










Shedding light with harmonic radar: Unveiling the hidden impacts of streetlights on moth flight behavior

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One of the most dramatic changes occurring on our planet is the ever-increasing extensive use of artificial light at night, which drastically altered the environment to which nocturnal animals are adapted. Such light pollution has been identified as a driver in the dramatic insect decline of the past years. One nocturnal species group experiencing marked declines are moths, which play a key role in food webs and ecosystem services such as plant pollination. Moths can be easily monitored within the illuminated area of a streetlight, where they typically exhibit disoriented behavior. Yet, little is known about their behavior beyond the illuminated area. Harmonic radar tracking enabled us to close this knowledge gap. We found a significant change in flight behavior beyond the illuminated area of a streetlight. A detailed analysis of the recorded trajectories revealed a barrier effect of streetlights on lappet moths whenever the moon was not available as a natural celestial cue. Furthermore, streetlights increased the tortuosity of flights for both hawk moths and lappet moths. Surprisingly, we had to reject our fundamental hypothesis that most individuals would fly toward a streetlight. Instead, this was true for only 4% of the tested individuals, indicating that the impact of light pollution might be more severe than assumed to date. Our results provide experimental evidence for the fragmentation of landscapes by streetlights and demonstrate that light pollution affects movement patterns of moths beyond what was previously assumed, potentially affecting their reproductive success and hampering a vital ecosystem service.

light pollution | harmonic radar | moth | orientation | barrier effect

The dramatic insect decline is one of the most concerning recent biological problems (1, 2). Among insects, pollinators are of particular importance. Because of their significance for insect-pollinated plants, ecosystem functioning, and food security, their decline will have severe implications for humans as well (3, 4). While great focus has been dedicated to finding the causes and mitigating the decline of diurnal pollinators (5, 6), nocturnal pollinator decline is less well understood. At night, moths belong to the most important pollinators (7, 8) and there is also evidence for their decline in abundance and distribution (9, 10). In addition to general drivers of insect decline (11), nocturnal pollinators are also threatened by light pollution (12–15).

Light pollution (16) is caused by artificial light sources that differ from natural light sources in spectrum, intensity, and timing (17). Thus, the still increasing extensive use of artificial light at night (ALAN) changes and disturbs natural night environments (18, 19) with negative impacts from individual species to whole ecosystems, potentially affecting biodiversity (20, 21). Furthermore, ALAN disrupts the natural visual cues nocturnal insects rely on for orientation (22–24). Most moths show a strong phototactic response which is generally described to end in a flight toward light sources (25, 26) and such behavior has been the focus of the majority of investigations (27, 28). Yet it remains unclear why many insects exhibit particular phototactic behavior, and none of the existing hypothesis provides a complete explanation for insect phototactic behavior (29). In a recently published study, a new model was presented that proposes the dorsal-light-response to explain why flying insects gather at artificial lights (30). However, since the attraction radius of a light source remains controversial in addition (31), it is not sufficiently understood to date which parameters ultimately elicit a flight toward the light in an individual approaching a light source from a distance.

Notably, as ALAN triggers maladaptive behavior, it creates an “evolutionary trap” that reduces survival and reproduction (32, 33). Because of methodological constraints, previous studies on the effects of streetlights were restricted to specific locations, using capture-recapture experiments (34, 35) and observations within the light beam of a single lamp (36) or theoretical models (37, 38). However, these results can only reveal the effects

Significance

Artificial light at night drastically changes the light environment nocturnal animals are adapted to with unknown consequences for their orientation performance. Due to methodological constraints, to date, little is known about the impact of streetlights on moth flight behavior whenever they are moving within nonilluminated parts of the landscape. The harmonic radar technique enabled us to overcome this limitation, demonstrating that streetlights significantly affected flight behavior long before an individual approached a streetlight. Since only 4% of the tested individuals finally flew toward a streetlight and showed the typical disoriented behavior of circling around the light source and crashing to the ground, the effect of light pollution might have been severely underestimated to date.

The authors declare no competing interest.

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but not the causes for the impact of ALAN on moth behavior. Understanding why streetlights affect movement behavior and orientation performance requires measurements of the entire flight trajectories inside and outside of the illuminated area. We therefore used harmonic radar technology on several nocturnal moth species, recording individual flight trajectories with a high spatial and temporal resolution within 1 km range.

