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E-Synthesis

An Ecological Perspective on Sleep Disruption

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abstract: Despite its evolutionary importance and apparent ubiquity among animals, the ecological significance of sleep is largely unresolved. The ecology of sleep has been particularly neglected in invertebrates. In insects, recent neurobehavioral research convincingly demonstrates that resting behavior shares several common characteristics with sleep in vertebrates. Laboratory studies have produced compelling evidence that sleep disruption can cause changes in insect daily activity patterns (via "sleep rebound") and have consequences for behavioral performance during active periods. However, factors that could cause insect sleep disruption in nature have not been considered nor have the ecological consequences. Drawing on evidence from laboratory studies, we argue that sleep disruption may be an overlooked component of insect ecology and could be caused by a variety of anthropogenic and nonanthropogenic factors in nature. We identify several candidate sleep-disrupting factors and provide new insights on the potential consequences of sleep disruption on individual fitness, species interactions, and ecosystem services. We propose an experimental framework to bridge the current gap in knowledge between laboratory and field studies. We conclude that sleep disruption is a potential mechanism underpinning variation in behavioral, population, and community-level processes associated with several aspects of global change.

Keywords: circadian activity, time budget, anthropogenic disturbance, sleep rebound, fitness, ecosystem services.

> An object in motion always attracts the attention of children, young and old; a butterfly flitting from blossom to blossom, a locust jumping before one in the dusty road, a bee rummaging in a flower, all arouse one's interest. But naturalists, like children, cease to pay attention to insects when the latter cease their activity. Thus the interesting problem of when, where and how insects sleep has been all but neglected. (Rau and Rau 1916)

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Sleep: An Underappreciated Component of Animal Ecology

Most animals have evolved in environments with rhythmic periods of light and darkness. These oscillations have selected for a variety of temporal patterns of neurological and behavioral activity. Animals often restrict their activity to certain periods of the daily cycle during which they must allocate their limited time to different, often mutually exclusive tasks (e.g., locomotion, feeding, mating, oviposition; Saunders 2002; Kronfeld-Schor and Dayan 2003). These circadian rhythms and associated time budgets determine when animals perform their ecological roles and when they interact with other species. However, periods of inactivity are seldom considered, and their ecological and physiological implications remain largely unexplored.

Sleep is a particular kind of behaviorally inactive state usually characterized by temporally consolidated periods of resting behavior, a specific body posture, reduced levels of neurological activity, increased arousal thresholds, and homeostatic regulation (Siegel 2008, 2009). Although often considered to have a restorative function, the adaptive value of sleep is still controversial (Siegel 2008, 2009; Hartse 2010; Vorster and Born 2015). Despite its ubiquity among animals (Vorster and Born 2015), sleep has mostly been studied in neurological and behavioral contexts under laboratory conditions, without considering its significance for animal ecology. In a recent article, Aulsebrook et al. (2016) convincingly argued for an integration of neuroscience, ecology, and evolutionary biology in order to better understand patterns of animal sleep in natural settings. Focusing on vertebrates, they advocated for measuring neurophysiological states of animals in nature and introduced the idea that anthropogenic disturbances could affect the timing, nature, and intensity of animal sleep.

In this article, focusing on insects—the most abundant and diverse animal group—we provide a complementary but distinct treatment with a unique focus on the ecological significance of animal sleep. We chose to focus on

Table 1: Selected examples of factors reducing the duration of insect sleep, and resulting consequences of total sleep deprivation or partial restriction for behavioral performance in the laboratory (if measured).

Causative factor and study organism	Sleep rebound observed	Performance effects of sleep deprivation	References
Mechanical disruption (shaking, rotation, manual tapping, sliding floor):			
Fruit fly *Drosophila melanogaster*	Yes	Impaired memory consolidation	Seugnet et al. 2008; Donlea et al. 2011; Le Glou et al. 2012
		Reduced courtship behavior	Seugnet et al. 2011; Kayser et al. 2014
		Lower courtship success	Kayser et al. 2014
		Reduced aggression	Kayser et al. 2015
		Compromised escape responses	Huber et al. 2004; Cirelli et al. 2005
		Higher reaction thresholds	Faville et al. 2015
		Premature death	Shaw et al. 2002
		Not measured	Joiner et al. 2006; Bushey et al. 2007; Dissel et al. 2015*a*
Honeybee *Apis mellifera*	Yes	Lower precision of social communication (waggle dance)	Klein et al. 2010
		Impaired navigation	Beyaert et al. 2012
		Reduced memory retention	Hussaini et al. 2009
		Higher reaction thresholds	Sauer et al. 2004
Cockroach *Leucophea maderae*	Yes	Not measured	Tobler 1983
Cockroach *Blaberus giganteus*	Yes	Increasing activity during recovery	Tobler and Neuner-Jehle 1992
Cockroach *Diploptera punctata*	No	Increased metabolic rate, premature death	Stephenson et al. 2007
Paper wasp *Polistes flavus*	No	Not measured	Klein 2003
Chemical exposure (caffeine, hydroxyzine, octopamine):			
Fruit fly *D. melanogaster*	Not measured	Not measured	Shaw et al. 2000; Crocker and Sehgal 2008; Donlea et al. 2011
Temperature (high nighttime temperatures):			
Fruit fly *D. melanogaster*	Yes	Reduced aggression	Kayser et al. 2015
		Reduced courtship behavior	Kayser et al. 2014
		Lower courtship success	Kayser et al. 2014
		Not measured	Parisky et al. 2016
Social interactions (exposure to male sex peptide):			
Fruit fly *D. melanogaster*	Not measured	Possible link to reduced life span	Isaac et al. 2009
Resource availability (starvation):			
Fruit fly *D. melanogaster*	Sometimes	No learning impairments	Thimgan et al. 2010
		Not measured	Keene et al. 2010; Erion et al. 2012

