## HUMAN IMPACTS

# The influence of human disturbance on wildlife nocturnality

Kaitlyn M. Gaynor[1]*, Cheryl E. Hojnowski[1], Neil H. Carter[2], Justin S. Brashares[1]

Rapid expansion of human activity has driven well-documented shifts in the spatial distribution of wildlife, but the cumulative effect of human disturbance on the temporal dynamics of animals has not been quantified. We examined anthropogenic effects on mammal diel activity patterns, conducting a meta-analysis of 76 studies of 62 species from six continents. Our global study revealed a strong effect of humans on daily patterns of wildlife activity. Animals increased their nocturnality by an average factor of 1.36 in response to human disturbance. This finding was consistent across continents, habitats, taxa, and human activities. As the global human footprint expands, temporal avoidance of humans may facilitate human-wildlife coexistence. However, such responses can result in marked shifts away from natural patterns of activity, with consequences for fitness, population persistence, community interactions, and evolution.

The global expansion of human activity has had profound consequences for wildlife. Research has documented the effects of habitat destruction and defaunation on species and ecosystems (1), but the indirect or nonlethal pathways through which humans alter the natural world have largely eluded quantification. Human presence can instill strong fear in wild animals, which may adjust their activity to avoid contact with humans (2). As in natural predator-prey systems, such risk avoidance can have important nonlethal effects on animal physiology and fitness, affecting demography and triggering trophic cascades (3).

The study of fear effects on animals has focused mainly on spatial avoidance, propelled by rapid advances in wildlife tracking, remote sensing, and computational methods (2, 4). However, as the human footprint expands (5), fewer areas are available for animals to seek spatial refuge from people. In places where wild animals co-occur with humans, animals may minimize risk by separating themselves in time rather than in space (6). Temporal partitioning is a common, even intrinsic, feature of ecological communities, shaping spatiotemporal patterns of predation and competition (6–8). Here we show that humans, as a diurnal apex "super predator" (9), are driving increases in nocturnal activity across diverse mammalian taxa.

To quantify temporal shifts in wildlife activity in response to humans, we conducted a meta-analysis of published literature on the activity of mammals across gradients of human disturbance. Our dataset included 141 effect sizes for 62 mammal species, representing 21 families and nine orders, and spanned six continents (Fig. 1A). We restricted our analysis to medium- and large-bodied mammals [>1 kg in body size (10)] because of their large space needs, potential for conflict with humans, and high levels of behavioral plasticity and because data on their 24-hour activity patterns were widely available. Within each study, we compared animal nocturnality under conditions of low and high human disturbance. We classified areas, time periods, or individual animals as being associated with low or high disturbance on the basis of categorical descriptions of the study system or binned distance or elapsed time from an anthropogenic disturbance (tables S1 and S3).

For each species in each study, we calculated the risk ratio (RR) as a measure of effect size. We compared the percentage of activity that occurred at night (as measured by motion-activated cameras, telemetry devices, and direct observation) at sites or during seasons of high human disturbance ($X_h$) with nighttime activity under low disturbance ($X_l$), with RR = ln($X_h/X_l$). A positive RR indicated a relatively greater degree of nocturnality in response to humans, and a negative RR indicated reduced nocturnality. We used meta-analytical random-effects models to estimate the overall effect of human disturbance on nocturnality and to compare responses across types of human disturbance, species traits, habitats, continents, and study methods. We also used multivariate models to explore the relative importance of these factors with an information-theoretic approach.

Our analysis revealed a marked increase in nocturnal activity. Overall, mammal nocturnality increased by a factor of 1.36 [95% confidence interval (CI), 1.23 to 1.51] in areas or time periods of high human disturbance relative to nocturnality under low-disturbance conditions. For example, an animal that typically split its activity evenly between the day and night would increase its proportion of nocturnal activity to 68% of total activity near human disturbance. Of the 141 effect sizes, 83% corresponded to an increase in nocturnality in response to humans (Fig. 1B). This finding

