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IMPACT OF OUTDOOR LIGHTING ON MOTHS: AN ASSESSMENT

KENNETH D. FRANK

2508 Pine St., Philadelphia, Pennsylvania 19103

ABSTRACT. Outdoor lighting has sharply increased over the last four decades. Lepidopterists have blamed it for causing declines in populations of moths. How outdoor lighting affects moths, however, has never been comprehensively assessed. The current study makes such an assessment on the basis of published literature. Outdoor lighting disturbs flight, navigation, vision, migration, dispersal, oviposition, mating, feeding and crypsis in some moths. In addition it may disturb circadian rhythms and photoperiodism. It exposes moths to increased predation by birds, bats, spiders, and other predators. However, destruction of vast numbers of moths in light traps has not eradicated moth populations. Diverse species of moths have been found in illuminated urban environments, and extinctions due to electric lighting have not been documented. Outdoor lighting does not appear to affect flight or other activities of many moths, and counterbalancing ecological forces may reduce or negate those disturbances which do occur. Despite these observations outdoor lighting may influence some populations of moths. The result may be evolutionary modification of moth behavior, or disruption or elimination of moth populations. The impact of lighting may increase in the future as outdoor lighting expands into new areas and illuminates moth populations threatened by other disturbances. Reducing exposure to lighting may help protect moths in small, endangered habitats. Low-pressure sodium lamps are less likely than are other lamps to elicit flight-to-light behavior, and to shift circadian rhythms. They may be used to reduce adverse effects of lighting.

Additional key words: conservation, evolution, flight, urban ecology, light pollution.

Since the invention of the incandescent lamp over a hundred years ago, outdoor lighting has progressively increased. The growth has been characterized by expansion into new geographic areas, development of new lamps with new spectral characteristics, and increases in total amount of light and radiant energy (Riegel 1973, Hendry 1984, Sullivan 1984). Outdoor lighting has transformed the nocturnal face of the earth (Croft 1978). However, despite universal awareness that electric light disturbs behavior of nocturnal insects, the ecological impact of outdoor lighting has never been comprehensively assessed.

The possibility that outdoor lighting may adversely affect our fauna

is well recognized. Lepidopterists have blamed outdoor lighting for declines in populations of North American moths, especially saturniids in the northeastern United States (Holland 1903, Ferguson 1971, Hessel 1976, Muller 1979, Worth & Muller 1979, Krivda 1980, Pyle et al. 1981). This view assumes a direct causal link between lamps and faunal change. Fundamental questions about such a link, however, have never been closely examined: What mechanisms might link lamps with changes in populations of moths? If lamps cause populations of moths to change, specifically what might the changes be? How important are effects of lighting compared to effects of other environmental disturbances? This study examines each of these questions. It investigates the hypothesis that outdoor lighting influences populations of moths.

The investigation is based on a review of literature. The presentation is organized into three sections. The first section describes distribution, growth, energy, and spectral composition of outdoor lighting. The second describes how lamps affect behavior, life functions and survival of individual moths. The third explores how such effects may disturb moth populations; it also discusses measures to reduce disturbances caused by lighting. Citations are deliberately extensive to facilitate retrieval of source material which is widely scattered among different disciplines.

LIGHTING

Nocturnal images of earth viewed from orbiting satellites show the distribution of outdoor lighting (Fig. 1). In the United States this distribution coincides with that of the country's population (Croft 1978). Nocturnal illumination is clustered around all large metropolitan areas, with greatest concentration in the Northeast corridor. Viewed from an airplane, nocturnal lighting delineates a web of interconnecting roadways lined with illumination from houses, parking lots, billboards, and other landmarks. Such aerial observation suggests that lighting forms an illuminated web that envelops the nocturnal environment of Lepidoptera. The web's density varies with human population density, and its distribution is continental.

The magnitude of lighting in a major metropolitan area is illustrated by Philadelphia's streetlighting (Table 1). Philadelphia has 100,000 high-pressure sodium streetlamps at a density of almost 300 lamps/km². The energy they radiate equals more than 10 kilowatts/km², an order of magnitude greater than the energy density of moonlight at full moon (Agee 1969). During the last 4 decades, lamp size (lumens) increased 7-fold, number of lamps tripled, and type of lamp changed from tungsten filament and mercury to high-pressure sodium (Figs. 2 & 3) (Wainwright 1961, C. A. Oerkvitz pers. comm.). Nationwide per capita consumption of electrical power for streetlighting is similar to that of

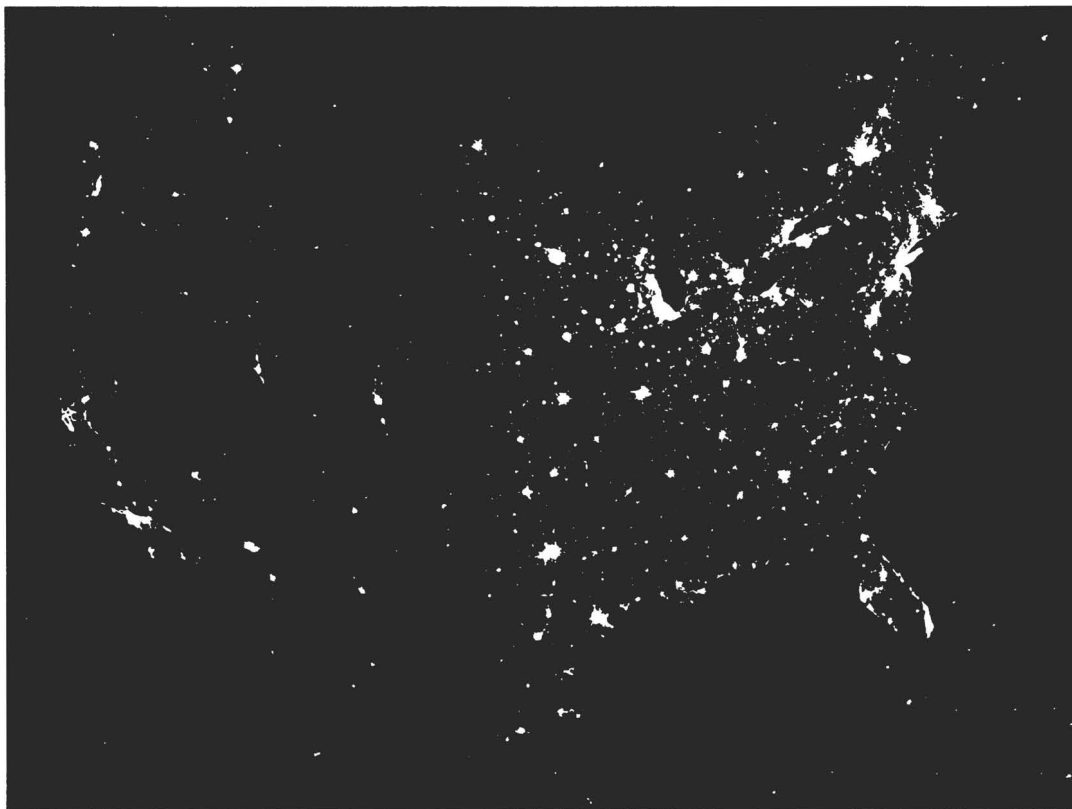


FIG. 1. Composite image of nocturnal United States, as viewed from orbiting satellite in fall 1985 (Defense Meteorologic Satellite Program). Photograph from National Snow and Ice Data Center, Campus Box 449, University of Colorado at Boulder, Boulder, Colorado 80309.