insect sleep disruption, including sleep deprivation (total sleep loss) and sleep restriction (partial sleep loss), because (i) although invertebrates have historically been neglected as models of sleep research, many studies measuring the consequences of sleep disruption are now performed in this group of animals due to their short life cycle and genetic tractability (Vorster and Born 2015), and (ii) they have enormous untapped potential for conducting field ecology studies. Drawing from a synthesized body of laboratory experimental work on insect sleep disruption, we propose the following: (1) there are a variety of biotic and abiotic factors that are likely to disrupt insect sleep in natural settings, (2) disruptions during the sleep period cause changes in circadian patterns and behavioral performance during active periods, and (3) the effects of sleep disruption may cascade beyond the individual to have population- and community-level consequences and affect the provision of insect-mediated ecosystem services. We aim to identify the current gaps in knowledge concerning the ecological relevance of insect sleep and propose a consolidated set of new hypotheses to be tested in the coming years as this new field of ecology emerges. As there is currently a complete lack of evidence from the field, our approach at this early stage will consist of extrapolating laboratory discoveries on insect sleep disruption to effects on insect ecology at different levels of biological organization. We highlight a need to understand the nature, strength, and frequency of sleep-disruptive factors in nature that could affect individual fitness, argue that sleep must be considered as

a central part of animal time budgets, and propose that sleep disruption is a mechanistically important missing link in the study of the behavioral ecology of animals.

Insect Sleep

The idea that resting states in insects are similar to sleep in humans and other vertebrates, and that they play an ecological role, goes back to at least the early 1900s (Fiebrig 1912; Piéron 1913; Rau and Rau 1916). However, it was not until the 1980s that comparative sleep research began to include insects (reviewed in Hussaini et al. 2009). Pioneering studies on honeybees (Kaiser and Steiner-Kaiser 1983; Kaiser 1988) and cockroaches (Tobler 1983) showed that insect resting states shared many common characteristics with vertebrate sleep at the neuronal or behavioral levels, including (i) consolidated periods of behavioral inactivity, (ii) rapid reversibility of the inactive behavioral state, (iii) increased thresholds needed for arousal, (iv) distinct behavioral postures during resting, and (v) and homeostasis (i.e., a "sleep rebound" following sleep loss). Then, at the turn of the century, two independent studies (Hendricks et al. 2000; Shaw et al. 2000) demonstrated that rest in *Drosophila* fruit flies is a sleeplike state. The discovery of sleep in a genetically tractable model organism launched a new field of sleep research, mostly focusing on the ontogeny, genetics, and neurology of *Drosophila* sleep (reviewed in Dissel et al. 2015*b*), with a handful of additional studies on other insect groups (table 1). In addition to widening the taxonomic scope of animal sleep research, this wave of recent studies has begun to show that depriving animals of sleep can have consequences for daily activity rhythms and behavioral performance.

Laboratory Sleep Disruption Studies

In order to demonstrate a potential adaptive value of sleep, one can experimentally test the consequences of sleep disruption. Because most of the studies on sleep have been performed in diurnal insects, we will predominately focus on the effects of sleep disruption that occurs during the night, when diurnal insects are sleeping. The most common method used to deprive insects of sleep in the laboratory is mechanical stimulation—usually involving shaking, manual tapping, or causing rapid falling—during consolidated sleeplike resting periods. Other factors that have been observed to cause reductions in insect sleep include ingestion of chemical substances such as caffeine, high nighttime temperatures, exposure to substances associated with mating, and starvation (table 1). The most thorough investigations have measured (i) the reduction in sleep caused by the disruption, (ii) the compensatory sleep rebound that occurs the following day (an increase in inactivity during a normally active period) or during the subsequent normal sleep period (an increased intensity of sleep; Tobler and Neuner-Jehle 1992; Sauer et al. 2004; Klein et al. 2010), and (iii) behavioral performance consequences for the individual (table 1). Although to date there are proportionally few studies that actually measure behavioral performance consequences of sleep disruption (table 1), there is already clear evidence that sleep loss/interference can have wide-ranging consequences for individual performance, including memory consolidation, courtship success, aggression level, navigation performance, and longevity (table 1; fig. 1). There is additional evidence that effects can vary as a function of factors such as starvation level, immune state, age, and genotype (Donlea et al. 2012; Erion et al. 2012; Yamazaki et al. 2012; Dissel et al. 2015*c*; Slocumb et al. 2015). Unfortunately, none of these studies has been conducted outside of the laboratory. However, analogous disruptive factors present in nature are likely to cause insect sleep disruption, and a large component of insect behavioral variation observed in field studies could be explained by these disruptions. We will first present candidate disruptive factors in nature and their relationship to laboratory analogues and will then propose perspectives on potential outcomes at several levels of biological organization.