Results and Discussion

Hardly Any Moth Terminated Its Flight at a Streetlight. To investigate the impact of ALAN on the flight behavior of moths, we recorded flight trajectories of 95 individuals (SI Appendix, Table S1) with harmonic radar (SI Appendix, Fig. S1). All these moths were captured with the help of light (Materials and Methods) to ensure that all tested individuals principally react to artificial light. Thus, our sample might not be representative for the whole population. Since we caught almost no females, all tested moths were males. The most common species were *Euthrix potatoria* (drinker, Lasiocampidae), *Laotloe populi* (poplar hawkmoth, Sphingidae), *Deilephila elpenor* (elephant hawk moth, Sphingidae), and *Sphinx ligustri* (privet hawk moth, Sphingidae), but we also captured individuals of *Smerinthus ocellata* (eyed hawkmoth, Sphingidae), *Catocala sponsa* (dark crimson underwing,

Noctuidae), *Noctua pronuba* (large yellow underwing, Noctuidae), and *Cossus cossus* (goat moth, Cossidae) (SI Appendix, Table S1). Because the radar signal of different individuals could not be distinguished, males were released one by one in the center of six circularly arranged high-pressure sodium streetlights (radius: 85 m, SI Appendix, Figs. S2–S4; see also Fig. 1B). All individuals were tracked until we lost the signal for more than 10 min. A similar number of individuals was tested each day with the streetlights either turned on or off to compensate for daily fluctuations in weather and ambient light conditions.

For analyzing whether individuals generally ended their flight at one of the streetlights, no knowledge about their biology was required. Thus, we included all released males in this analysis (SI Appendix, Table S1), even if we collected only one individual of a certain species. Out of the 50 animals that were released with the streetlights turned on, only two individuals (4%) terminated their flights directly at a streetlight (Fig. 1A, flight trajectories of the two individuals Fig. 1C). This was surprising, all especially because all individuals we tested were captured utilizing light. We therefore expected a much higher proportion of males to fly into the illuminated area of a streetlight, ending up there showing the typical disoriented behavior. However, since even these light-captured individuals rarely flew to the streetlights, the proportion might be even less when considering the whole population.

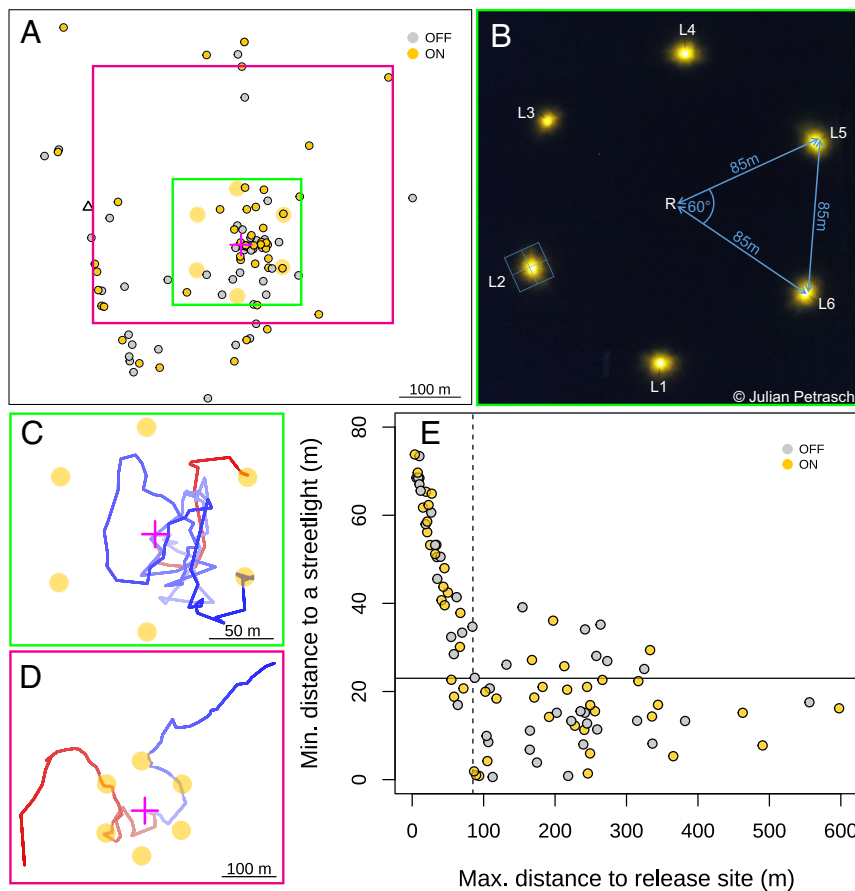


Fig. 1. Final positions of tracked moths and flight proximity to a streetlight. (A) Final recorded positions of all tracked moths ($n = 95$). (B) Arrangement of the six high-pressure sodium streetlights used in the experiment imaged from a drone (picture taken by Julian Petrasch). The distance between the release site and each streetlight as well as the distance between them was 85 m. Note that light cones of single streetlights did not overlap. Representative illuminance measurements of one streetlight (L2) are indicated by the blue square and corresponding values are illustrated in SI Appendix, Fig. S3. (C) Flight trajectories of the only two individuals that terminated their flight at a streetlight. (D) Two representative flight examples of individuals that passed an illuminated streetlight closer than 10 m and continued their flight ($n = 6$). These individuals belonged to both families, hawk moths ($n = 3$) and lappet moths ($n = 3$). (E) Maximum distance to the release site and minimum distance to a streetlight at any time during a flight for all tracked moths ($n = 95$). The attraction radius of 23 m (indicated by the solid horizontal line) was calculated in a previous experiment using the same type of streetlights (39). Since each of the six streetlights was located 85 m away from the release site, this distance marks the minimum flight distance to arrive at a streetlight, as indicated by the dashed vertical line. (A–D) All figures are aligned to the north.