TABLE 1. Streetlamps in Philadelphia, 1983. Total lamps, lumens, and demand (watts) from C. A. Oerkvitz (pers. comm.). Radiant energy calculated from GTE Products Corp. (Sylvania) (1977b). Demographic data from *World Almanac* (1986).

Streetlamp parameter	Number		
	Total	Per capita	Per km ²
Lamps	1.0×10^5	5.8×10^{-2}	2.8×10^2
Lumens	1.8×10^9	1.1×10^3	5.0×10^6
Radiant energy (watts) emitted for wavelengths 350–700 nm	5.6×10^6	3.3	1.6×10^4
Electric power demand (watts)	2.2×10^7	1.3×10	6.1×10^4

Philadelphia, and growth in lumens has been comparable or higher (Riegel 1973, Edison Electric Institute 1971, 1985, Sullivan 1984).

Conversion from mercury to high-pressure sodium lamps reduces radiant energy at the short-wavelength end of the spectrum. However, high-pressure sodium light is spectrally broad and does include radiant energy in the blue spectral region (Fig. 2B).

In contrast to high-pressure sodium light, low-pressure sodium light is spectrally narrow. It excludes practically all energy in the ultraviolet, blue, and green regions of the spectrum (Fig. 2A). Viewed through a spectroscope, its spectrum contains a bright yellow-orange line (actually 2 spectral lines very close together) near 589 nm. Because the human eye is particularly sensitive to light in the 589 nm region, low-pressure sodium lamps can provide bright illumination with comparatively little radiant energy (Finch 1978). Compared to other lamps used for outdoor lighting, low-pressure sodium lamps minimize environmental exposure to radiant energy both in number of wavelengths and number of watts. These lamps are used for streetlighting and other outdoor lighting, but much less frequently than are high-pressure sodium lamps.

Conversion of streetlamps from mercury to high-pressure sodium has changed the spectral distribution of outdoor lighting, but it has not changed it as much or as clearly as one might suppose. Mercury lamps, for example, are still used for residential and commercial lighting in Philadelphia, and for streetlighting in neighboring areas. Tungsten filament (Fig. 3), low-pressure sodium, metal halide (Fig. 2C) and fluorescent lamps (Sorcar 1982) all contribute to spectral diversity of outdoor lighting in the city. While density and distribution of outdoor lighting have increased, spectral composition has diversified.

EFFECTS ON INDIVIDUAL MOTHS

Vision

Bright light can lower sensitivity of moth eyes 1000-fold (Bernhard & Ottoson 1960a, Höglund & Struwe 1970, Agee 1972, 1973, Eguchi

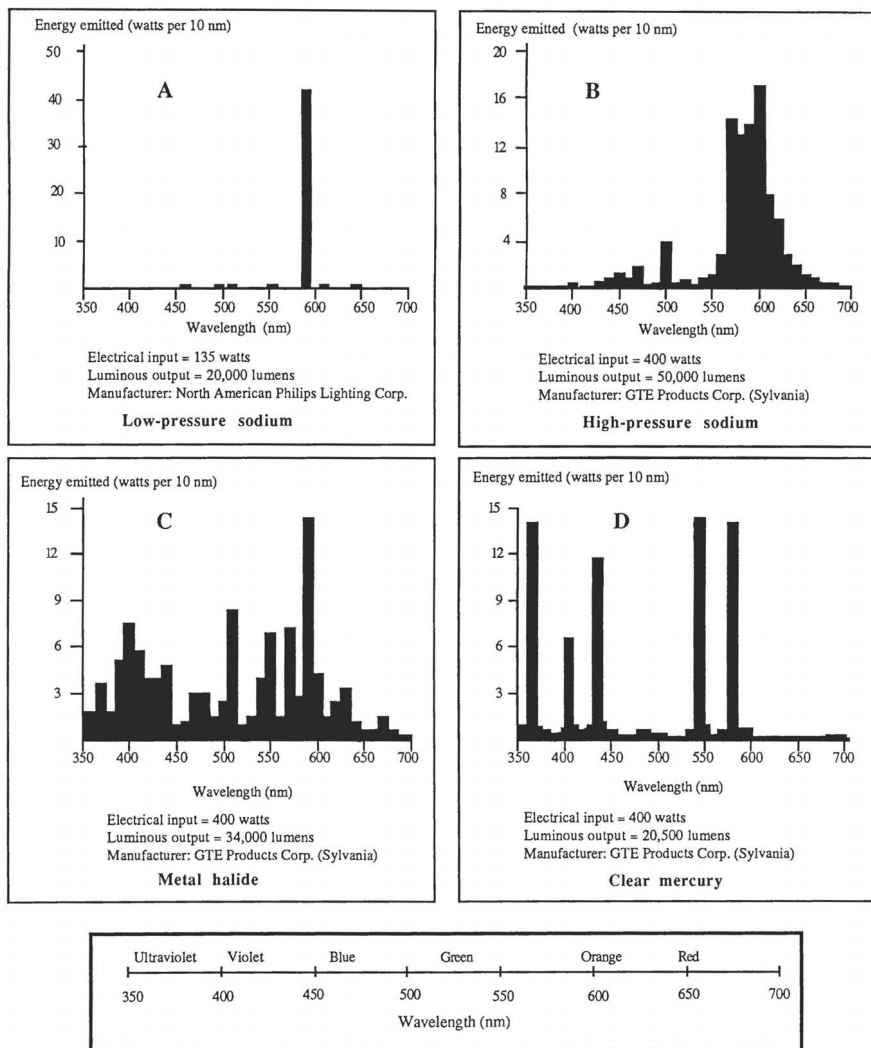
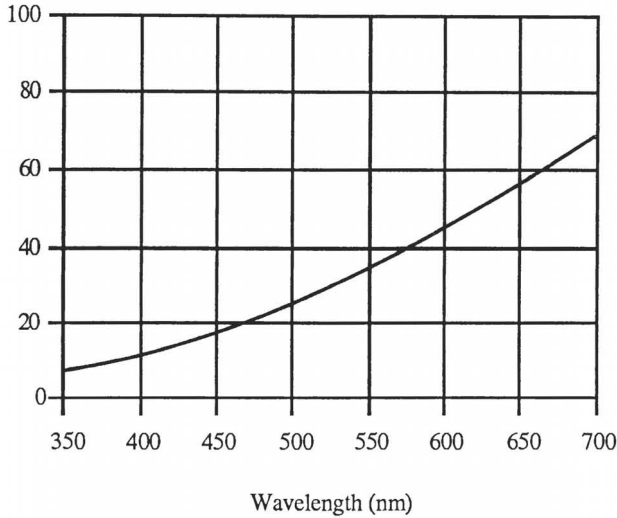