Potential Factors Causing Insect Sleep Disruption in Nature

Night Warming

Over the past 5 decades, night temperatures have been increasing faster than day temperatures as the climate changes (IPCC 2013). This asymmetry has not yet been given enough consideration, especially in terms of its impact on small, free-living, diurnal ectotherms (e.g., many insects) whose nighttime sleep, along with other fitness-related traits, may be sensitive to heat exposure. For instance, in the grain aphid *Sitobion avenae*, successive exposures to warm nights depressed adult performance (longevity and fecundity) during the following days (Zhao et al. 2014). In addition to the observed impacts on various life-history traits, we propose that higher nighttime temperatures could disrupt sleep and—in light of evidence from laboratory studies—elicit a sleep rebound and decrease performance (Kayser et al. 2014, 2015; table 1), although this may not be the case for all species (see "Special Cases: Nocturnal and Around-the-Clock Insects?"). Warm nights could cause sleep disruption by desynchronizing the photoperiod with the thermoperiod by affecting the central oscillator responsible for daily activity patterns (Beck 1980) or by affecting insect time perception and resetting their internal clock (Dunlap 1999). Moreover, warmer nighttime temperatures may result in higher energy expenditure during sleep in diurnal insects, especially if climate warming allows insects to be active later in the year, when daylight periods are shorter (Joschinski et al. 2015). Night warming could prove to be a sleep-disruptive mechanism that