The positions of last waypoints of all other flights were widely scattered within the detection range of the radar (Fig. 1A) and there was no significant difference in the distance of the last recorded waypoint to the nearest streetlight between “light on” and “light off” conditions (linear model, estimate = -0.73 , $P = 0.97$, $df = 94$). Since the harmonic radar technique requires a certain handling procedure for the attachment of the necessary antenna, we confirmed in control experiments that the handling procedure did not significantly affect behavior (*Materials and Methods*). To ensure that the light sources used in the experiments (*SI Appendix, Figs. S2–S4*) generally triggered the disrupted behavior described in literature (40), we released seven moths of the species *S. ligustri* in front of a streetlight at a distance of 10 m. All these males showed the typical behavior of circling around the light at different heights and crashing to the ground from time to time until they stay motionless on the ground (31). This indicates that the streetlights we used influenced the behavior in the expected, disruptive way within a close range (≤ 10 m) when the light source was above the moth at the time of release. Yet, in free flight, only 4% of the tested individuals ended their flight at a streetlight and showed this behavior. Considering that all tested individuals already showed a clear positive phototactic response as they were collected using artificial light (*Materials and Methods*), this low fraction of individuals getting trapped within the beam of a streetlight raises the question how well light traps commonly placed at the lamp post can reflect the real impact of streetlights.

Next, we analyzed whether the males we released at the release site passed a streetlight within the attraction radius, i.e., the distance to a light that is assumed to cause the animal to fly toward its source, as individuals might have left the circle of the six streetlights without entering into any attraction radius. The attraction radius of high-pressure sodium streetlights is estimated to be 23 m for moths in general (39). We therefore expected that all individuals that enter any streetlight’s attraction radius (Fig. 1E, solid horizontal line) would show a positive phototactic response and thus terminate their flight at the light source (Fig. 1E, dashed vertical line). In total, 28 individuals entered the attraction radius of a streetlight (Fig. 1E, all individuals displayed with yellow circles below the solid horizontal line). Besides the two individuals that actually terminated their flight at a streetlight and showed the typical disrupted behavior of circling around the streetlight and crashing to the ground from time to time (Fig. 1C), only another two males ended their flight within the attraction radius but were not seen within the illuminated area. All other 24 individuals continued their flight and left the attraction radius again. Moreover, the distance to streetlights passed during a flight in the light on and light off condition did not differ significantly [general linear model (glm), estimate = -1.1 , $P = 0.67$, $df = 55$] for moths that left the circle of streetlights (Fig. 1E, Right of dashed line). Thus, we could not show attraction by streetlights for most individuals, even though they entered the attraction radius. Six moths (12%) even passed an illuminated streetlight closer than 10 m without interrupting their flight (representative flight examples: Fig. 1D), a distance we have demonstrated to elicit the typical disruptive behavior when the animal was released from the ground (see above). Although the harmonic radar did not provide any information about the flight altitude, the flight direction could be communicated during the flight to the experimenter at the release site. This allowed the experimenter at the release site to monitor the illuminated area of the communicated streetlight by eye as soon as the experimenter at the radar monitored an individual approaching it on the screen. Since we did not see any of the six individuals that passed a streetlight, but continued their

flight, within the illuminated area, we hypothesize that they passed above the streetlight. We therefore suggest that flight altitude may be critical when assessing the attraction radius of a streetlight.

Streetlights Increased the Tortuosity of Flights. The tortuosity of an animal’s path is a key parameter in orientation, including search behaviors, and is inversely related to the efficiency of the orientation mechanism involved for oriented flights while it reflects searching intensity for local search flights (41) (*Materials and Methods*). Thus, it is important to know whether the investigated species live in the habitat where experiments were performed, as one would expect different flight behaviors (directed or search flights) in either case. For hawkmoths, we could rely on extensive knowledge about their biology to identify suitable habitats, all of them located outside the experimental area. Indeed, all hawk moth species investigated in our study were collected outside of the experimental field (*Materials and Methods*), corroborating our assumption that the test site was not a preferred habitat at this time of the year.

Lappet moths, on the other hand, were supposed to inhabit the experimental field, enabling us to investigate a local species with a high abundance and sufficient body size to carry the radar transponder easily. Also for this species, we could corroborate our assumption, as it was caught adjacent to the experimental field (*Materials and Methods*). According to Benhamou (41), the tortuosity of flights needs to be calculated differently for oriented (aiming to leave the experimental field) and search flights (to find local resources): While the tortuosity of oriented flights (hawk moths) needs to be calculated based on a straightness index, the tortuosity of local search flights (lappet moths) can be reliably estimated by a sinuosity index (*Materials and Methods*). To investigate the effect of streetlights on orientation and search behaviors, we therefore analyzed whether turning on the streetlights elicited a change in the tortuosity of flights (Fig. 2) based on the index appropriate for the species.