FIG. 2. Spectral energy distribution of vapor discharge lamps. Sources for A: Judd 1951, Finch 1978, Illuminating Engineering Society 1981, North American Philips Lighting Corp. 1982. Sources for B, C, and D: GTE Products Corporation (Sylvania) 1977a, 1977b, 1979.

& Horikoshi 1984). Electoretinographic studies suggest what happens to the visual sensitivity of a moth that flies to a lamp. If the moth remains at the lamp and then flies away, full visual sensitivity may not return for 30 min or longer (Bernhard & Ottoson 1960a, 1960b, Agee 1972). This effect requires exposure to the lamp over a period of time, probably 10 min or longer (Day 1941, Höglund 1963, Yagi & Koyama

Relative energy



Electrical input: 1000 watts
 Luminous output: 23,100 lumens
 Color temperature: 3030° Kelvin

FIG. 3. Spectral energy distribution of tungsten filament ("incandescent") lamp. Sources: GTE Products Corporation 1972, 1974.

1963). A moth flying away from a lamp into relative darkness on a cloudy, moonless night may be functionally blind until enough time has elapsed for it to become fully dark-adapted.

Continuous exposure to bright electric lamps could in theory "dazzle" moths. This means it could stimulate the moth retina so intensely that the retina could not respond to additional increases in light. The result would be functional blindness so long as the moth remained exposed close to the lamp. Electroretinographic evidence, however, suggests that lamps do not dazzle moths (Eguchi & Horikoshi 1984).

Net effects of electric lighting on moth vision may vary according to local conditions as well as moth behavior. Urban lighting increases background illumination which in turn may help moths see. Electric lighting in some areas has increased nocturnal sky brightness as much as 20-fold (Hendry 1984). However, the spectral composition, polarization and spatial distribution of outdoor lighting varies widely in different settings. In some locations they may differ so much from that of natural nocturnal light that they create visual artifacts and distortions. One

outcome of disturbed vision is flight to outdoor lamps, but many disturbances in visual function and behavior are possible.

The suggestion that urban lighting influences nocturnal vision of moths may appear paradoxical. Municipal light sources have shifted away from mercury lamps and toward high-pressure sodium lamps. One might suppose that moth retinas are insensitive to the relatively long wavelengths which characterize most of the energy contained in high-pressure sodium light (Fig. 2B). Moths, for example, do not fly to the 589 nm light of low-pressure sodium lamps (Fig. 2A), or do so rarely (Robinson 1952). Such a supposition, however, is incorrect: electroretinograms of moths consistently demonstrate sensitivity to light in the 589 nm region, and most studies have found maximum sensitivity in the green rather than ultraviolet part of the spectrum (Jahn & Crescitelli 1939, Höglund & Struwe 1970, Hsiao 1972, Mikkola 1972, Agee 1973, MacFarlane & Eaton 1973, Langer et al. 1979, Mitchell & Agee 1981, Eguchi et al. 1982). Retinal sensitivity extends farther into the long-wavelength end of the spectrum than flight-to-light behavior typically would suggest (Mikkola 1972, MacFarlane & Eaton 1973, Mitchell & Agee 1981).

Navigation

Diversion to lamps. Three hundred fifty-six species of Macrolepidoptera, or about a third of those species found in all of Great Britain, were collected at a single light trap in England (Williams 1939). Comparable findings have been reported in Britain and North America (Dirks 1937, Robinson & Robinson 1950a, Beebe 1953, Bretherton 1954, Moore 1955, Langmaid 1959, Hosny 1959, Holzman 1961, Moulding & Madenjian 1979). Tens of thousands of moths have flown to a single lamp in a single evening (Robinson & Robinson 1950a), and huge swarms of moths have aggregated around urban light sources (Howe 1959). On the other hand, some species of nocturnal moths rarely fly to lamps even though large populations of them may be flying nearby (Bretherton 1954, Taylor & Carter 1961, Janzen 1983). A variety of physiologic, behavioral and environmental factors may determine which species of moths fly to light and when (Geier 1960, Gehring & Madsen 1963, Milyanovskii 1975, Mazokhin-Porshnyakov 1975, Janzen 1983, 1984).

Large numbers of moths flying to lamps may give a false impression that lamps divert moths from great distances. Effective radius of a 125-watt mercury vapor light trap was initially reported to be 91 m, but later estimates reduced the figure to 17 m, and the most recent analysis cut the distance to 3 m (Robinson & Robinson 1950a, Robinson 1960, Baker & Sadovy 1978). Other studies have shown flight-to-light dis-

tances of 10 m or less (Stanley 1932, Hamilton & Steiner 1939, Hartstack et al. 1971, Plaut 1971). Long-distance estimates ranging up to half a kilometer represent either extrapolation, artificial conditions or both (Graham et al. 1961, Hsiao 1972, Agee 1972, Stewart et al. 1969, Plaut 1971, Bowden & Morris 1975).

If the mechanism by which a lamp disturbs moths depends on diversion of flight paths to the lamp, then the moths disturbed must be limited to those flying in the geographic area immediately adjacent to the lamp. In this sense any direct effects of a particular lamp would tend to be local, except when topography (Beebe 1949, Beebe & Fleming 1951), foodplants, pheromones, or other factors concentrate moths near the lamp. Only in urban regions would density and distribution of lamps be great enough to influence large populations of moths over broad geographical areas.

Effects of electric lamps in urban areas, however, may be much smaller than one might expect. Robinson & Robinson (1950a) noted that lamps in isolated phone booths appear to be much more effective in eliciting flight-to-light behavior than are clusters of bright urban lamps located immediately adjacent to areas with large populations of moths. They demonstrated that lamps interfere with each other's capacity to elicit flight-to-light behavior, and the closer together the lamps, the greater the interference. The high density which characterizes distribution of urban lamps suppresses flight-to-light behavior.