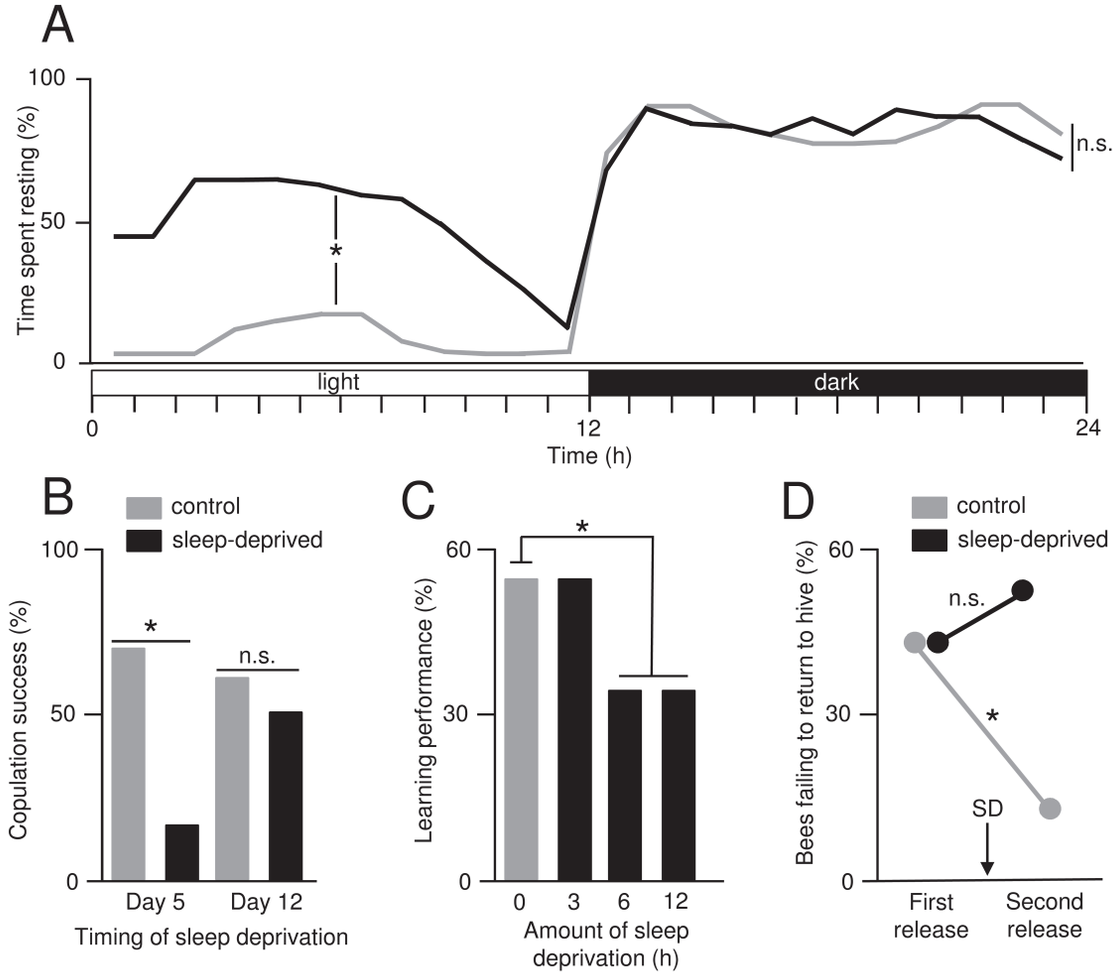

Figure 1: Selected examples of behavioral consequences of sleep deprivation in insects. *A*, Mechanical sleep deprivation (gray line) during the previous nighttime resting period increases the amount of daytime but not nighttime sleep by *Drosophila melanogaster* relative to undisturbed controls (black line; modified from Shaw et al. 2000). *B*, Sleep deprivation due to high nighttime temperatures results in reduced courtship behaviors and copulation success in *D. melanogaster* but only when administered early in their adult life (5 days after emergence; modified from Kayser et al. 2014). *C*, Mechanical sleep deprivation administered for a duration of 6 or 12 h following learning that an odor paired with an aversive stimulus (shock) reduces learning performance in *D. melanogaster* (modified from Seugnet et al. 2008). *D*, Mechanically sleep-deprived honeybees (*Apis mellifera*) fail to consolidate navigation memory following a first release (arrow with SD indicates sleep deprivation during the intervening night) and as a result more often fail to return to the hive when compared to controls with no sleep deprivation that remembered the first release (modified from Beyaert et al. 2012). Note, however, that in the latter study there was no control for daytime stress. Asterisks indicate statistical differences; n.s. indicates no significant difference.

has a larger impact on ectothermic animals (whose metabolism is more dependent on environmental temperature), which would have asymmetric effects on terrestrial food webs.

Noise and Vibrations

In humans, noise exposure causes several physiological and neurological problems, as well as sleep disturbances (World Health Organization 2011). There is growing evidence of numerous effects of anthropogenic noise on nonhuman animals from different taxa, such as changes in foraging behavior and reproductive success (Barber et al. 2010). Although the consequences of sleep disruption caused by noise have not been directly tested in laboratory studies of insects, there is evidence that their mechanosensory systems could be sensitive to this perturbation either through substrate-borne vibrations or receptivity to far-field sound, depending on the taxon in question. Some insect species have evolved very complex hearing systems that are similar to those found in vertebrates, mostly serving intraspecific communication and predator detection functions (Göpfert and Hennig 2016). Morley et al. (2013) recently reviewed why and how inver-

tebrates are likely to be affected by anthropogenic noise, although they did not consider sleep disruption as a potential mechanism. Similar to noise, and analogous to mechanical techniques in laboratory experiments that have induced sleep disruption (shaking, sliding, rotation, tapping), many anthropogenic activities (e.g., construction activities, farm equipment, traffic) produce vibrations in urban and agricultural settings and may disrupt insect sleep patterns as a result. For example, a recent study found that *Drosophila* flies can synchronize their daily locomotor activities, as well as the daily oscillations of their protein concentrations controlling clock neurons, to specific sequences of vibrations and silence (Simoni et al. 2014). Finally, adverse weather conditions such as wind and rain, although understudied compared to other environmental factors in the context of insect behavior (but see Weisser et al. 1997), could act similarly to vibrations by dislodging insects from their resting places and mechanically disrupting their sleep. Since both anthropogenic activities and extreme weather events are likely to increase into the future and could have synergistic effects, it will be important to study their impacts on insect ecology while considering sleep disruption as a potential mechanistic driver.

Night Light

Because light is both a resource and a source of information, artificial lighting during the night can be a major stressor for diurnal organisms via effects on multiple aspects of their behavior (Rich and Longcore 2006), including sleep disruption (Raap et al. 2015, 2016). Gaston et al. (2013) reviewed the ecological impacts of nightlight anthropogenic pollution and discussed how this stressor can disrupt the partitioning of activities between night and day by affecting circadian clocks and photoperiodic responses. In insects, exposure to light at inappropriate periods of the circadian cycle can reset the internal clock in addition to strongly affecting flight behavior, the timing of mate finding, foraging behavior, and the risk of exposure to predators (Rich and Longcore 2006). Both nocturnal and diurnal insects are vulnerable to effects of artificial lighting, especially in and around the cities where important declines in insect biodiversity have been reported around the world (Eisenbeis and Hänel 2009). Nightlight is known to affect sleep patterns in vertebrates (Aulsebrook et al. 2016), but this has not yet been directly investigated in insects. These effects should also be investigated in insect species whose internal clocks are circalunar (dependent on moonlight) instead of circadian (Kronfeld-Schor et al. 2013).

Exposure to Chemical Substances

For insects, exposure to synthetic chemical substances in nature is a likely occurrence, especially in agroecosystems where pesticides and other chemical compounds are omnipresent and where their residues persist over time. Similar to the effects of drugs (e.g., caffeine, octopamine) in laboratory experiments (Crocker and Sehgal 2008; Nall et al. 2016), chemical substances present in ecosystems may act on specific brain receptors and the endocrine system involved in daily rhythmicity and sleep expression, causing sleep deprivation or restriction. There is already evidence that circadian rhythms in insects influence their responses to pesticides; for instance, *Drosophila* are more sensitive to pesticide exposure during some phases of the daily cycle than others (Hooven et al. 2009). To our knowledge, however, the reverse hypothesis—that behavioral responses to chemical pesticides affect circadian rhythms (including sleep)—has not been tested.