Since none of the hawk moth species tested were native to the experimental field, we expected them to leave in a straight line, as this provided the fastest possible route to reach a more suitable habitat. Based on this, we assumed for all hawk moth species that they rely on straight-line orientation and therefore omitted a detailed investigation of possible fine-scaled differences between species. Indeed, when the streetlights were turned off, we observed such straight flights, represented by a low tortuosity, especially when the moon was visible above the horizon (Fig. 2A, beta regression with post hoc tests see *SI Appendix, Table S2*). Switching on the streetlights significantly increased the tortuosity of flights when the moon was above the horizon, meaning that flights became less directed (Fig. 2A). Lappet moths, which were native to the experimental field, were expected to search for resources. Indeed, they generally had less directed flights compared to those of hawk moths when the streetlights were turned off, which likely reflects their search activity for local resources. When streetlights were turned on, the tortuosity of flights increased significantly when the moon was below the horizon (Fig. 2B, Beta regression with post hoc tests see *SI Appendix, Table S3*). Thus, our experiments revealed for both moth groups a significant change in flight behavior when the streetlights were turned on.

Although the sample size was moderate for some test conditions, especially for hawk moths when the streetlights were turned off and the moon was above the horizon, the tortuosity of flights when streetlights were turned off did not differ remarkably within both moth groups when the moon was present or absent (Fig. 2). Moreover, even this subsample consisted of two different species (*S. ligustri* and *L. populi*), minimizing the risk of incorrectly

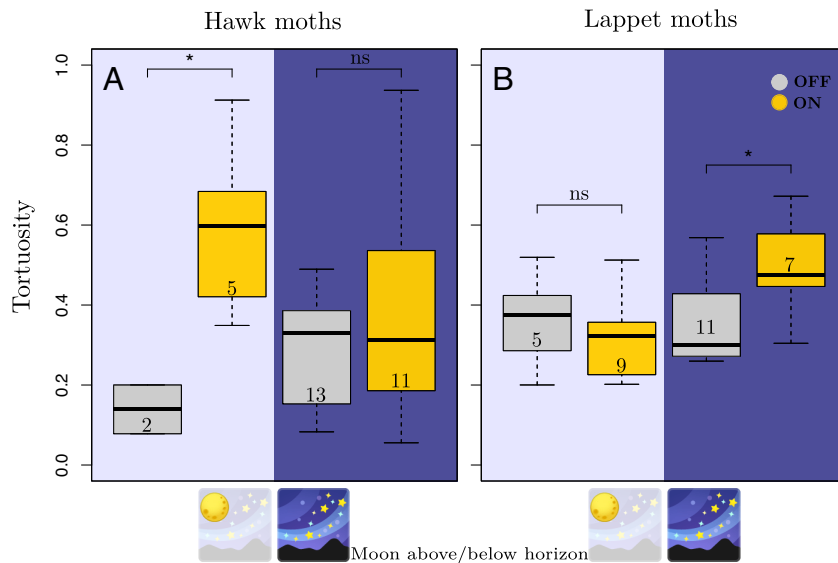


Fig. 2. The effect of artificial light on the tortuosity of flights. (A and B) Tortuosity of flights when streetlights were off or on in the presence or absence of the moon. The tortuosity of oriented flights [hawk moths (A)] is inversely related to the efficiency of the orientation mechanism involved, while it reflects searching intensity for local search flights [lappet moths (B)]. A value of 0 represents a perfectly straight flight and a value of 1 a very curvy flight. Values are displayed separately for hawk moths (A; $n = 31$) and lappet moths (B; $n = 32$), and nights when the moon was above the horizon (Left) or below the horizon and therefore not visible (Right). Box plots show the median (black line), the interquartile range (grey or orange box), and the minimum and maximum value within 1.5 times the interquartile range of the box (whiskers). The number within each box plot gives the sample size (only flights longer than 85 m and with at least five waypoints are included in this analysis). Statistics: glm to account for unbalanced and small sample size, significant differences ($P < 0.05$) are marked by*.

assigning the significant effect to the genus instead to a specific species. The unbalanced design goes back to the implementation of a key finding retrieved in another study demonstrating that the moon is of crucial importance for the orientation performance of the hawk moth *S. ligustri* (42). In more detail, we found that the moon was the strongest factor determining the ambient brightness, brightening every sector of the sky as soon as it appeared above the horizon. Moreover, neither distant artificial light sources nor clouds had a significant impact on flight behavior, indicating that the significant decrease in flight duration of males to reach females was predominantly caused by the presence of the moon. Thus, by integrating the moon as a critical factor in our analysis, we were able to find that the increase in tortuosity is not solely based on the presence of artificial light but on complex interactions between natural and artificial light in addition.

