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Sensory Ecology: Night Lights Alter Reproductive Behavior of Blue Tits

Research on songbirds indicates that streetlights influence timing of dawn chorus, egg-laying and male success in siring extra-pair young, providing new evidence that artificial lighting is an ecologically disruptive force.

Travis Longcore

Daily, monthly, and seasonal fluctuations in ambient lighting were reliable elements of the physical environment until the introduction of widespread gas and electric lighting by humans in the late 1800s and 1900s. Natural variation in light from the sun, moon, and stars provided both a reliable *Zeitgeber* for daily and seasonal rhythms and defined the visual environment within which characteristics affecting fitness evolved (e.g. [1]). Although the expansion of artificial night lighting as a global phenomenon tracks growing population, economic activity and energy consumption (Figure 1) [2], research has only recently focused on the biological implications of these dramatically changed conditions [1,3]. In a recent issue of *Current Biology*, Bart Kempnaers and colleagues [4] report on a new finding that begins to illustrate the effects of artificial night lighting on reproductive behavior of songbirds, and, importantly, shows the potential interference of altered light environments with indicators of individual fitness.

The timing of bird song and reproductive development relative to ambient and artificial illumination have long been studied [5,6]. Under natural conditions, dawn song initiates soon after a critical illumination threshold is met [5]. An influence of artificial illumination on the time of singing is well known for a variety of passerines

(see references in [6]. Nocturnal and early morning singing associated with territorial defense and reproductive behavior can be affected by artificial lighting. For example, male Northern Mockingbirds (*Mimus polyglottos*) sing at night under artificial lights and full moon conditions when unmated, while mated males rarely sang at night except under artificial lighting. Likewise, the time of initiation of songs by American Robins (*Turdus migratorius*) advances both along a geographic gradient of increased ambient lighting and between historic (less lighting) to current (more lighting) ambient conditions at the same location [7]. There is also evidence for an earlier start to seasonal breeding of birds in urban (lighted) environments than rural (dark) environments [8,9], although co-varying factors such as food availability were not ruled out [6]. Such early breeding could be stimulated by an extended day-length cue produced by artificial lighting that triggers testosterone production and gonad development [6,10].

Research on the effects of artificial night lighting on the non-lethal physiological responses of organisms *in situ* is increasing. Mechanisms of lethal effects of lights on animals have received considerably more attention, including the long history of documented avian mortality at lighted structures [11], and the attraction and mortality of insects and sea turtles at lights (see reviews in [1]). The effects of artificial lights at night extend beyond

instances of direct mortality; night lighting changes the very essence of the environment in which species interact at night and upon which they depend to make decisions about risk. The effects of artificial night lighting on species interactions, especially predator-prey dynamics, is therefore receiving attention [12–14], as are the consequences for movement and foraging behavior [15,16].

The new paper by Kempnaers *et al.* [4] is pathbreaking in that it documents and connects a behavior affected by artificial light (timing of dawn song) with reproductive outcomes (laying date and obtaining extra-pair copulations). Kempnaers *et al.* [4] worked with a community of songbirds in Vienna that were monitored over six years, from 1998–2004. The layout of their study area provided a natural experiment with three distinct zones: forest interior, forest edge, and forest edge adjacent to streetlights with high pressure sodium lamps. They recorded the dawn chorus in each of the zones to investigate the time of initiation for five bird species, and also used a database of extensive banding and DNA sampling of Blue Tits (*Cyanistes caeruleus*) breeding in nest boxes to investigate laying date, paternity gain and loss, and other fitness-related traits.

Consistent with earlier research, each of the five species within 50 m of streetlights initiated dawn songs earlier than in the forest interior or edge habitats without lighting. Furthermore, for Blue Tits, females nested earlier in the year by 1.5 days on average and males had greater success siring extra-pair young in the light-influenced areas. The number of extra-pair couplings decreased exponentially with distance to lights, reinforcing the conclusion that lights were the causal mechanism. Yearling birds especially



Figure 1. Night lights.

Kempnaers *et al.* [4] researched the effect of artificial night lighting on birds in a forest reserve on the outskirts of Vienna, Austria. This photograph of downtown Vienna illustrates various types of light that influence biological systems, including the yellowish glow of low pressure sodium streetlights (similar to those studied by the authors), white from full spectrum lights (fluorescent, metal halide, and other types), and red obstruction lighting on tall buildings. Although sodium vapor lights are generally thought to be less ecologically disruptive because they emit little ultraviolet light, which is attractive to insects, and blue light, which is a powerful physiological signal, the new research illustrates that these lights do disrupt timing of bird song and other reproductive behavior. Photo: iStockphoto.com/Ziutograf.

benefitted from location near lights, with these birds gaining extra-pair copulations at rates equaling those reached by mature birds in lit areas, while yearling birds in unlit environments rarely sired any extra-pair offspring. The authors convincingly rule out male quality as an explanation for these observed differences.

Kempnaers *et al.* [4] propose that the increase in extra-pair copulations near artificial lights can be attributed to earlier initiation of the dawn song, which in turn influences female extra-pair behavior. Under natural conditions, early dawn song is an indicator of male quality [4], which attracts females to early singing males. Thus, in areas influenced by artificial night lighting, previously reliable indicators of fitness are being rendered unreliable.