Ecological Interactions

Disturbances of insect sleep patterns may arise from ecological interactions such as competition, predation, parasitism, or social interactions. As an adaptation to avoid temporal niche overlap, species are often active at different times of the day and could thus influence each other's sleep patterns. For instance, some sympatric species of carabid beetles are active at night, while others are active during the day (Thiele 2012). Thus, the foraging behavior of one species could interrupt sleep in the other by direct inadvertent physical disturbances, analogous to mechanical sleep disruption in laboratory experiments (table 1). In terms of antagonistic interactions, some animals have been shown to shift from nocturnal to diurnal activity in response to the presence of a competitor (Harrington et al. 2009; Yerushalmi and Green 2009). The effect of predation pressure on the sleep patterns of prey animals is well known in vertebrates (Acerbi and Nunn 2011) but has not been evaluated in insects. Predator presence is likely to have a strong effect on insect sleep through both direct (e.g., predation attempts, prey-predator physical contact) and indirect (e.g., cues of predator presence) effects. Some of these effects could be mediated by chemical signaling among insect prey. In aphids, for example, alarm pheromones emitted during predator attack trigger defensive behavior (dropping off the plant) by other colony members (Vandermoten et al. 2012). The question of sleep disruption caused by interactions with other insects could be particularly interesting when applied to social insects that have evolved a caste-dependent "clock of the colony," in which some specialized individuals could act as an alarm clock to other individuals (Moore 2001; Klein and Seeley 2011; Klein et al. 2014).

Potential Consequences of Sleep Disruption

Effects on Individual Fitness

If sleep serves a crucial restorative and consolidative function, individual animals are expected to face a trade-off in

terms of allocating their time between sleeping and carrying out the daily activities (e.g., foraging, mating, habitat seeking) required to support their survival and reproduction. Too much time spent sleeping could result in missed opportunities for engaging in other activities that increase fitness (Aulsebrook et al. 2016), while not sleeping enough could result in a variety of performance deficits that result in decreased fitness (table 1; fig. 1). From a behavioral ecology perspective, we would expect animal sleep schedules to optimize this trade-off under a particular set of local biotic and abiotic conditions. While barely explored to date (but see Acerbi et al. 2008), behavioral and ecological models that incorporate trade-offs between (i) activity levels and behavioral performance and (ii) time spent sleeping and the opportunities for fitness-related activities could be used to create and test hypotheses relating to optimal sleep schedules under different sets of ecological conditions. Including the sleep-disruptive effects of natural and anthropogenic factors described above in these models would allow investigators to test hypotheses related to the fitness costs associated with these perturbations. Among the sleep disruption–sensitive aspects of performance identified by laboratory studies to date (table 1; fig. 1), reduced courtship performance and impaired learning (which is important for insect foraging behaviors; e.g., Fatouros et al. 2008) could have particularly important impacts on individual fitness.

Future studies should also consider the possibility that insects may be able to habituate to sleep-disrupting factors, minimizing negative effects on individual fitness. While habituation to the sleep-disrupting effect of noise is known to occur in humans over successive noise-exposed nights (Muzet 2007), the hypothesis that other animals can habituate to sleep-disruptive factors in natural settings remains untested. It is, however, likely that frequently occurring sleep disruptors (e.g., wind) may first lead to an initial disruption, followed by habituation. The impact of sleep disruption on individual fitness and the possibility that individuals can habituate will likely depend on the nature, frequency, predictability, magnitude, and synergistic effects of the candidate sleep-disrupting factors discussed above.

Population-Level Effects

The individual-level effects of sleep disruption are likely to have cascading effects on population-level variables such as attack rates (via increased or reduced predator activity or performance) and virginity rates (through reduced copulation success). Furthermore, several studies have found evidence for within- and among-population variation in insect sleep patterns (Donlea et al. 2012; Slocumb et al. 2015; Svetec et al. 2015), suggesting that natural selection maintains variation in sleep schedules and that the frequency of different sleep strategies could shift depending on the prevalence of sleep-disruptive factors. For example, Donlea et al. (2012) found a trade-off between sleep deprivation resistance (in terms of short-term memory retention) and starvation resistance in naturally occurring genetic variants of *Drosophila melanogaster*. In cases like this, one might expect that the relative frequency of different genotypes in different environments should depend on the balance between ecological variables such as resource availability and the prevalence of sleep-disruptive factors. Furthermore, some insect populations may be more susceptible to disturbances affecting their sleep than others. Direct links between ecological variables and insect susceptibility to sleep disruption have not yet been made in observational or experimental ecology studies conducted in the field.