The interaction between artificial and natural light was not universal, however, as the tortuosity of flights in presence of illuminated streetlights was significantly increased for hawkmoths when the moon was above the horizon, but for lappet moths when it was below the horizon (Fig. 2). Based on the data acquired in this study, we speculate that moonlight had an opposing effect on responses to ALAN due to context-dependent reliance on visual cues for orientation. For hawk moths, the moon plays a key role in the orientation of males (42) and can therefore facilitate straight-line orientation when it is above the horizon. Thus, introducing point light sources might disrupt their orientation more strongly when the moon is present and they rely on it, resulting in an increase of flight tortuosity predominantly under these conditions. The local search behavior of lappet moths, on the other hand, might be more affected by local lighting patterns. Without moonlight, the contrast between illuminated and dark areas is more pronounced, eventually preventing them from leaving the circle of light and thereby increasing tortuosity of flights as they can only move within this enclosed space. As soon as the moon appears above the horizon, the experimental field is brightened, and therefore, the contrast between the light cone of artificial light sources and the surrounding environment is reduced, possibly

enabling individuals to leave the circle of light. In this case, the increased tortuosity would be a consequence of the high contrast. In order to understand this interaction in detail, targeted experiments are certainly required.

Usually, we lost track of individuals at some point, either because individuals flew too high or too low to be detected by the radar, lost their transponder, stopped their flight to sit down in the grass, or were eaten by a predator. Thus, all data shown in Fig. 2 go back to moths that were tested only once. A fortunate coincidence allowed us to test a single animal (hawk moths, *L. populi*) repeatedly, as it could be caught at the light trap set up several hundred meters away after it performed its first flight when streetlights were turned off. We brought this individual back to the experimental field and waited 40 min before we tested it again with streetlights turned on, since the return to full ocular sensitivity takes around 30 min in moths (7). This individual performed a rather straight flight (tortuosity: 0.19) when lights were turned off and the moon was below the horizon and a rather curvy flight (tortuosity: 0.68) when lights were turned on and the moon was above the horizon (SI Appendix, Fig. S5). Thus, this individual corroborates our general findings for hawk moths.

Streetlights Induced a Barrier Effect for Lappet Moths. The six streetlights placed in the experimental field created a circle of light that might have created a barrier effect, an “invisible wall” the moths were incapable of passing. We indeed found such a barrier effect for lappet moths under certain conditions (SI Appendix, Fig. S6). Taking the presence of the moon into account, lappet moths were significantly prevented from leaving the circle of streetlights once these were turned on and the moon was not visible (Fig. 3 C and D, $P = 0.039$, $n = 32$; see SI Appendix, Table S5 for entire model output). Thus, the illuminated circle of streetlights created a barrier effect for lappet moths, but only when the moon was not visible as a natural celestial cue. Although we cannot determine which feature of moonlight enabled lappet moths to leave the illuminated circle of streetlights, the results confirm earlier findings showing that the moon can have a strong