Urban lighting may suppress flight to light for a number of reasons. Light trap collections vary with the lunar cycle and are lowest at full moon (Williams et al. 1956, Agee et al. 1972, Nemec 1971, Dufay 1964, Bowden & Church 1973, Janzen 1983, Stradling et al. 1983). A similar correlation with moonlight cannot be demonstrated when nocturnal flight is measured by suction traps (Williams et al. 1956, Danthana-rayana 1986), pheromone-baited traps (Saario et al. 1970, Janzen 1984) or radar (Schaefer 1976). Moths active at dusk typically appear in suction traps before they appear in light traps (Taylor & Carter 1961). Eye pigment must be in a position of dark adaptation before moths will fly to light (Collins 1934), and even relatively dim background light can cause the pigment to move away from this position (Bernhard & Ottoson 1964). Diffuse urban light, like moonlight and twilight, reduces the darkness essential for flight-to-light behavior.

The moon not only increases background lighting but also constitutes a concentrated source of light by which insects may be able to orient (Sotthibandhu & Baker 1979). Moths flying by lunar navigation may bypass lamps (Baker & Sadovy 1978). Lamps may provide navigational cues which suppress flight to other lamps.

Light sources that emit large amounts of ultraviolet energy are gen-

erally most effective in eliciting flight-to-light behavior (Williams et al. 1955, Glick & Hollingsworth 1955, Klyuchko 1957, Deay et al. 1965, Mazokhin-Porshnyakov 1969, 1975, Mikkola 1972, Sargent 1976, Mitchell & Agee 1981). Conversion of mercury streetlamps to high-pressure sodium and metal halide streetlamps has undoubtedly tended to reduce flight to streetlamps. On the other hand, moths do fly to high-pressure sodium and metal halide lamps, and a small minority of species may fly preferentially to lamps with little or no ultraviolet emission (Klyuchko 1957, Mikkola 1972). Unlike high-pressure sodium lamps, however, low-pressure sodium lamps rarely elicit flight-to-light behavior (Robinson 1952).

In summary, increases in electric lighting do not necessarily impair nocturnal vision and navigation. Under some conditions they may improve moths' nocturnal vision and suppress flight-to-light behavior.

Diversion away from lamps. Electric lamps may also divert moths away from them (Robinson & Robinson 1950a, Robinson 1952, Herms 1929, 1932, Nomura 1969, Nemec 1969, Hsiao 1972). These effects may depend in part on spectral output of the lamp (Mazokhin-Porshnyakov 1969, 1975, Nomura 1969). Several theories attempt to explain this behavior (Hsiao 1972), but none accounts for diversity of flight paths at lamps (Janzen 1984): while some moths make spiral or circular flights around lamps and land several meters away, others make a beeline straight to lamps and crash into them. Flight paths approaching lamps may zig-zag or be totally chaotic (Holzman 1961, Mazokhin-Porshnyakov 1969, Janzen 1984). Diversion away from lamps has been debated (Bretherton 1950, Robinson & Robinson 1950b). Evidence that moths avoid large illuminated areas (Herms 1929, 1932, Nomura 1969, Nemec 1969) is inconclusive, but this behavior is more difficult to demonstrate than flight to lamps.

Lamps suppress flight of moths that fly to them. Moths approaching lamps may land near them and remain quiescent for a moment or for the entire night. Lamps suppress flight of some species more than others (Blest 1963, Graham et al. 1964). In some cases lamps do not appear to suppress flight; in other cases they excite quiescent moths into flight (Collins 1934, Hsiao 1972). Diurnal moths occasionally fly at night to lamps (Engelhardt 1946, Janzen 1983), but here it is unclear whether the lamps help to initiate nocturnal flight.

Diversion and suppression of flight may impair orientation and navigation based on lunar, stellar or other visual celestial cues (Mazokhin-Porshnyakov 1969, Sotthibandhu & Baker 1979, Wehner 1984) including polarization of celestial light (Danthanarayana & Dashper 1986). It also may impair navigation and orientation based on geomagnetic, gravitational, barometric, aerodynamic, inertial, olfactory, acoustic or

visual terrestrial cues (Baker & Kuenen 1982, Baker & Mather 1982, Janzen 1984, Schöne 1984, Riley & Reynolds 1986). How much electric lighting disturbs use of particular cues may be expected to vary in part according to which cues the moth happens to be using at the moment it encounters the lamp.

Migration and Dispersal

Light sources divert moths engaged in migratory or dispersal flights (Cockerell 1914, Williams 1937, Beebe & Fleming 1951, Wolf et al. 1986). Urban lighting surrounds habitats isolated by urban sprawl, so that moths may have to traverse dozens of kilometers of densely illuminated territory to arrive at potential breeding sites. Moths flying high (Glick 1965) may fly to urban light sources on tall buildings (Stanley 1932, Glick 1961). Because location of natural flyways is poorly documented for North American moths, one cannot determine the extent urban lighting may intersect long-range natural migration routes here. In Venezuela, vast numbers of migrating moths aggregated around lamps near a narrow mountain pass which functions as a natural flyway (Beebe 1949, Beebe & Fleming 1951). Lighting along roads following topographical features such as valleys, rivers, and coastlines might selectively interfere with North American moth migrations (Fig. 1).

Oviposition

Electric lighting can disturb oviposition. Light-trap surveys have shown that the vast majority of females collected at lamps are gravid (Dirks 1937, Ficht et al. 1940, Glick & Hollingsworth 1954, Geier 1960, Gehring & Madsen 1963) although males usually outnumber them (Dirks 1937, Williams 1939, Sargent 1976, Worth & Muller 1979, Janzen 1984). Flight to light can shift oviposition to sites located near the lamp (Ficht et al. 1940, Martin & Houser 1941, Pfrimmer & Lukefahr 1955, Beaty et al. 1951, Nemec 1969, Brown 1984). Eggs may be deposited on lampposts, window screens, buildings, and other unsuitable sites near lamps. Egg densities may be several-fold higher on plants near lamps (Martin & Houser 1941). The result may be larval overcrowding and increased susceptibility to starvation, microbial infection, and predation.

Lamps shift the distribution of oviposition sites toward them probably by diverting ovipositing females and not by stimulating oviposition. In cornfields, *Ostrinia nubilalis* (Hbn.) (Pyralidae) tends to oviposit near lamps (Ficht et al. 1940, Beaty et al. 1951), but in the laboratory nocturnal illumination suppresses *O. nubilalis* oviposition (Skopik & Takeda 1980). Similar observations have been reported in *Pectinophora gossypiella* (Saund.) (Gelechiidae) (Pfrimmer & Lukefahr 1955, Lu-

kefahr & Griffin 1957, Henneberry and Leal 1979). Outdoor lighting may decrease oviposition by *Cydia pomonella* (L.) (Tortricidae) and *Heliothis* spp. (Noctuidae), although the mechanism is unclear (Hermes 1929, 1932, Nemec 1969).