Community-Level Effects

Sleep rebound resulting from sleep disruption could change the temporal structure of insect communities. A sleep-deprived insect will be less active during the following day or the next sleeping period, and its period of activity might become temporally mismatched with its antagonistic or mutualistic partner. These kinds of mismatches are well documented for phenological changes (e.g., diapause) at the seasonal scale (Visser and Holleman 2001; Tylianakis et al. 2008; Chaianunporn and Hovestadt 2015) but have not been explored at finer temporal scales in the context of sleep rebounds. It is increasingly being recognized, however, that disruptive anthropogenic factors such as intensifying levels of artificial night lighting could modify several characteristics of ecological communities (Davies et al. 2012). Sleep disruption could be one of the mechanisms explaining how these disruptive factors could impact community structure, species interactions, and ecosystem functioning. For example, in a well-conducted outdoor mesocosm experiment, Sanders et al. (2015) showed that insect parasitoids and their host aphids were impacted by artificial night light exposure. They observed considerable changes in host-parasitoid interactions (e.g., host density, parasitoid behavior) as a result of artificial night lighting, with particular negative impacts on parasitoids. Modifications of parasitoid searching behavior, reduced parasitoid fecundity, and increased host resistance were proposed as mechanisms underlying these changes. It is tempting to speculate that parasitoid sleep disruption as a result of artificial night lighting could have contributed to this result as well. While still seldom considered in ecological studies of anthropogenic disturbance, the effects of sleep-disrupting factors could cascade through food webs through their effects on individual performance, as well as through variable impacts on different members of interacting insect communities (fig. 2).

Sleep Disruption and Ecosystem Services

Several groups of insects are beneficial to humans because of the ecosystem services they provide in the form of pollination (e.g., bees, other insect pollinators) and pest control (e.g., predators and parasitoids of agricultural pests). Naturally present beneficial insects may provide ongoing ecosystem services in open agricultural production (e.g., field crops) or in other cases are bred, reared, and mass released in either open or closed (e.g., greenhouse production) systems. From an applied perspective, the time that beneficial insects spend inactive (sleeping or simply resting) rather than pollinating or killing pests is wasted and undesirable, unless (1) insects would be ineffective ecosystem service providers during the time they are sleeping anyway (e.g., because host/prey/flower resources are not available or detectable) or (2) a lack of sleep would compromise their ability to provide ecosystem services. Hypothesis 1 is unlikely to be true in all cases: in insect parasitoids, for example, periods of inactivity can make up the vast majority of their time budget, even during daytime periods when hosts are readily available and detectable (e.g., Lauzière et al. 2000). If hypothesis 2 is true, variation in the quality of naturally present ecosystem services provided by beneficial insects could be compromised by disruptive natural and anthropogenic factors (fig. 2), including production and shipment methods for beneficial insects prior to release. On the other hand, if there are minimal relevant performance trade-offs associated with reduced sleep or they can be effectively mitigated (e.g., by providing nutritional supplements)—although this has not yet been demonstrated—strains of beneficial insects with reduced sleep period could potentially be selected from naturally present genetic variants (Donlea et al. 2012) or artificially selected as part of breeding programs for mass releases.

Methodology for Studying Sleep Disruption in Nature

For the most part, experimental studies of insect sleep to date have been performed in the laboratory with laboratory-reared insects. To properly study sleep's role in insect ecology, this field of research must move into natural settings. Addressing this point, Aulsebrook et al. (2016) point out that using behavior as a proxy for sleep can sometimes be misleading and that sleep under field conditions could be measured using wireless electroencephalography (EEG) technology deployed on wild animals. While brain activity of sleeping insects has been measured using probes inserted into tethered individuals in the laboratory (Kaiser and Steiner-Kaiser 1983; Nitz et al. 2002; van Alphen et al. 2013), there are currently no methods available to measure neurological states of free-moving insects, most of which are too small to accommodate currently available wireless EEG technology. In the meantime, we believe that behavioral proxies will continue to be useful for assessing the patterns and effects of insect sleep disruption in ecological studies, particularly in combination with other techniques. We suggest three complementary approaches.

Approach 1: Laboratory Quantification in Field-Collected Individuals

An indirect way to measure an insect's sleepiness in natural populations would be to bring field-collected individuals into a controlled environment and measure how much they sleep during the following 24 h (i.e., their sleep rebound), compared to a set of controls that had been collected the previous day and allowed to rest unperturbed during the night (e.g., kept individually in sheltered enclosures in the field). This would constitute a modification of the captive cohort method for estimating population age structure (e.g., Carey et al. 2012) but applied to the ecology of sleep. This approach would come with the same caveats as the captive cohort method in terms of potential laboratory confinement (see Papadopoulos et al. 2016), especially during the first day, which may have confounding effects on sleep incidence and structure.

Approach 2: Molecular Markers

Cross-translational studies in flies and humans (Seugnet et al. 2006; Thimgan et al. 2010) have begun to identify specific, conserved biomarkers of animal sleep deprivation (e.g., *amylase*, lipid storage droplet 2). If the utility of these markers extends to other insects, they could be measured in individuals collected from natural populations to quantify their level of sleep disruption, depending on ecological factors such as predator presence, population-level variables (demography, population density), and adverse weather conditions. Issues may arise from the use of generalist stress markers if they cannot distinguish the more general effects of environmental stressors in the field from true sleep disruption. Encouragingly, markers produced in response to other forms of environmental stresses (e.g., starvation) are typically not involved in the response to sleep deprivation (Seugnet et al. 2006; Thimgan et al. 2010), suggesting that specific markers of sleep deprivation (i.e., that do not mark any other type of stress) may exist. However, before using a given marker in field study, its reliability in the face of environmental variation will need to be thoroughly investigated. As metabolomic (biochemistry) and transcriptomic (gene expression) profiles of sleep-deprived model insects continue to be developed and begin to be validated in other species, the power of this approach will increase.

