

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With the expansion of human habitation near and within natural habitats, fragile ecosystems are increasingly exposed to artificial night lighting. Amphibians (particularly frogs and salamanders) are important components of many forest and aquatic ecosystems. Amphibians are particularly sensitive to environmental changes and, thus, are important indicators of the health of ecosystems. Amphibian populations have been declining world-wide as a result of environmental perturbations including increases in UV -B radiation (due to ozone depletion), global warming and climatic change, habitat loss and destruction, and acidification caused by acid rain. Light pollution may also contribute to global decline of amphibians, because many amphibians are nocturnally active or have biological rhythms regulated by light. This paper will summarize methods of conducting research designed to determine the impact of light pollution on amphibians, including laboratory experiments, field experiments, and natural (observational) studies. Laboratory experiments, in which night lighting is manipulated under controlled conditions, have resulted in information about changes in hormone production, growth, and metabolism resulting from the introduction of light during normal dark periods. Field experiments, in which the introduction of artificial night lighting is controlled, have provided evidence for short-term changes in activity and reproduction of amphibians in response to the additional of artificial night lighting. Natural (observational) studies have demonstrated an effect of artificial night lighting on foraging activity of toads, but few other natural studies have been conducted on amphibians. Results of all these studies demonstrate that artificial night lighting has the potential to affect foraging and breeding as well as growth and development of frogs and salamanders. Thus, artificial night lighting should be considered an additional factor that negatively impacts amphibian populations and more research is needed to assess the potential magnitude of such impacts on biological diversity of amphibians.

Introduction

Light pollution seems to have a widespread, negative impact on many different species[1]. The evidence for the impact of light pollution in migratory birds[2] hatchling sea turtles[3], and insects[4] is striking, because of the large-scale mortality that has occurred as a result of artificial night lighting. Such mortality makes the impact of light pollution on these species more obvious and quantifiable. However, for other taxa, the impact of light pollution on populations may be more subtle, yet equally important. In such species, light pollution may affect such aspects of the biology of these species as physiology (e.g. growth and metabolism) and behavior (e.g. reproduction and foraging activity) causing stress that negatively affects populations exposed to this environmental pollutant.

Amphibians, including frogs and salamanders (very little is known about the basic light-relevant ecology of caecilians), are good models for examining the impact of light pollution on wildlife for several reasons. First, many species are nocturnally active, such that reproduction and activity primarily occur during dark periods. Secondly, amphibian species are widespread, abundant, and important components of terrestrial and aquatic ecosystems as both predators and prey. For example, the redback salamander, *Plethodon cinereus*, is a major predator of invertebrates in the forest of Eastern North America.[5] In some areas, the total biomass of these salamanders is higher than for any other vertebrate species.[6] Third, many amphibians are sensitive to changes in habitat[7] and thus are considered indicator species, such that amphibian populations are often among the first to show declines in degrading habitats.[8,9] Finally, amphibians are undergoing global decline for a variety of reasons including habitat loss, ultraviolet radiation (UV-B), acid rain, water pollution, exploitation, climate change, and infection (e.g. fungal disease, chytridiomycosis)[7,10]. However, a combination of these factors, or other "enigmatic factors" (sensu Stuart et al.[10]), may be the cause of population declines in some species[7,10].

Light pollution is a potential stressor that may exacerbate declines in populations of amphibians. Light pollution increases ambient illumination, disrupts photoperiod, and changes spectral properties of night light that may affect the physiology, behavior, ecology, and evolution of frog[11] and salamander[12] populations. Unfortunately, only a few researchers have directly examined the effects of light pollution on amphibians. The focus of this paper is to (1) discuss ways in which the impact of light pollution can be studied and monitored in amphibians, especially when direct mortality is not a likely outcome; and (2) provide examples from the literature and unpublished studies of the results obtained from these types of studies.