Mating

Outdoor lighting does not prevent mating in certain Saturniidae: male *Hyalophora cecropia* (L.) and *Samia cynthia* (Drury) complete long-distance mating flights to virgin females at night across illuminated urban territory, and breed in urban habitats (Rau & Rau 1929, Pyle 1975, Sternburg et al. 1981, Waldbauer & Sternburg 1982). Most freshly emerged female saturniids do not fly at all until they have emitted pheromone and mated (Blest 1963, Nässig & Peigler 1984, Waldbauer & Sternburg 1979). Male sphingids and saturniids fly to virgin females before they fly to nearby electric lamps (Allen & Hodge 1955, Worth & Muller 1979, Janzen 1984). Almost all female *Cydia pomonella* collected at black lights have already mated (Gehring & Madsen 1963). Although more males than females typically fly to lamps, the capacity of males to mate with more than one female (Rau & Rau 1929, Allen & Hodge 1955, Lukefahr & Griffin 1957, Vail et al. 1968) may moderate the reproductive impact of disproportionate harm to males.

In contrast, electric lighting may have a major effect on mating in certain Noctuidae. *Heliothis zea* (Boddie) is an example. The peak time of night during which *H. zea* flies to light traps coincides with the period of copulation (Graham et al. 1964, Stewart et al. 1967). Only a third to a half of female *H. zea* collected at light sources have mated (Gentry et al. 1971, Vail et al. 1968). In the laboratory, *H. zea* will not mate unless its eyes are in a state of dark adaptation, as indicated by the presence of eye glow. Light intensity must be below $0.015 \mu\text{W}/\text{cm}^2$, the intensity of light of a quarter-moon (Agee 1969). The suggestion is that *H. zea* females fly to light sources whose radiant energy suppresses mating.

A criticism of this scenario is that unmated *H. zea* females that fly to light may be migrating (Raulston et al. 1986) and therefore sexually immature (Johnson 1969). Female *H. zea* in the laboratory do not mate for 30–60 h after eclosion (Agee 1969). However, even if unmated females at lamps were sexually immature migrants, the lamps could disrupt reproductively important behavior, such as flight to locations where courtship and mating would be likely to occur. Furthermore, outdoor lighting may interfere with *H. zea* mating regardless of flight to light. Levels of light that suppress mating in the laboratory (Agee 1969) are well below ambient levels of light in electrically illuminated environments outdoors. Low levels of incandescent light (Nemec 1969)

and moonlight (Nemec 1971) have influenced activities of *Heliothis* spp. in the field.

Other evidence suggests that lighting may interfere with mating. Unmated females of four other noctuid species fly to lamps (Vail et al. 1968). Male sphingids caught in light traps baited with virgin females do not seek out the females (Hoffman et al. 1966). In the laboratory, even dim electric light (0.3 lux) suppresses female *Trichoplusia ni* (Hbn.) (Noctuidae) pheromone release and male response to pheromone (Shorey & Gaston 1964, 1965, Sower et al. 1970). Electric light also suppresses female pheromone release and male response to pheromone in *Dioryctria abietivorella* (Grt.) (Pylalidae) (Fatzinger 1979). Mating by *Pectinophora gossypiella* requires a period of relative darkness lasting at least 7 h (Lukefahr & Griffin 1957).

Feeding

Moths may feed in illuminated environments. Sphingids and noctuids visit food sources in full view of electric lamps located sometimes less than a few meters away, or they fly to electric light sources after they have completed feeding (Bretherton 1954, Milyanovskii 1975, Mazokhin-Porshnyakov 1975, Janzen 1983, 1984). I have observed *Buddleja* (Gentianaceae) blossoms covered with noctuids at night (2300 h) virtually directly under a tungsten filament street lamp illuminating a heavily traveled road in Quisset, Massachusetts. Light from automobile headlamps and from a flashlight did not alter the moths' activities.

Electric lamps, however, may interfere with feeding. Orchard illumination has reduced the number of *Cydia pomonella* feeding at bait (Herms 1932). In Japan, orchard illumination has been used to protect fruit from damage by fruit-piercing noctuids (Nomura 1969). Light has disturbed nectaring sphingids (Brown 1976). Diversion of moths away from light may explain why lamps interfere with feeding. Suppression in feeding is moot for the large number of moth adults that never feed (Norris 1936).

Electric lighting theoretically could injure larval foodplants. Sodium vapor lighting may harm plants by disrupting photoperiodic regulation of growth and development (Sinnadurai 1981, Cathey & Campbell 1975, Shropshire 1977), but such effects are apparently greater indoors in greenhouses than outdoors on the street (Andresen 1978).

Time Keeping

Electric lighting can delay or advance vital activities of moths and their larvae, and these shifts could affect the insects as much as changes in the activities themselves (Beck 1980, Saunders 1982). This possibility has been the basis for proposals to exploit biological clocks for purposes

of pest control (Barker et al. 1964, Nelson 1967). In a field trial, however, light exposure failed to prevent diapause in larvae of *Adoxophyes orana* (F.R.) (Tortricidae) (Berlinger & Ankersmit 1976). The trial suggests that it is easier to manipulate biological clocks indoors than outdoors where temperature and other factors cannot be controlled.

Biological clocks of flying insects, however, may be much more susceptible to outdoor electric lighting than those of larvae. This is because flight to light increases exposure to radiant energy. Exposure to a pulse of light lasting only 15 min is sufficient to attenuate a circadian rhythm in *Drosophila*; light 10^3 times more intense produces the same effect after only 10 sec; light 10^5 times more intense does it after an exposure of less than 0.1 sec (Chandrashekar & Engelmann 1976). Energy for even a minute fraction of a second (photoflash) can disturb photoperiodic clocks in larvae of Lepidoptera (Barker et al. 1964). The anthropomorphic observation that quiescent moths adjacent to a lamp are "asleep because they think it is daytime" may be close to the truth.

Shifts in timing of nocturnal behavior of moths at lamps do not necessarily imply shifts in phase of endogenous rhythms. Changes in timing of behavior could represent other responses to light, or they could represent complex mixtures of responses. Regardless of these possibilities, magnitude and character of responses may vary according to when in the circadian cycle exposure to light occurs (Pittendrigh & Minis 1971, Skopik & Takeda 1980). Responses may also vary depending on spectral output of the lamp. For example, *Pectinophora gossypiella* has two light-sensitive clocks, only one of which responds to the 589 nm light emitted by low-pressure sodium lamps (Bruce & Minis 1969, Pittendrigh et al. 1970).