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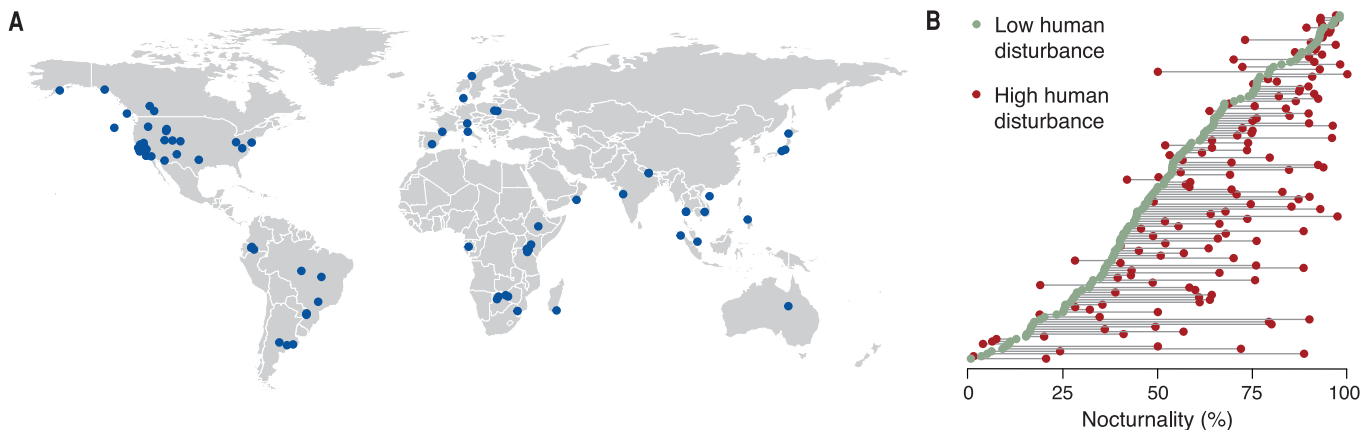*Corresponding author. Email: kgaynor@berkeley.edu

**Fig. 1. Mammals become more nocturnal to avoid humans throughout the world.** (**A**) Map illustrating the locations of the 76 studies included in the meta-analysis. (**B**) Paired measures of nocturnality (percentage of activity that occurs in the night) in areas of high human disturbance ($X_h$) and low human disturbance ($X_l$), displayed for each species in each study ($n$ = 141 effect sizes, ordered from high to low $X_l$). The relative change in nocturnality in response to human disturbance was used to calculate the effect size (RR) for the meta-analysis, where RR = ln($X_h/X_l$).

**Fig. 2. Increase in large mammal nocturnality in relation to human activity types, trophic level, and body size.** Points represent the estimated overall effect size (with 95% CIs) for each category. Positive values indicate a relative increase in nocturnal activity in areas of higher human disturbance. The number of effect sizes in each category is indicated in parentheses (human activity categories were nonexclusive). Mammals exhibit a significant increase in nocturnal activity in response to all types of human activity, with similar patterns across trophic levels and body sizes. Back-transforming the overall (mean) RR (0.31; CI, 0.21 to 0.41) indicates that nocturnality increased by a factor of 1.36 (CI, 1.23 to 1.51) in response to human activity.
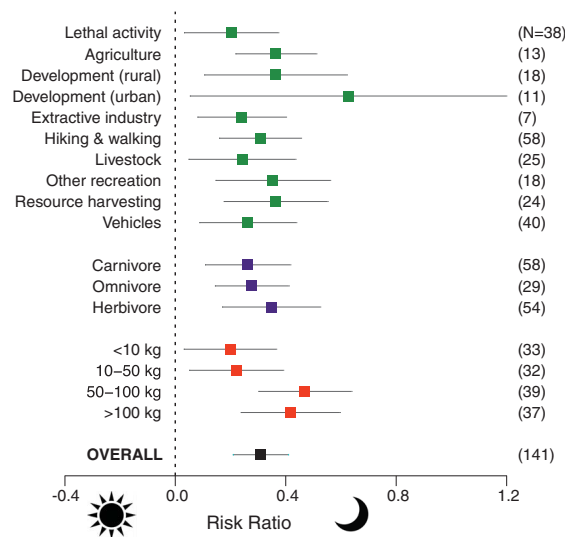
indicates a widespread increase in nocturnality among mammals living alongside people.