I advocate a multilevel, or multidisciplinary, approach when studying the impacts of light pollution. This approach should include both laboratory and field experiments, as well as natural (observational) studies. Each methodological approach has its benefits and limitations[13], such that a combined approach will allow us to understand 1) the mechanisms by which light pollution affects species, and 2) the overall effect on populations. Laboratory experiments are conducted using controlled environmental conditions in the laboratory in which only the ambient illumination is manipulated between control (dark conditions) and experimental treatments (lighted conditions), while all other environmental factors such as temperature, food, and humidity can be kept constant between treatments. However, laboratory experiments lack the realism of the natural world[13] (Fig. 1), and may only provide information about the potential effects of the variable on natural populations and specific effects of light at night on the physiology or behavior of the study organism. In field experiments, the ambient illumination in lighted treatments, but not in unlighted control treatments, can be controlled by the researcher; whereas other environmental factors are allowed to vary naturally. However, field experiments lack the very high level of control that is characteristic of laboratory experiments because the organisms are also exposed to variable environmental conditions. The benefit of field experiments over laboratory experiments is that the results are more representative of the effects of night lighting under natural conditions[13] (Fig. 1). Natural (observational) studies are conducted using existing sites that differ in light levels (e.g. naturally dark habitats and artificially lighted habitats). There is no control over ambient illumination or other environmental factors by the researcher (the researcher can only measure existing levels). Thus, in natural studies, there is very little control over the variable of interest or other environmental factors, but the results are much more likely to reflect what is occurring under field conditions[13]. (Fig. 1).

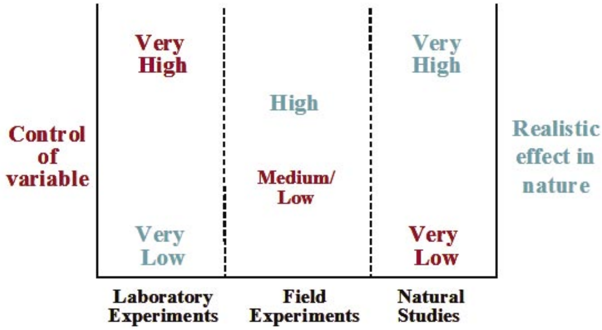

Figure 1. A multi-level approach to studying the ecological effects of artificial night lighting on wildlife. Methodologies include laboratory experiments, field experiments, and natural studies. For each type of design, there is a trade-off in control over variables (in red or darker shade if grayscale) and the realism of the results, i.e. how likely these results would occur in nature (in blue or lighter shade if grayscale). Laboratory experiments provide a high level of control to determine the physiological and behavioral effects of night lighting, but there is very little realism. Field experiments provide less control (medium/low amount); light levels can still be manipulated, but other environmental factors may increase the variability of the results. Field experiments provide more realistic results. Natural studies use existing levels of light in the natural habitat; thus, there is very little control over the system. However, these studies provide realistic evidence of the effect of light in natural habitats. Theoretical concept modified from Diamond[13].

Using a multi-level, combined approach involving all three types of studies will allow us to understand 1) the mechanisms by which artificial night lighting affects organisms (e.g. the cellular, physiological, and behavioral effects of light on organisms) and 2) the overall effect of artificial light at night on population size and structure. Laboratory experiments examining cellular physiology, including cell division, cellular function, and periodicity (i.e. melatonin production and the natural rhythms of cells) will allow us to understand the effect of light at the most fundamental level of the organism. Laboratory and field experiments, using controlled conditions, and natural studies can be used to examine the effects of light at night on systems physiology, such as hormonal and metabolic changes as the result of artificial light and the effects on growth and reproductive development (i.e. day length has a widespread effect on timing of gonadal maturation in a wide variety of organisms[14]). Additionally, these methodologies can be used to determine the effect of lights at night on behavior, such as activity patterns, aggression, foraging, and reproduction, and ecology such as population distribution (e.g. avoidance of or attraction to light), population size, and species interactions (e.g. competition and predation). In this paper, I will provide examples of laboratory experiments, field experiments, and natural studies for both frogs and salamanders when possible. The examples I have included in this paper are provided as generalizations of the types of research done at each level, and are not meant to be a comprehensive review of the field. For a comprehensive review of the effects of light pollution on amphibians see review of frogs by Buchanan[11] and salamanders by Wise and Buchanan[12]. For each example, I will explain the methods used to examine the impact of light at night, the variables that were measured, the results, and the implications for the impact of artificial light at night for amphibians.