Approach 3: Manipulative Field and Semifield Experiments

Ultimately, manipulative field experiments will be needed to test hypotheses regarding the causes of sleep disruption

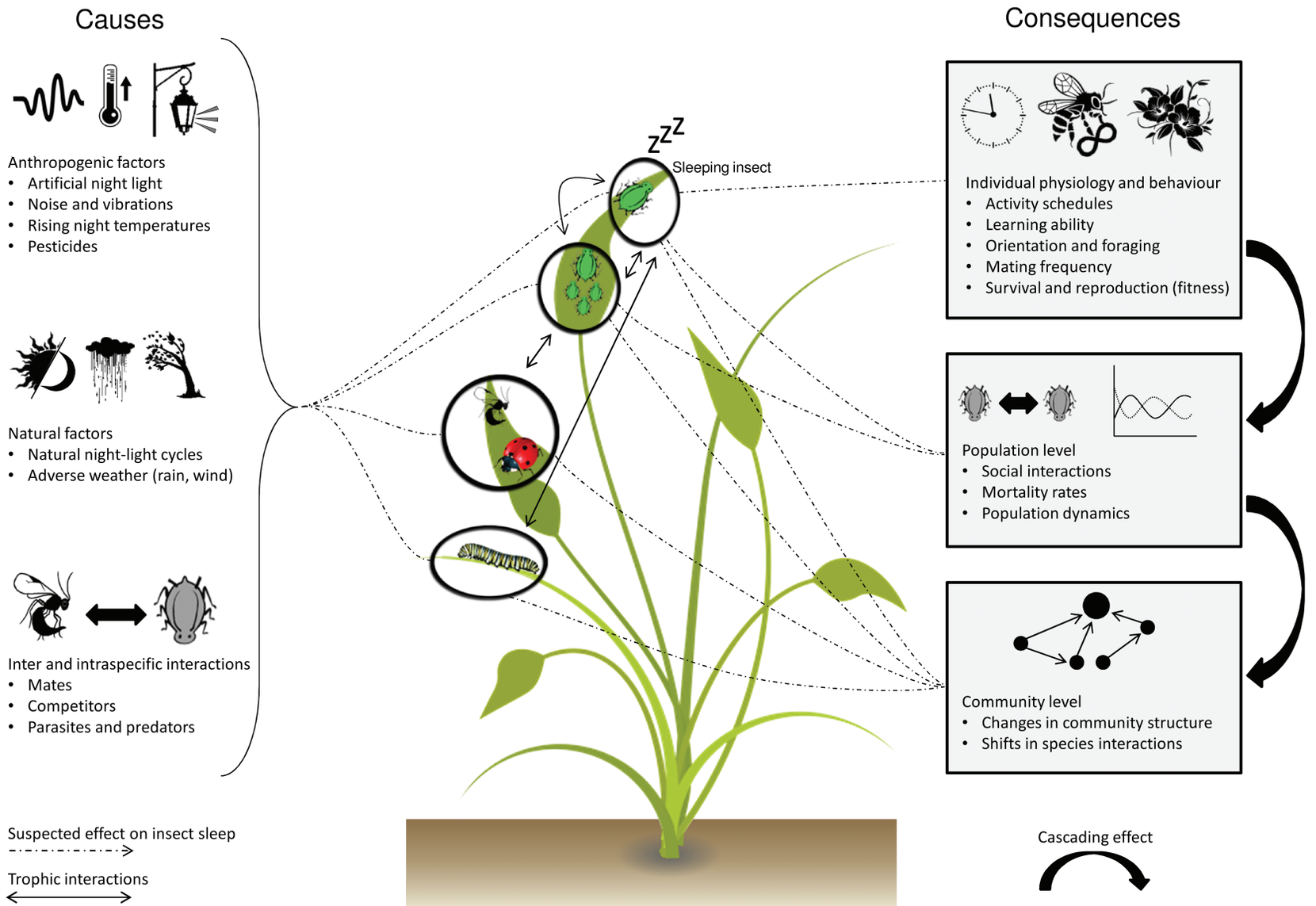

Figure 2: Graphic summary of major causes and consequences of insect sleep deprivation. Principal causes of sleep deprivation are listed as anthropogenic factors, natural abiotic factors, and biotic interactions. Sleep-disrupting factors act on the different components of the food web. Hypothesized consequences range from individual to community level with both direct effects of the disruptive factors and cascading effects among different ecological scales.

and the consequences it has for ecological processes. Using cages or shelters to exclude sleep-disrupting factors, or adding sleep-disrupting factors to some experimental plots and not others, could be used to connect sleep disruption to observed population-level consequences (e.g., predation rates, population growth). To distinguish sleep disruption from other causes of reduced behavioral performance (e.g., stress, energy expenditure), appropriate controls will have to be included; in past laboratory studies these have typically consisted of additional treatments where the same disruptive factors are applied during periods when insects are not sleeping (see studies in table 1). These approaches could be particularly powerful in combination with the first two methods listed above, which would allow experimenters to connect behavioral/biochemical markers of sleep disruption with the observed ecological outcomes.