Our analysis spanned a wide range of human disturbances associated with diverse stimuli representing different levels of risk to wildlife, including lethal activities (e.g., hunting and retaliatory persecution), nonlethal activities (e.g., hiking and natural resource extraction), and human infrastructure (e.g., urban development, road construction, and agriculture). There was a significant increase in nocturnality in response to all forms of human presence (Fig. 2), signaling the robustness of our findings. Surprisingly, nonlethal human activities generated shifts in wildlife diel patterns similar to those from lethal activities (Fig. 2), suggesting that animals perceive and respond to humans as threats even when they pose no direct risk.

We expected temporal responses of wildlife to vary across species, given interspecific differences in biology such as variation in morphology and behavior. Body sizes of the 63 species analyzed ranged from 1.13 kg for the common opossum (*Didelphis marsupialis*) to >3,500 kg for the African elephant (*Loxodonta africana*). Mammals of all body size classes showed a strong response to human activity, although there was a slight trend toward a greater response among larger-bodied species (Fig. 2), perhaps because they are more likely to be hunted and harassed or because their space needs force them into more frequent contact with people. Across trophic levels, species also exhibited similar responses to human activity (Fig. 2). Even apex carnivores, which from an evolutionary perspective have typically faced little or no predation risk from other species, responded to humans by becoming more active at night. Species that are typically diurnal showed an increase in nocturnality, and even crepuscular and nocturnal species became more strongly nocturnal around humans (fig. S3A). Human activity increased wildlife nocturnality across continents and habitat types (fig. S3, B and C). The study method (camera trap, teleme-

try, or direct observation), human disturbance treatment (space or time), and continent were included as predictors of effect size in the best multivariate models (tables S5 and S6).

The absence of increased nocturnal activity by wildlife in many of the studies examined does not necessarily indicate an absence of human impact. Differences in age, sex, reproductive status, and personality may shape responses and mask patterns at the population level (*11*). For example, in one population of brown bears (*Ursus arctos*), human recreation induced temporal shifts among adult males that created additional daytime feeding opportunities for females, which are often otherwise outcompeted by males for access to resources (*12*). Alternatively, ecological and morphological constraints may limit behavioral plasticity, causing individuals to remain active during the daytime in the presence of humans, thereby incurring the cost of increased stress or energetically expensive antipredator behaviors (*13*). Animals living alongside humans in disturbed ecosystems may face additional constraints (e.g., limited food resources) that limit their ability to respond temporally (*14*). At the community level, strictly diurnal species may also entirely avoid areas of human activity, opening niches for more nocturnal competitors, including invasive species (*15*).

In addition to changing diel patterns of activity in response to human disturbance, wildlife species may alter temporal patterns of specific behaviors. During the day, animals often choose more protected habitats or microhabitats in areas of human disturbance (*16*) or more strongly avoid anthropogenic features like roads and buildings (*17*, *18*). Some species also modify daytime and nighttime movement speed and tortuosity (*19*) and temporal patterns of antipredator behavior such as vigilance (*20*). Furthermore, in addition to shifting activity from the day to the night, animals often decrease their overall activity throughout the 24-hour period in response to human disturbance, spending more time rest-

ing and less time foraging or engaging in other fitness-enhancing behaviors (*21*).

We assert that fear of humans is the primary mechanism driving the increase in wildlife nocturnality, given its prevalence across activity types and the widespread evidence that mammals perceive and respond to risk from people (*2*, *4*). In some of the studies included in our analysis, fear of humans may have interacted with other factors, such as food provisioning (through anthropogenic food sources such as livestock, crops, and food waste), to drive increased nocturnal activity (rather than spatial avoidance) by generalist species in areas of human disturbance (*22*, *23*). Furthermore, nighttime light cues or increased visibility around permanent human infrastructure may also promote an increase in nocturnal activity in these areas (*24*). However, for animals wary of humans or more fearful of predators in lit areas, anthropogenic light may also be perceived as a source of risk and thus may limit the magnitude of a shift to nocturnality (*25*).

The global increase of nocturnality among wildlife in human-dominated areas demonstrates the high degree of behavioral plasticity of animals in a human-altered world, with great implications for ecology and conservation (Fig. 3). On the positive side, temporal partitioning may facilitate human-wildlife coexistence at fine spatial scales and effectively increase available habitats for species that are able to adjust (*26*). The separation of humans and wildlife in time, if not space, may also limit contact rates between people and dangerous animals and therefore reduce some forms of negative encounters between the two, such as disease transmission and attacks on people. In situations where humans pose a lethal threat to wildlife, increased nocturnality may be advantageous to individual animals and has been linked to increased probability of survival (*27*). In this case, increased mortality among more diurnal individuals may even drive selective pressure for behavioral plasticity and nocturnal activity (*27*).