Theoretical Effects

To what extent nocturnal flight to light affects timing of nocturnal behavior has never been formally investigated. For example, if a moth flies to a light source, receives intense irradiation for 15 min, and flies away, how will its activities during the rest of the night be affected? If a male, will its mating period still coincide with that of females not exposed to light? If a female, will pheromone release still occur during the flight period of males? Shifts in mating times could cause sympatric, closely related species to attempt to mate with each other; such species normally do not mate with each other in part because their different mating periods keep them temporally segregated (Tuttle 1985).

Synchronization of activities with lunar rhythms may help moths navigate, mate, and avoid predators (Danthanarayana 1986). Lamps may disturb oviposition synchronized to lunar rhythms (Nemec 1969, 1971). To what extent moth activity synchronizes with lunar rhythms,

and to what extent electric lighting may disturb such synchrony warrants investigation.

Predation

Bats, birds, skunks, toads, and spiders hunt moths flying to lamps (Stanley 1932, Thaxter 1957, Holzman 1961, Krivda 1980, Covell 1985, Brower 1986). Lamps increase predation by clumping prey, and directly exposing them to attack (Turnbull 1964). Concentrated experience with particular species may help birds learn to defeat defenses based on surprise, novelty, or deceit (Blest 1957, Wickler 1968, Coppinger 1970, Sargent 1973b, Pietrewicz & Kamil 1979). Lamps also can destroy defensive behavior, such as that required for crypsis (Sargent & Keiper 1969, Sargent 1973a, 1976). The outcome is exemplified by a dark, bark-colored moth conspicuously resting on a white wall near a lamp at dawn. Lamps may help birds learn to recognize unpalatable species, but moths unpalatable to some birds may be acceptable to others (Löhr 1979). Lamps may enable different birds to pick and choose among different possible prey. Because moths often land before they arrive at lamps, lamps may provide predators with far more prey than one might expect from the moths immediately adjacent to the lamp (Hartstack et al. 1968).

Parasitoids of Lepidoptera fly to electric light sources (Collins & Nixon 1930, Cline et al. 1983). Electric lighting could reduce predation on Lepidoptera by suppressing populations of parasitoids (Worth & Muller 1979). It may divert parasitoids used for biological control of pest Lepidoptera in warehouses (Cline et al. 1983). Even brief exposure to intense sources of radiant energy (photoflash) may sterilize minute hymenopterous parasites which survive the radiation (Riordan 1964). Theoretically, lighting could affect secondary parasites, thus potentially disturbing the food chain at three levels, and producing changes in populations which would be difficult to predict (Frank 1986).

EFFECTS ON MOTH POPULATIONS

Evidence Against Effects

Migration and dispersal. Even though lamps may contribute to the destruction of vast numbers of moths, the impact on moth populations may be negligible. For example, more than 10 000 *Autographa (Plusia) gamma* (L.) (Noctuidae) were collected in a light trap in one season in England (Robinson & Robinson 1950a). In England the population of *A. gamma* is maintained almost entirely by immigration in spring from southern Europe (Ford 1972). A particular light source in England should have a negligible influence on the breeding stock which annually

replenishes the population of *A. gamma* around it. Seasonal movement of moths over long distances is not rare (Williams et al. 1942, Williams 1958, Johnson 1969, Ford 1972) and may be sustained by wind transporting moths at altitudes sometimes hundreds of meters above most electric light sources (Glick 1965, Mikkola 1986, Raulston et al. 1986, Wolf et al. 1986).

Failure to suppress agricultural pests and other species. One might expect that light traps could substantially reduce or eliminate some moth populations. However, elaborate efforts to exploit such traps for pest control have failed, and successes could not be consistently replicated (Cantelo 1974, Hienton 1974). The failure has been attributed to influx of moths from outlying areas, but light trapping may fail to control insect populations even on small islands. On St. Croix, United States Virgin Islands, 250 black-light traps were deployed during a period of 43 months. The island is 208 km² in area. Although decreases in light-trap collections suggested that traps were depleting the island's sphingids (Cantelo et al. 1972a, 1972b), other studies using the same traps at the same time found similar decreases in collections of *Heliothis zea* even though traps collected only a minute fraction of the island's *H. zea* population (Cantelo et al. 1973, 1974, Snow et al. 1969). Furthermore, light-trap collections of sphingids were beginning to increase at the time the study was terminated. Meteorologic and density-dependent ecological forces may determine the size of moth populations exposed to lighting, even on isolated islands.

Failure of light traps to reduce insect populations extends beyond species of agricultural interest. Williams (1939) examined 150 species of Noctuidae and Geometridae collected in his stationary light trap during a 4-year period in Rothamsted. Comparison of numbers of individuals of each species collected from year to year provided no evidence of any consistent declines in populations, except possibly in the case of one geometrid. More recent observations at Rothamsted extended Williams' studies. Taylor et al. (1978) tabulated annual number of species and number of specimens of each trapped at Rothamsted from 1966 to 1975, and also calculated an index of diversity for each year. No downward trends are apparent, despite wide fluctuations from year to year.

Prevalence of urban moths. The above studies did not simulate urban conditions where lighting is dense and widespread. However, large numbers of species have been collected in urban areas in Britain and the United States (Langmaid 1959, Lutz 1941). Collections based on a nationwide network of 172 light traps in Britain suggest that moth populations in areas undergoing urban changes can substantially recover despite electric lighting (Taylor et al. 1978). In North America, some

saturniid species not only tolerate urban lighting but may actually thrive better in urban than in rural habitats. *Hyalophora cecropia* and *Samia cynthia* are two examples. The ecology of both species is complex, and numerous factors other than lighting can account for changes in their abundance in illuminated environments (Sternburg et al. 1981, Frank 1986). In New England, eight species of *Catocala* (Noctuidae) thrive in illuminated urban or suburban areas. Seven of these species can be found within a mile of downtown New Haven, and one occurs in downtown Boston. Several depend almost entirely on urban-suburban shade trees (D. F. Schweitzer pers. comm.).

Extinctions unrelated to lighting. Most declines and extinctions in moth populations can be linked to specific circumstances unrelated to lighting (Bretherton 1951, Ford 1972, Heath 1974). These include deforestation, agriculture, and draining of fens. Destruction of habitats as a cause of widespread declines in Lepidoptera populations has been described in detail for European butterflies (Kudrna 1986). In Britain, many species of moths became scarce around the middle of the last century, but after World War I the situation reversed, probably because of favorable climatic changes (Heath 1974). Declines in numbers of *Malacosoma americanum* (F.) (Lasiocampidae) in Winnipeg, Manitoba, have been attributed to English sparrows (*Passer domesticus* L., Passeridae) eating the moths at lamps (Krivda 1980), but *M. americanum* populations fluctuate at intervals independent of changes in lighting. Interval duration is about 10 years (Johnson & Lyon 1976). Attacks by microbial and parasitic agents probably account for periodic reductions in populations of this species (Lutz 1941).