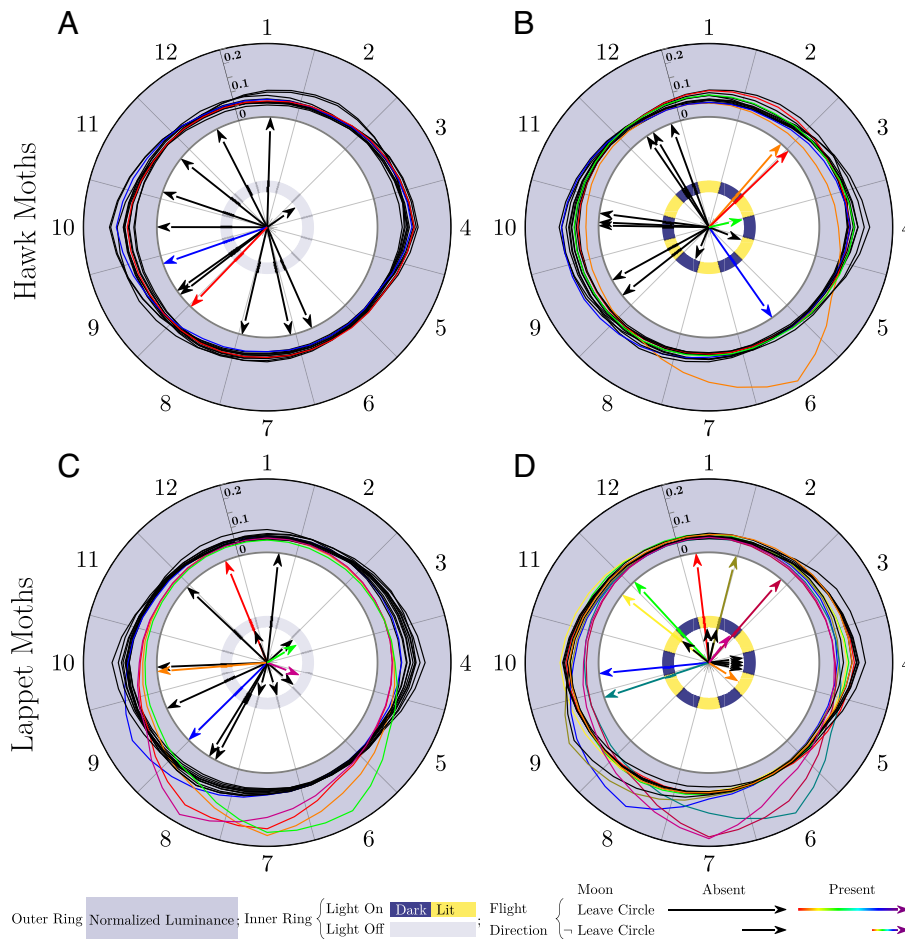


Fig. 3. Linking flight directions and distances to the light environment. Flight directions were analyzed separately for hawk moths (A and B) and lappet moths (C and D) and the conditions when lights were turned off (A and C) or on (B and D). Animals that did not leave the circle of streetlights are displayed with short arrows and those that left the circle by long ones (only flights longer than 85 m with at least five waypoints and an all-sky image are included in this analysis). Furthermore, individuals that performed their flight when the moon was below the horizon are displayed with black arrows and those that were released when the moon was above the horizon by colored ones. In the latter case, arrows were color coded to relate the flight direction to the light environment impacted by the moon (circular curves in the same color as the corresponding flight). For the analysis of the relation between flight direction and light environment, we defined 12 sectors spanning 30° each, with odd-numbered sectors representing the position of a streetlight. The sectors are numbered clockwise in each plot, with the flight directions displayed as one arrow for each individual. We divided all-sky images taken in parallel to the experiment (*Materials and Methods*) into the same sectors and calculated the mean luminance (“brightness”) for each single sector to link moth’s flight direction to the luminance of the surroundings. Luminance was normalized to compare light distribution patterns independent of varying light conditions of different nights (*Materials and Methods*) and the corresponding scale is displayed at the *Left* boundary of sector one. Arrows when the moon was visible above the horizon are displayed in color, matching the corresponding luminance distributions. Except when fully overcast ($n = 4$), the brightness was always highest in the sector where the moon was located, allowing to assess the flight direction with respect to the position of the moon. When the moon was below the horizon, flight directions as well as the corresponding brightness values are displayed in black.

influence on the orientation of moths (42). In general, many individuals did not leave the circle of light in both, the lights off and lights on condition (Fig. 3 C and D). However, this result is not surprising, as this species was expected to search for local resources in contrast to hawk moths that were expected to leave the experimental field.

For hawk moths there was indeed no indication of a barrier effect (*SI Appendix, Fig. S7*), irrespective of the presence of the moon as a natural celestial cue (Fig. 3 A and B; exact logistic regression for leaving the circle with moon present or absent and lights on or off: $P = 0.57$, $n = 27$; see *SI Appendix, Table S6* for entire model output). In general, almost all individuals (23 out of 27) left the circle of light, irrespective of the moon or testing condition (Fig. 3 A and B). It is important to note that all individuals included in this analysis initiated their flight properly and vanished from the field of view of the observer shortly after take-off. In case they landed in the grass after they started properly, we consider this behavior to be one possible consequence of a barrier effect.

Although we conducted the experiments in a relatively dark area, the surroundings featured a considerable amount of artificial light, ranging from streetlights of the close-by village Großseelheim to skyglow from distant cities (for details, see *Materials and Methods*). We quantified the light environment at the beginning of every flight via an all-sky image (43) (*Materials and Methods*). Because the nocturnal light environment varied considerably between different nights, we normalized luminance for each image to identify the brightest sectors (Fig. 3). We found that the sectors with skyglow emerging from the towns Kirchhain and Stadtallendorf (Fig. 3, sector 4) and Marburg (Fig. 3, sector 10) were usually the brightest ones, with the moon overriding this pattern (e.g., Fig. 3B orange curve). If individuals had flown toward the brightest sectors caused by skyglow, we would expect a higher frequency of flights within sectors 4 and 10. However, flight directions were widely scattered in all cases, resulting in overlapping CI (Bayesian projected normal regression models for circular deviation of flight direction from the brightest horizontal light source) in response to moon above vs. below the horizon and

street lights turned on or off (*SI Appendix, Table S4*). We could not show that moths flew into the direction of greatest sky brightness, respectively (weak) skyglow. In addition, we tested whether individuals preferred to fly in direction toward the moon when it was the brightest spot in the sky. Our results indicate that the corresponding individuals (Fig. 3, flight directions (arrows) and brightness distribution (curves) are color coded) did not fly directly in the direction of the moon (*SI Appendix, Table S4*).

General Discussion

The harmonic radar technique revealed a significant impact of streetlights on the flight behavior of different species of moths even beyond the illuminated area. In addition to the barrier effect on lappet moths, the significant increase in the tortuosity of flights caused by streetlights is of particular importance, because it relates to the orientation of individuals. Our results demonstrate that streetlights affect the orientation of moths although they do not terminate their flight at the light source. This finding adds a unique dimension to the impact of light pollution on local movements of moths, which was previously not considered due to methodological constraints.