Laboratory Experiments

Most laboratory experiments examining the effects of light on physiology and behavior of amphibians were conducted to determine the extent to which light acted as an environmental cue for circadian or seasonal changes in hormone levels, growth, metabolism, and reproduction (reviewed by Buchanan[11] and Wise and Buchanan[12]). Researchers often examined such effects by exposing animals to constant light, constant dark, or varying photoperiods. These researchers often did not report detailed information about the spectral properties or illuminations used during these studies[11,12]. These experiments are simple in that the intensity of light at night is not varied (and in many studies light intensities at night were the same as those used during daylight hours), but the number of hours per day these amphibians are exposed to light is varied. Varying the intensity of light at night to levels similar to those produced by artificial night lighting (directly or from sky glow), will allow for extrapolation to a variety of potential artificial lighting conditions. Regardless, these earlier experiments have provided information about the impact of light at night on the physiology and behavior of frogs and salamanders. Currently researchers are investigating directly the effect of artificial night lighting on physiology and behavior, and include more sophisticated measurements of light intensity and spectral characteristics of light, as well as treatments that vary light intensities. Such experiments are important in determining the direct impact of artificial night lighting on physiology and behavior in controlled conditions. The results of these experiments provide predictions for the effects we might see in natural habitats, where controlled conditions are not possible to create and causal factors may be more difficult to determine.

Gern et al.[15] performed a representative physiological experiment examining the impact of light (and temperature, another important environmental cue for amphibians) on the concentration of plasma melatonin in neotenic tiger salamanders (*Ambystoma tigrinum*). Melatonin is a master hormone that is regulated by photoperiod (production occurs during dark periods and is inhibited by light[16]. As part of a larger study, Gern et al. examined the effect of continuous light or a 12L:12D photoperiod (lighted during the day and complete darkness at night) on plasma melatonin concentrations. They found higher plasma melatonin concentrations during the dark cycle of the 12L:12D photoperiod than during the daylight period, but when in constant light, there was no difference in melatonin

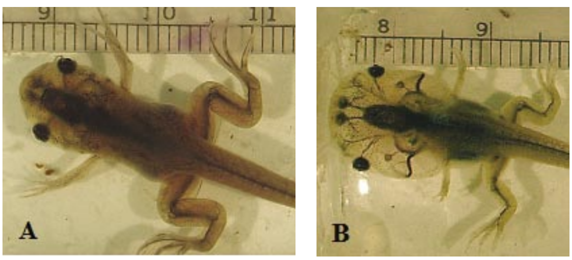

Figure 2. Tadpoles of the same age exposed to different nocturnal illuminations. The tadpole in A, from the darkest lighting treatment, is metamorphosing. The tadpole in B still retains the larval body form and is not yet ready to metamorphose.

levels over the 24-hr period. Melatonin production was lowered in salamanders kept under constant light. In amphibians, melatonin is important in the regulation of thyroid hormones (involved in metamorphosis of frog tadpoles), gonadal development, reproductive behavior, skin coloration, thermoregulation, and ability to adapt visually to darkness[14,17].

In a more recent study by H. Savage, K. Bingel, B. Buchanan, and S. Wise (not yet published), a variety of nocturnal illuminations were used to measure the effect of light at night on growth and metamorphosis in tadpoles of the African clawed frog, *Xenopus laevis*. These researchers exposed tadpoles to a 12L:12D photoperiod, with daytime light levels of 100 lx (comparable to bright room lighting) and varying nocturnal illuminations of 0.0001 lx (very dark night), 0.01 lx (comparable to bright moonlight), 1 lx (comparable to dawn or dusk), and 100 lx. The researchers found that the tadpoles differed in amount of growth in the different nocturnal light treatments; at the end of the experiment, a greater proportion of frogs in the darkest lighting treatment metamorphosed than in the other lighting treatments (Fig. 2). Even small amounts of light at night (comparable to bright moonlight, or artificial lights from anthropogenic sources) may delay metamorphosis. If this finding applies to other species of frogs that are limited in the length of the larval stage by drying (such as those in temporary ponds) or temperature (those in vernal pools), such delayed metamorphosis may decrease the chance of escaping a pool before it dries or cools and may increase mortality in tadpoles exposed to artificial light at night.