Though human-wildlife coexistence may be a positive outcome of increased nocturnal activity of wildlife, this shift may also have negative and far-reaching ecological consequences. Humans may impose substantial fitness costs on individual animals, analogous to predation risk effects in predator-prey systems, in which costly antipredator behavior compromises prey reproduction and survival and alters trophic interactions (*28*). An increase in nocturnality may also eventually alter evolution through selection for morphological, physiological, and behavioral adaptations to nighttime activity. The human "super predator" has already been implicated in evolutionary changes through selective harvest (*29*), but as with other predators (*3*), the nonlethal effects of humans may have an even stronger influence on fitness and evolutionary trajectories.

Risk effects induced by a temporal response to human presence are expected to be particularly strong, as an increase in nocturnal activity can cause mismatches between morphology and environment for historically diurnal species. The

diel cycle provides a reliable set of environmental cues against which ecological and evolutionary processes play out (30). Behavior at different times of the diel cycle influences and is influenced by morphology [e.g., corneal size (31)], physiology [e.g., opsin proteins (32)], and ecology [e.g., group living and predation risk (33)]. Although most mammals possess some sensory adaptations to nighttime activity due to nocturnal mammalian ancestors, many species have evolved traits that optimize diurnal behavior (34, 35). When active at other times, diurnally adapted animals may suffer from reduced hunting and foraging efficiency, weakened antipredator strategies, disruption of social behavior, poor navigational capacity, and higher metabolic costs, all of which can compromise reproduction and survival (36, 37).

By altering typical activity patterns in some wildlife species, human disturbance initiates behaviorally mediated trophic cascades and transforms entire ecological communities (38, 39). Fear-based behavioral responses by apex predators to humans may diminish their ability to hunt and thus perform their ecological role at the top of a trophic web (40). Animals that are increasingly nocturnal may drastically alter their diets toward prey or forage that are more accessible at night, reshaping lower trophic levels (41). Predators may also abandon kills near human settlements in the daytime, resulting in increased overall predation rates (42). Human-induced increases in nocturnality among prey species can also increase their vulnerability to nocturnal predators (43). Differential responses to human disturbance among mammal species also alters patterns of predation and competition. Predators may increase nocturnality in response to humans, creating temporal human shields, in which a prey species will then decrease nocturnality near human disturbance to avoid predation, analogous to spatial human shields (44, 45). Alternatively, some prey species may instead seek out human-dominated areas at night to escape nocturnal predators that spatially avoid humans (46).

Human-induced change in diel activity is a growing field of inquiry, as indicated by the large number of studies in our meta-analysis (table S1). However, very few studies have examined the individual-, population-, or community-level consequences of these behavioral changes. Given the widespread nature of increased nighttime activity, there is ample opportunity and need to study not just the magnitude of this effect but also its consequences for individual fitness, species interactions, and natural selection. Additional research and synthetic analyses are also needed for nonmammalian taxa, which may also exhibit diel shifts in response to humans (47).