Saturniid populations in the northeastern United States declined in the 1950's. This observation is supported by dates of last capture for species represented in regional collections, and by surveys of collectors (Ferguson 1971, Hessel 1976, D. F. Schweitzer pers. comm.). Populations of some saturniid species have since shown signs of recovery, whereas other saturniids, especially the two *Citheronia* species native to the area, have failed to recover in several states (D. F. Schweitzer pers. comm.). Declines that occurred in the 1950's coincided with widespread aerial spraying against gypsy moth, and recoveries coincided with drastic curtailment of this spraying (D. F. Schweitzer pers. comm., Gerardi & Grimm 1979). Whether pesticides can account for changes in saturniid populations is unclear. However, changes in populations of saturniids as a group correlate poorly with changes in outdoor lighting.

Evidence for Effects

Small colonies exposed to lighting. Evidence that outdoor electric lighting has the capacity to affect populations of moths is illustrated by

Hydraecia petasitis Doubleday (Noctuidae) in Finland. Only three or four isolated colonies are known to exist in the country. The isolation is not due to urbanization but rather to the fact that the species in Finland is at the extreme tip of its range. Two small colonies were studied, one covering 700 m², the other 800 m². A mark-recapture experiment conducted during 48 days in one colony demonstrated that a trap equipped with an 80-watt mercury lamp captured 53% of males in the colony and 30% of females at least once. The colony was estimated to consist of 218 individuals. These and other observations suggest that continuous light trapping could destroy this population. The authors point out that this species is only mildly attracted to light, and that the effect of light trapping might be more severe for other Lepidoptera (Väisänen & Hublin 1983). The number of moths the authors trapped probably underestimated the number that flew to the lamps (Hartstack et al. 1968).

The Finnish light-trap study demonstrates that a substantial proportion of individual moths within a geographically small colony may fly to an electric lamp. It is conceivable that disturbances in oviposition, mating, feeding, vision, navigation, dispersal, crypsis, circadian rhythms or photoperiodism would be sufficient to disrupt an already shaky population or to impede establishment of a new one. Disruptive effects would be even greater when caused by lamps in special conditions. These include lamps in traps equipped with electrocuting grids ("bug zappers") and lamps near bird feeders and bird houses. Lamps may incinerate or desiccate moths trapped inside poorly constructed or broken luminaires. Lamps near hostplants may disturb females attracted to the plants, or they may disturb males attracted to the females. Lamps in open garages and pavilions may direct moths into areas from which they cannot escape. Automobile headlamps and streetlamps divert moths into the paths of moving vehicles.

Urbanization and fragmentation of habitats. The same urban changes that increase outdoor electric lighting also tend to fragment habitats (MacArthur & Wilson 1967). The result is creation of small colonies exposed to electric illumination. Man has made many species of British moths in effect relict faunas, remnants of a bygone era when their habitats were much more widespread (Bretherton 1951, Ford 1972). Three species of noctuids once plentiful in southern California have been reduced to small, isolated colonies, in one instance in the vicinity of the Los Angeles International Airport (Hessel 1976). Urban gardens and parks now function as important faunal reservoirs (Frankie & Ehler 1978, Davis 1978, 1982, Owen 1978, Schaefer 1982). Urbanization increases both vulnerability and exposure of moth populations to lamps.

Lighting as a selective force. Outdoor lighting may act as a selective

force against particular individuals within a population. For example, it may select against individuals that tend most strongly to exhibit flight-to-light behavior. In the Finnish light-trap study, such individuals would include those that flew into traps most frequently. Industrial melanism demonstrates that urban change may cause evolutionary change in populations of moths, and that disturbances in crypsis can generate the selective forces needed to produce such evolution (Kettlewell 1973, Cook et al. 1986). Electric lighting disturbs crypsis, but also a multitude of other functions. That some species of noctuids and other nocturnal moths do not fly to nearby light sources, or do so only rarely (Bretherton 1954, Taylor & Carter 1961, Janzen 1983), suggests that evolutionary modification of flight-to-light behavior has already occurred, although the causes are unknown.

Responses to selective pressures produced by lighting may be diverse. For species active at dusk, natural selection could favor individuals that fly at the beginning of the population's flight period, rather than at the end when flight to light occurs. The evolutionary response would be a shift in flight period rather than a specific change in flight-to-light behavior. Biological clocks are in part genetically controlled, and clock mutants affecting time of eclosion and locomotor activity have been identified in *Drosophila* (Konopka & Benzer 1971, Yu et al. 1987). In moths, different races or strains of a single species exhibit different photoperiodic behavior (Gardiner 1982, Ankersmit & Adkisson 1967), and selective pressures can account for such differences (Tauber & Tauber 1978, Hoy 1978, Waldbauer 1978). On the other hand, advancing or delaying flight times could disturb species segregation mediated through allochronic flight periods (Tuttle 1985), or it could expose moths to increased predation by birds or bats that fly only at certain times. Any evolutionary response to selective pressures generated by electric lighting would have to represent a net response to opposing selective pressures.

The diversity of moth behavior around lamps suggests a multitude of possible mechanisms for reducing adverse effects of electric light. The degree to which moths of different species fly to lamps may depend on the degree to which they respond to alternative navigational cues that compete with the lamps (Janzen 1984). Suppression of flight-to-light behavior could take the form of increasing responsiveness to competing stimuli such as olfactory, geomagnetic, aerodynamic, gravitational and inertial cues, plus alternative visual cues (Baker & Kuenen 1982, Baker & Mather 1982, Schöne 1984, Janzen 1984, Riley & Reynolds 1986). Within a population of moths, variation exists not only in tendency of different individuals to fly to light, but also in tendency to linger at the light or fly past it. Variation may also exist in tendencies

to avoid lamps or oviposit near them. Evolutionary changes in response to electric lighting may be complex.

Forces opposing evolutionary reduction of flight-to-light behavior, however, are difficult to understand and assess in individual cases. Studies have employed suction traps to measure aerial densities of moth populations and at the same time light traps to measure flight to light. These studies suggest that *Xestia (Amathes) c-nigrum* (L.) (Noctuidae) is 5000 times as likely to fly to light as *Amphipyra tragopoginis* (Cl.) (Noctuidae) (Taylor & Carter 1961). Why these two noctuids behave so differently around lamps is a mystery. Failure to evolve seemingly advantageous adaptations has been well described in Lepidoptera (Ehrlich 1984). Populations of moths may resist strong selective pressures to evolve defenses against adverse effects of electric light.