Special Cases: Nocturnal and Around-the-Clock Insects?

In this article we have focused our discussion on diurnal insects, mostly because the majority of sleep studies has been performed in *Drosophila* and honeybees, which are diurnal. However, many insect species are nocturnal (e.g., Morse and Fritz 1983) and would thus experience a different suite of factors that could disrupt their sleep during the daytime. The only studies of nocturnal insect sleep to date have been conducted in cockroaches (table 1) and have shown evidence of behavioral changes during the night when disruptive stimuli are administered during the day. However, it is still too early to conclude whether causes and consequences of sleep disruption differ between diurnal and nocturnal insects.

Are detrimental effects of insect sleep disruption inevitable, or are there some species or situations where negative effects of sleep disruption are minimal? There are many animal species, including insects, in which no clear circadian pattern can be distinguished (at least not for every individual). Such around-the-clock activities may have an adaptive value and be selected in animals (reviewed in Bloch et al. 2013), and the resulting sleep loss may not always lead to a decrease in performance. For example, during a 3-week period of strong competition for access to females, some male birds are able to reduce their time spent sleeping without showing signs of neurological impairment (Lesku et al. 2012). Additionally, male birds that slept the least sired the most offspring. It thus appears that sleep can sometimes be disrupted without strong negative consequences when there is a strong advantage to staying awake. In principle, this could also apply to insect species that undergo long-distance migrations, display nearly continuous feeding activity (e.g., phloem-feeding species such as aphids; Dixon 1985), or undergo intense consolidated bouts of mating activity, although nothing is known about sleep expression during these activities in insects. Future research on ecological consequences of sleep disruption must account for potential plasticity in the central oscillator system that governs sleep, in order to better understand the impact and ecological significance of around-the-clock activities.

Concluding Remarks

Sleep disruption must be regarded as a potential driver of daily rhythms and behavioral performance when considering the consequences of environmental perturbations on insect ecology. At present, there are many outstanding questions. Knowledge on how the effects of sleep disruption change through ontogeny, across seasons, and in different habitats is completely lacking. Potential synergistic effects of different stressors that cause sleep disruption remain to be explored. When performing these studies, we urge experimenters to not only measure ecological outcomes but also explore evolutionary consequences in terms of effects on individual insect fitness. In addition, there is enormous untapped potential for exploring evolutionary patterns of sleep in insects, due to their incredible diversity and range of lifestyles. Previous comparative analyses of vertebrate groups (Roth et al. 2006; Lesku et al. 2008, 2009) could serve as jumping-off points for these investigations. Ultimately, the question of how and why animals sleep is an evolutionary ecology question (Aulsebrook et al. 2016), with applications for global change biology and ecosystem services. The basic form of this question as applied to insects was first posed at least a hundred years ago, and we still do not have an answer.

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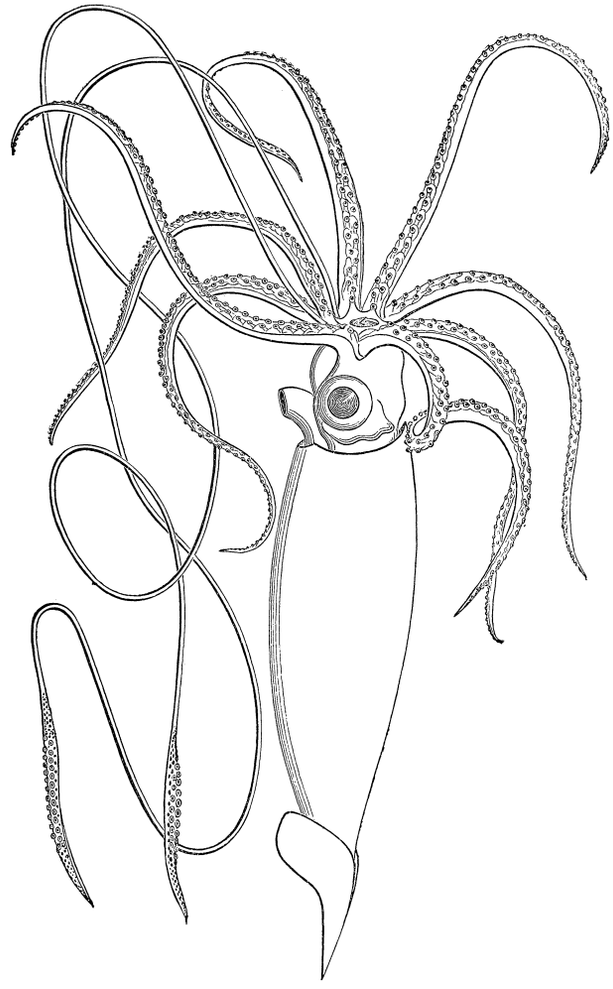

"The most complete specimen [of *Architeuthis monachus* Steenstrup, figured] that has ever come under scientific observation was captured in November, 1873, at Logie Bay, near St. John's, Newfoundland. It became entangled in herring-nets and was secured by the fishermen with some difficulty and only after quite a struggle." From "The Colossal Cephalopods of the North Atlantic" by A. E. Verrill (*The American Naturalist*, 1875, 9:21–36).