Field Experiments

Most field experiments have examined only the short-term effects of artificial light at night on behavior of amphibians. In these experiments, artificial illumination under the control of the researcher is introduced into natural habitats. The control treatment, no artificial light, is an important additional treatment that must be present in such designs. However, this control may be difficult to achieve in light-polluted habitats, particularly where sky-glow is a problem. Two such simple, short-term experiments are explained below. More complex designs should incorporate variation in light levels, manipulated by the researcher, to determine the effect of low-intensity and high-intensity illumination on the behavior or population distribution of amphibians. Additionally, long-term experiments, examining the effect of artificial light on amphibian behavior, reproduction, and population distribution over longer periods of time (e.g. a season or a year) need to be done.

Baker and Richardson[18] examined the reproductive behavior (calling) and movement activity of male green frogs, Rana clamitans melanota, in Ontario, Canada that were exposed to artificial light (flashlight or torch) or a control (no artificial light) on moonlit nights (higher natural ambient illumination) or darker nights (new moon or cloudy nights, lower natural ambient illumination). In the artificial light treatment, frogs were illuminated using the flashlight for 5 min before observations began (habituation period, so that the eyes of the frogs could partially adapt to the rapid increase in illumination). Observations were made using an infrared (IR) viewer, because frogs cannot use IR light for vision[19]. In the control treatment, behavioral observations were made using the IR viewer under natural ambient illumination after a 5-min habituation period. Baker and Richardson found a reduction in number of calls and an increase in movements by males in the artificially lighted treatment compared to the control treatment, regardless of the natural ambient illumination (moonlight or no moonlight). A reduction in the number of calls by males may affect selection of mates (mate choice) by females[20]. If such an effect is long-term and widespread, the result may be changes in the population dynamics of frogs exposed to artificial night lighting.

Wise and Buchanan (unpublished) conducted a field study examining the short-term effect of artificial night lighting on the foraging activity of the redback salamander, Plethodon cinereus. These salamanders occupy the leaf litter in eastern North American deciduous forests, maintaining territories under cover objects (rocks and logs) that provide protection from predation and desiccation[21,22]. Their above-ground foraging activity is limited by moisture during rainy or humid nights, these salamanders emerge from under the leaf litter and cover objects to forage on the forest floor[21,22]. To determine the effect of artificial night lighting on foraging activity of redback salamanders, transects were established in forested areas at the Mountain Lake Biological Station in Virginia, U.S.A. Half were lighted by strings of white minilamps placed in the transects (Fig. 3), whereas the other control transects were not lighted by minilamps. Light levels were 0.01 lx (comparable to bright moonlight) on the forest floor in the lighted areas and 0.0001 lx in the control areas. The researchers systematically walked each transect in random order beginning 1 hr after dark (2200-2310 h) and counted the number of salamanders found on the forest surface. There were significantly more salamanders active on the forest floor in the dark transects than in the lighted transects. This field experiment demonstrated a short-term reduction in activity of salamanders that were exposed to artificial night lighting. These salamanders, like many other species, are limited to foraging on the forest floor during moist periods at night. The introduction of light at night reduced this activity. If chronic exposure to artificial night lighting has similar long-term effects on salamanders, artificial night lighting has the potential to limit foraging opportunities, which may ultimately reduce growth and reproductive output, survival during winter hibernation (during which salamanders presumably do not feed and must rely on stored fat for energy[23]), and population size and distribution.

Natural Studies

There are very few natural (observational) studies that examine the effect of artificial night lighting on amphibians. Natural studies provide information about the impacts of existing artificial light on wild amphibian populations. However, in natural studies experimental and environmental factors are not controlled and other factors, besides artificial light, may be responsible for detected differences in lighted and unlighted areas. For example, artificial lighting often occurs in areas where there is habitat destruction or fragmentation. Thus, it is very important to have a control treatment (dark areas) that is similar in as many ways as possible to the habitat in lighted areas. Additionally, light levels should be measured when possible, although natural studies are valuable even without such information. Natural studies can be used to study short-term and long-term effects of artificial night lighting on populations, and may provide especially valuable

Figure 3. Transects used for field experiment by Wise and Buchanan (unpublished). These transects, placed in forested areas (A), were either lighted with strings of minilights (B) or were left dark (as controls).

evidence for the impact of chronic artificial night lighting on amphibian populations over seasons or years.