As research on the pattern and consequences of increased nocturnality advances, we urge that similar progress be made to incorporate knowledge of temporal dynamics into conservation planning. Currently, spatial ecology informs commonly used land-planning tools (48), but new tools are needed that explicitly address temporal interactions. Approaches may include diurnal "temporal zoning," analogous to spatial zoning, that would restrict certain human activities during times of the day when species of conservation concern are most active or when the likelihood of negative human-wildlife encounters is highest. Similar strategies already restrict human activity at certain times of the year, such as during breeding seasons (49). Systematic approaches to understanding and managing temporal interactions between humans
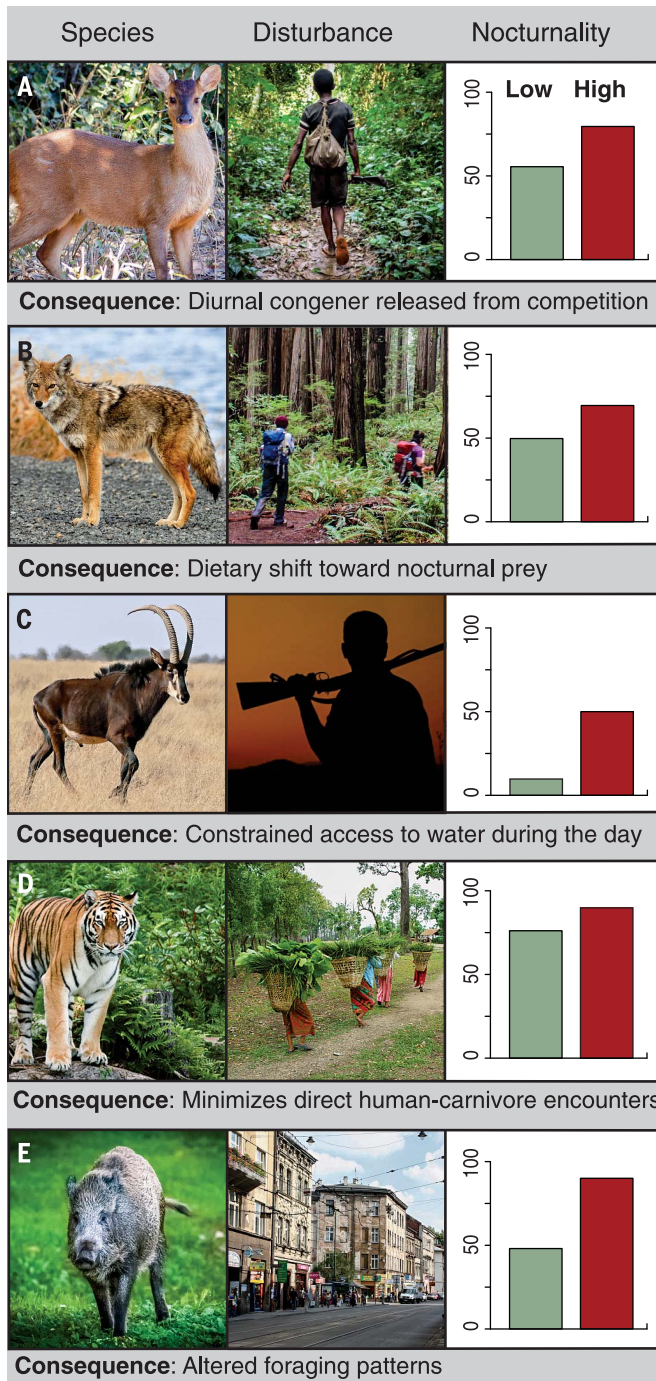


**Fig. 3. Case studies demonstrate the diverse consequences of human-induced increases in nocturnality.** (**A**) Red brocket deer (*Mazama americana*) and subsistence hunting, Atlantic Forest, Argentina (50). (**B**) Coyote (*Canis latrans*) and hiking, Santa Cruz Mountains, CA (51, 52). (**C**) Sable antelope (*Hippotragus niger*) and sport hunting, Hwange National Park, Zimbabwe (53). (**D**) Tiger (*Panthera tigris*) and forest product collection and farming, Chitwan National Park, Nepal (26). (**E**) Wild boar (*Sus scrofa*) and urban development, Cracow and Białowieza Forest, Poland (54). Green bars represent nocturnality (the percentage of total activity that occurs in the night) in areas of low human disturbance ($X_l$), and red bars represent nocturnality in areas of high human disturbance ($X_h$).

and wildlife can open up new domains for conservation in an increasingly crowded world.

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# Science

## The influence of human disturbance on wildlife nocturnality

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### Nocturnal refuge

As the human population grows, there are fewer places for animals to live out their lives independently of our influence. Given our mostly diurnal tendencies, one domain that remains less affected by humans is the night. Gaynor *et al.* found that across the globe and across mammalian species—from deer to coyotes and from tigers to wild boar—animals are becoming more nocturnal (see the Perspective by Benítez-López). Human activities of all kinds, including nonlethal pastimes such as hiking, seem to drive animals to make use of hours when we are not around. Such changes may provide some relief, but they may also have ecosystem-level consequences.
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