Fewer moths at urban lamps. Evolutionary changes in wing coloration can be documented by inspection of collections of moths obtained over a period of time (Kettlewell 1973). Evolutionary changes in flight-to-light behavior cannot be documented in this way. Observations a century ago, however, are worth noting. Riley (1892: 51) advises collectors where to look for moths: "... nowadays the electric lights in all large cities furnish the best collecting places, and hundreds of species may be taken in almost any desired quantity." Denton (1900:35) was more explicit:

While employed in Washington, D.C., I made a splendid collection of the moths of that region simply by going the rounds of a number of electric lights every evening. The lamps about the Treasury Building were sometimes very productive of fine specimens and the broad stone steps and pillars were frequently littered with moths, May flies beetles, etc., where one could stand and pick out his desiderata with little difficulty. I captured several of the Regal Walnut moths (*Citheronia regalis*) and a number of our largest and handsomest sphinxes. Besides making the acquaintance of a number of insects new to me, I met several entomologists who, like myself, had been attracted to the lights by the abundance of specimens.

Today lamps in big cities such as Washington, D.C., Philadelphia, and Boston rank among the worst places to collect moths or meet entomologists. Reductions in numbers of moths flying to lamps have been noted in other locations (Hessel 1976, Muller 1979, Janzen 1983). Decreases in moths at urban lamps can be explained by many factors, including declines in moth populations, dilution of moths among thousands of city light sources, and suppression of flight-to-light behavior as a result of diffuse background light. However, reductions in numbers of moths flying to urban lamps are what one would expect if urban moths today were genetically less inclined to fly to lamps than were those a century ago.

In densely illuminated urban environments, lighting may have favored species that either fly during the day, do not fly to lamps, or do

not fly at all. Urban pests exemplify such species. These include sesiids (Engelhardt 1946) and domestic tineids (Ebeling 1978). Species with flightless females include the bagworm moth, *Thyridopteryx ephemeraeformis* (Haw.) (Psychidae), gypsy moth, *Lymantria dispar* (L.), (Lymantriidae), white-marked tussock moth, *Orgyia leucostigma* (J. E. Smith) (Lymantriidae), and fall cankerworm, *Alsophila pometaria* (Harris) (Geometridae) (Lutz 1941, Drooz 1985). The two urban saturniids, *Hyalophora cecropia* and *Samia cynthia*, do not commonly fly to urban light sources (G. P. Waldbauer pers. comm., Covell 1984). The extent to which lighting may have influenced the kinds of moths inhabiting densely illuminated urban environments is unclear.

METHODS TO REDUCE DISTURBANCES

Low-pressure sodium lamps may be used to reduce disturbances caused by lighting. Low-pressure sodium lamps elicit flight-to-light behavior less frequently than do other lamps (Robinson 1952). They do not disturb certain circadian rhythms of Lepidoptera and other insects (Frank & Zimmerman 1969, Bruce & Minis 1969, Pittendrigh et al. 1970, Truman 1976). The low-pressure sodium lamp radiates less energy than does any other kind of lamp of equal illuminance (Finch 1978).

A variety of measures may protect moths from adverse effects of outdoor lighting. Lamp-free reserves such as sheltered hollows shielded from lighting have been suggested to save the glow worm, *Lampyrus noctiluca* L. (Coleoptera: Lampyridae), a species whose survival in Britain may be threatened by outdoor lighting (Crowson 1981). To reduce lighting impact in habitats already exposed to lamps, the most effective action is to turn off the lamps. Low-pressure sodium lamps may replace other lamps when illumination is essential. Filters to block ultraviolet light may be installed over mercury vapor lamps, and shields may be placed around lamps to block stray light. Low-watt orange-colored incandescent lamps ("bug lights") may replace ordinary incandescent lamps, but some moths fly to these lamps. Bird feeders may be removed from windowsills, lampposts, and other sites close to light sources. "Bug zappers" should be turned off. Natural light-traps such as open garages may be closed to prevent entry of insects. Operators of nearby commercial light sources such as illuminated billboards may be contacted and invited to save money and moths by turning lamps off during those hours of night and early morning when billboards are rarely seen.

Although the feasibility of such changes may be questioned, several North American cities have taken similar steps to reduce light pollution. Light pollution interferes with astronomical work at observatories (Hen-

dry 1984). These cities have converted streetlamps to low-pressure sodium, required ultraviolet-blocking filters over mercury lamps, imposed curfews on the use of commercial lighting, and mandated shielding of luminaires (Hendry 1984). Low-pressure sodium lighting, however, has provoked political controversy on aesthetic and other grounds (San Jose Committee of the Whole 1980).

CONCLUSION

Effects of outdoor lighting may be divergent. They vary according to species, lamps, and habitats. Improved levels of illumination may increase nocturnal vision, but creation of visual artifacts may disturb vision. Increased numbers of lamps may promote flight-to-light behavior, but high levels of background light may suppress this behavior. Expansion of streetlighting may increase flight to streetlamps, but shifts from mercury to sodium lamps may decrease it. Diversion of moths to lamps may increase numbers of moths in illuminated areas, but diversion of moths away from lamps may decrease numbers. Lamps may suppress oviposition in the laboratory, but oviposition may increase or decrease near lamps in the field. Clumping of moths near lamps may increase predation by birds and bats, but destruction of parasitic wasps and flies at lamps may decrease predation. Disturbances such as habitat destruction and urbanization may further confound effects of outdoor lighting.

Several conclusions emerge from the observations on lighting. Outdoor lighting may destroy vast numbers of individual moths without apparently suppressing populations of moths. However, it disturbs some populations more than others, and it disturbs some individuals more than others in the same population. It generates selective pressures favoring adaptations for protection against adverse effects of lamps. The result may be evolutionary changes in behavior, or changes in the kinds of moths inhabiting illuminated environments. These changes may increase through time as urban expansion fragments habitats and exposes smaller moth populations to electric illumination.

Conservation efforts need to consider adverse effects of outdoor lighting. If one wishes to protect Lepidoptera in small, endangered habitats exposed to outdoor lighting, reducing or changing exposure may be helpful. In such habitats light traps including "bug zappers" may deplete populations of moths. Some cities have attempted to reduce light pollution to protect astronomical observatories. Whether similar large-scale restrictions on lighting might help to conserve Lepidoptera has yet to be demonstrated.

Future research could help clarify lighting impact. Despite abundant evidence that outdoor lighting affects individual moths, few studies

have attempted to quantify lighting effects on moth populations. Evidence that lighting has suppressed populations of particular moths such as saturniids is weak. Studies similar to those on the effects of illumination of orchards and cotton fields (Herms 1929, 1932, Nomura 1969, Nemec 1969) could be extended to other settings and species. Faunal surveys, life history studies, and ecological studies could examine Lepidoptera in differently illuminated environments. Behavioral and physiological studies could investigate the possible evolution of tolerance to adverse effects of lighting. The method might include comparison of Lepidoptera sampled from large geographic regions that possess different levels or kinds of outdoor illumination.

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