Baker[24] examined the impact of artificial night lighting on distributions of common (European) toads, *Bufo bufo*, at Walton Lake, Milton Keynes, U.K. Tadpoles of this species often metamorphose into juvenile frogs simultaneously; thus, there is often a mass emigration of newly metamorphosed toads away from their aquatic environments. During one of these mass emigrations, Baker counted the number of young toads aggregating in lighted areas under street lamps and in darker control areas between these lamps (Fig. 4). He found more toads under lighted areas than in unlit areas. Baker hypothesized that toads aggregated under street lamps because of the increased insect abundance (prey for toads) found there. Although such aggregations may be beneficial in providing toads with an abundant, conspicuous food source, Baker hypothesized that such aggregations may also make toads more susceptible to mortality as a result of bicycle or automobile traffic. Mazerolle et al.[25] demonstrated that amphibians are vulnerable to mortality by automobile traffic, and lights, such as headlamps may increase the risk of mortality in some species of amphibians.

Conclusion

The ecological impact of light pollution on wildlife is a relatively new field of study, especially for taxa other than insects, sea turtles, and birds. The effect of light pollution on amphibians is only beginning to be intensely examined. In studying the effect of artificial night lighting on amphibians as well as other taxa, it is important to use a multi-level approach that includes the use of laboratory experiments, field experiments, and natural (observational) studies. For amphibians, most information about the potential effects of artificial night lighting comes from laboratory studies that have examined

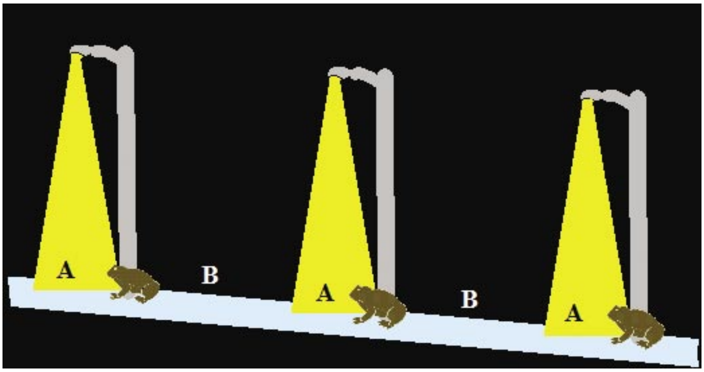

Figure 4. Baker counted the number of newly metamorphosed toads aggregating in lighted areas under street lamps (A) or in unlighted (control) areas in between the lighted areas (B).

the effects of variation of photoperiod or continuous lighting on hormone levels, growth, metabolism, activity, and foraging. These studies demonstrate that light at night affects basic physiological and behavioral biology of a wide variety of amphibians. More recent studies by Savage, Bingel, Wise, and Buchanan (unpublished) have examined the intensity-specific effects of different nocturnal light levels (from relatively dark to relatively bright) on growth and development of frogs. However, such complex, controlled studies need to be done on a variety of species before making generalizations about the potential impacts of artificial night lighting on all amphibians.

Very few field experiments and natural studies of light pollution have been performed using amphibians. Field experiments are conducted in more natural settings under controlled conditions, i.e. the researcher should have the ability to manipulate light levels and include appropriate dark control conditions. To date, field experiments include only those that have examined the short-term effect of artificial night lighting on amphibian behavior such as reproduction, activity, and foraging (e.g. studies by Baker and Richardson18 and Wise and Buchanan, unpublished). Long-term field experiments are needed to examine the chronic impact of artificial night lighting on aspects of amphibian populations such as foraging behavior, reproductive behavior, reproductive output, population distribution, and population size. Even fewer natural (observational) studies have been performed. Natural studies are important in providing evidence of the effect of light pollution on populations under existing conditions. These studies are often difficult to conduct, because lighted habitats must be matched with unlighted habitats (control) to make appropriate comparisons.

Currently, there is no comprehensive research incorporating laboratory experiments, field experiments, and natural studies for any single species of amphibians. This lack of intensive study at multiple levels may be because the potential importance of artificial night lighting as an environmental pollutant has only recently become a concern in the amphibian ecological and conservation literature. In order to understand the widespread impact of artificial lighting on amphibians and other taxa, more comprehensive research needs to be conducted. Regardless, the limited information we have indicates that artificial light at night negatively impacts a wide variety of amphibian species.

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