Our finding that only very few moths terminated their flight at the light source although many entered the attraction radius of a streetlight raises the question why only such a low fraction flew to the light source. Generally, high-pressure sodium streetlights are considered to be “insect-friendly” because of the spectral composition of their light emissions (*SI Appendix, Fig. S4*; see also ref. 31), yet various studies have documented that nocturnal moths get attracted by and fly toward this type of lights (44–46). This is particularly true for hawk moths and lappet moths as demonstrated by light-trap catches (39). Because we found that only very few moths terminated their flight at the light source, the observation of moths trapped at streetlights might only concern a small fraction of individuals that pass a streetlight in free-flight. Since we showed that their flight behavior can be significantly affected by streetlights, light-trap catches might underestimate the impact of ALAN since only individuals that fly toward the light source are sampled. Traditional streetlights, like those tested in this study, are increasingly being replaced by LEDs worldwide, and as these can vary considerably in spectrum and intensity, the repeatability of our results will need to be specifically investigated for the different LEDs in the future (47, 48). Our study demonstrates that ALAN can also affect individuals not showing a positive phototactic response and flying directly to the light source, raising the question which conditions elicit a positive phototactic response. Although low-intensity skyglow can cause a spatial shift toward open habitats at night (49), we found no indication that skyglow affects flight direction, consolidating findings of previous studies (42).

Based on the results retrieved with the radar, especially the finding that 12% closely passed a streetlight without interrupting their flight, we emphasize the hypothesis that a flight toward the light source is triggered as a function of flight altitude, extending the attraction radius to a three-dimensional space. Thus, flight altitude might be of utter importance in this context and should be investigated in free-flying moths, using promising new methods that allow 3D-tracking once these have been fully developed for such demands (50, 51).

The flight altitude of individuals may also explain why we found a barrier effect of streetlights for lappet moths but not for hawk moths (Fig. 3), since altitude is crucial for the perception and susceptibility of ALAN for all air-borne organisms (52). While lappet moths already inhabited the exact meadow where the experiments were performed, hawk moths did not, making it reasonable

to assume that lappet moths fly at lower altitudes to search for local resources while hawk moths may increase their flight altitude quickly after take-off to reach more favorable habitats. However, as the harmonic radar cannot resolve flight altitude, the proof for this would require a new 3D tracking method not available to date. The barrier effect of streetlights on lappet moths is of particular importance, as it provides experimental evidence for the commonly postulated fragmentation of habitats by streetlights (13, 39, 40). Since the distance between the streetlights and thus the dark areas between the lights were unusually large compared to standard streetlighting (Fig. 1B), it is likely that the barrier effect would be even stronger with the typical streetlight design. For example, in Europe pole distances of municipal streetlights for roads are between 25 and 45 m (53). Furthermore, we show a clear interaction between moonlight and ALAN, which should be taken into consideration for future studies on the impact of ALAN on nocturnal animals. Moon elevation and disk illumination should be reported in all studies, as effects of moonlight might mask or amplify the effects of ALAN.

Taken together, the harmonic radar technique revealed that streetlights affect moth orientation even if individuals do not fly toward the light source and circle around the light, indicating a unique dimension of impact at a local scale. This is of crucial importance for the probability of survival and mating success and supports the findings of Giavi et al. (54) that ALAN can affect ecosystem functioning in areas not directly illuminated. Since it has also been shown that ALAN is a threat to pollination (55) and potentially even alters diurnal plant–pollinator interactions (56), a reduced orientation performance of moths might represent a further threat to pollination networks. As the reduced orientation performance occurred independent of a disoriented behavior within the illuminated area of a light source, we conclude that the negative effects of light pollution on moths have been underestimated to date.

Materials and Methods

Experimental Design. The study site was located on an open flat pasture close to the small village Großseelheim, Germany. In the main experiment, all animals were released at the same location in the field (50°48'50.3"N, 8°52'32.7"E). The edge of Großseelheim was only about 430 m away from this release site and the towns Amöneburg, Kirchhain, and Stadtallendorf (distance to release site: 3.7 km, 3.7 km, and 10 km, respectively) as well as the cities Marburg and Giessen (distance to release site: 7 km and 30 km) were not too far away. Nevertheless, the study area was relatively dark and not strongly impacted by skyglow (*SI Appendix, Fig. S9*). We introduced typical streetlights (GeoTechnik; c. 3.5 m high) equipped with high-pressure sodium illuminants [(2,000 K, 6,700 lm; NAV-E 70/E SON E27 70 W; Osram, Munich; Germany, s.a. Perkin et al. (57))] to the study area (*SI Appendix, Figs. S2–S4*). In total, we positioned six of these streetlights uniformly in a circle around the release site (Fig. 1B). Each of these lights had a distance of 85 m to the release site and to its nearest neighbors. We used this type of streetlights to obtain representative results for the impact of common street lighting, since they are still one of most prevalent types (58). The lights were either switched off to record the flight trajectories under conditions without near-by artificial lights, or switched on to test the influence of streetlights on flight behavior. It is important to note that the light cones of the lights did not overlap (Fig. 1B).