The early laying date near night lights documented by Kempnaers *et al.* [4] may be maladaptive. Changes in phenology risk desynchronizing biological processes important for survival. For example, Bewick's swans (*Cygnus columbianus bewickii*) exposed to artificial night lighting on wintering grounds lay down fat more

rapidly and migrate earlier in the spring than those not under lights, potentially arriving at breeding grounds out of synchronization with local phenology [17]. Disruption of light signals that cue seasonal behaviors and associated physiological adjustments can lead to even more direct adverse effects. For example, social voles (*Microtus socialis*) that were exposed to light interruption in the form of 15 minutes of cool fluorescent light every 4 hours at night in the winter exhibited disruptions to their thermoregulatory system [18] that led to death in a field experiment [19].

The profound global change represented by the introduction and expansion of artificial night lighting over the past century has not yet been adequately investigated by biologists. More field studies will be needed that evaluate the effects on species interactions, physiology, circadian rhythms, foraging, social behavior and fitness to complement laboratory studies. For research on nocturnal species, researchers should be aware of the ability of many species to discern and respond to gradations of darkness that the human eye is unable to detect [1,3]. The current research by Kempnaers *et al.* [4] concerns

diurnal species with effects decreasing rapidly at illuminations of less than 0.1 lux. As researchers investigate other species, they should be aware that natural darkness ranges in orders of magnitude dimmer than 0.1 lux (10^{-3} to 10^{-5} lux) and sensitive equipment is required to measure these illuminations. The extent and rapid growth of artificial night lighting globally, and its significance in urban, rural and even aquatic environments [20], makes the effects of artificial light an inescapable consideration for biologists seeking to understand biodiversity and its conservation in the modern world.

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Actin Crosslinkers: Repairing the Sense of Touch

Cells use actin bundles infused with myosin to exert contractile forces on the extracellular environment. This active tension is essential for cellular mechanosensation. Now, the role of actin crosslinkers in stabilizing and repairing the actin bundles is coming into clearer view.

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In order to thrive in complex environments, eukaryotic cells have developed a range of sensory machineries that can respond to chemical, electrical and mechanical signals. While chemical and electrical signals can act over long distances through the diffusion of molecules or the transmission of currents, mechanical signals are decidedly local. In order to 'feel' forces or sense the stiffness and texture of the environment, the cell must 'touch' the immediate surroundings. This cellular haptic sensory perception has been studied extensively in many laboratories [1-5]. Recently, it has been recognized that the mechanical properties of the extracellular environment are important in many aspects of differentiation and development, including the differentiation of pluripotent cells into more specialized cells [6,7], developmental patterning [8], and the metastatic process in cancer [9]. Thus, there is a growing recognition for the role of mechanics and forces in cell biology and beyond. In a recent paper published in *Developmental Cell*, Smith et al. [10] have now provided new molecular details of mechanical stress events in the cell and have revealed how the cell maintains actin structures and mechanical tension. This work will open new avenues for in-depth understanding of cellular mechanosensation.

The essential cellular components involved in mechanosensing have been

identified: integrin and cadherin adhesions connect the cell to the extracellular matrix (ECM) and to other cells, respectively [11]. A host of regulatory proteins connect the actin cytoskeleton to the transmembrane integrin and cadherin adhesions. Non-muscle myosin II is needed to provide the contractile force that tugs on the cytoskeleton and the adhesions. Indeed, active generation of forces by the cell seems to be central to mechanosensing [1,5]. Previous work has provided insight into the regulation of active force generation at the molecular level [12] and a large number of proteins have now been implicated in cellular mechanosensing [11].

Yet, if we dig a little deeper, a number of fundamental questions still remain. The assembly and movement of adhesions in response to forces and ECM properties are poorly understood, although direct measurements of mechanical forces on adhesion proteins have been recorded [13]. The precise roles of adhesion and cytoskeleton proteins involved in mechanosensing are not clear. The regulatory circuitry of adhesions and myosin has not been mapped. Mechanical properties of eukaryotic cells are also complex and, depending on where you look, the cytoplasm can be liquid-like or solid-like [14]. The cell also actively regulates its mechanical properties by changing the crosslinking and bundling between cytoskeletal filaments. Indeed, in response to ECM and substrate properties, cells often form strong F-actin bundles that are called stress

fibers. Actin stress fibers terminate at focal adhesions and are important in regulating the cell's sense of touch. Recently, mechanical modeling offered some clues on how and why the stress fibers are built [15]: crosslinking and bundling proteins make transient connections between actin filaments and affect the sliding friction between these filaments. When the filaments are parallel, crosslinking and bundling friction reaches a maximum and can resist the contractile force exerted by myosin, generating a stable stress fiber structure. In this process, adhesions, myosin and actin crosslinking activity work together to change the cytoskeleton organization. This modeling analysis also revealed that the substrate stiffness strongly influences the formation of stable stress fibers [15].

The work by Smith et al. [10] focuses on mechanical failure events in the stress fiber and on zyxin, a LIM domain protein that has been associated with adhesions and mechanosensing. These authors point out that stress fibers often exhibit thinning events that can lead to catastrophic breaks. They find that, to guard against these failures, zyxin is recruited to sites where there is large stress fiber movement and damage. Zyxin also recruits α -actinin, which is a known crosslinker of actin filaments. Recruitment of zyxin and α -actinin appears to stabilize damaged stress fibers. Consistent with these results, earlier work has reported that zyxin is only recruited when the stress fiber is contracting [16,17]. Thus, zyxin appears to sense mechanical failure and control the sequence of crosslinking events that mediate the stabilization and contraction of stress fibers. One possible mechanism is that, during a failure event, there is an increase in the free barbed ends of F-actin at the site of mechanical strain, which might be targeted by zyxin. When taken together, these findings