A harmonic radar (Raytheon Marine GmbH, Kiel, NSC 2525/7 XU) was used to track the flight paths of individual moths (*SI Appendix, Fig. S1A*). This technique is well established for the investigation of navigation and orientation in honeybees (59, 60), bumblebees (61, 62) and butterflies (63, 64). It was possible to transfer the procedure established for honeybees to moths. This procedure commenced with gluing a number tag (Opalithplättchen, Bienen-Center Shop, <http://www.bienencenter.com>) onto the thorax of the moth using nontoxic shellac (Bienen-Center Shop, <http://www.bienencenter.com>). After a curing time of 5 to 10 min

(depending on humidity), a transponder (*SI Appendix, Fig. S1B*) was affixed to this number tag using double-sided sticky tape (Pattex, Kleben statt Bohren, bis 120 kg). Such a transponder had a weight of 10.5 mg and a length of 12 mm. It returned signals to the radar at twice the original transmitted frequency, enabling to determine the position of individual moths while they were in flight (65). The energy to operate the transponder is delivered by the illuminating radar, so no “on-board” battery is required (66). The procedure to attach the transponder to the thorax of a moth took about 30 s and required some light. To ensure that the moths’ vision did not get affected, we used only red light, which is not perceivable by most moth species including Sphingidae (67). Additionally, we tested a possible impact of the handling procedure, including the use of red light, during the control experiments (see below). We were able to follow the animals’ flights for up to 1 km with the position updated every 3 s.

The experiments were performed from 10 June 2018 until 29 July 2018 during warm summer nights (> 10 °C, maximum: 19.8 °C) as moths did not take flight at lower temperatures. Moreover, experiments were not performed during rain or strong wind (maximum wind speed recorded: 10.5 km/h; 83.2% of flights were performed with wind speeds below 5 km/h), because the harmonic radar could not be operated with high wind speeds. In total, we recorded 95 flights of 94 individuals of various species, nearly all of them either belonging to the family of lappet moths or hawk moths (*SI Appendix, Table S1*). All hawk moths were collected with a large light trap that was built up every night at changing locations in the surroundings of the experimental area, far enough away to exclude visibility from the release site. Lappet moths were captured at the experimental field before the start of experiments. To this end, field paths were slowly followed with a car. Once a lappet moth got into the spotlight of the car, it typically made uncoordinated movements on the ground and could be captured easily. Independent of the trapping method, only male moths could be caught.

After a moth was captured, it was kept in the dark and transported to the release site. Between capture and release of a moth there was a minimum acclimation time of 40 min (usually more than 60 min), and we assume that animals were dark-adapted at the time of take-off since the return to full ocular sensitivity takes around 30 min in moths (9). When the animals were kept for longer times, they were fed with sugar solution (2 M) to ensure that they had enough energy to perform a flight (except for *E. potatoria* that do not assimilate food as adults).

Light Environment. Moon phase and position were retrieved from <https://www.timeanddate.de>. Except for eight flights that were recorded at full moon, all flights were recorded at waxing moon or waning moon. The nocturnal light conditions were monitored with a calibrated all-sky camera (Canon EOS 6D, Sigma EX DG 8 mm fisheye lens 180°) see refs. 42, 43, and 68. By obtaining an image at the start of each flight, we were able to measure spatially resolved sky brightness for each flight. For the analysis, luminance (L_v , unit mcd/m^2) was calculated for each pixel with the software “Sky Quality Camera” (version 1.8.1, Euromix, Ljubljana, Slovenia).

Illuminance and spectra of each streetlight were measured with a spectroradiometer in irradiance mode with a cosine-corrected detector head facing the zenith (JETI Specbos 1211UV, Jena Technische Instrumente, Jena, Germany) at a height of 1.5 m because the vegetation did not allow a measurement exactly at ground level. Illuminance measurements were performed in a grid using a 2 m spacing along the main axis of the streetlight up to a distance of 10 m. Outer grid points were obtained in a 5 m spacing. An example grid is shown in *SI Appendix, Fig. S3* and an example spectrum in *SI Appendix, Fig. S4*. Apart from the main axes, we measured at intervals of 5 m. The illuminance measurements and the drone image obtained at the beginning of the experiment revealed that lamp 3 had to be replaced to ensure equal brightness for all six lamps.

Control Experiments. To assess possible effects of the preparations needed for flight tracking via harmonic radar on natural flight behavior (69, 70), we performed four different control experiments with other males of the species *S. ligustri* than those tested during the experiment with the harmonic radar. To this end, males were released from the same release site as the ones of the radar experiment, but the six streetlights were not turned on at any time. To create goals in the field, females (also *S. ligustri*) operating as pheromone traps were positioned north and south of the release site in a distance of 105 m. We were therefore able to record the arrival frequency as well as the time males needed to reach the females using a stopwatch. The same males were released within four

different conditions: 1) prepared with a transponder and fed with sugar solution (2 M) more than 3 h before they were released. Afterward, they were stored on a little wooden plate below a tin until the start of experiments, allowing a release without the need of the handling procedure to attach the transponder or the use of any light (9 releases, 9 individuals; median flight duration: 1.8 min). On another day, these males were 2) prepared with a transponder directly before the flight (14 releases, 13 individuals; median flight duration: 1.7 min), 3) experienced the same handling procedure as the animals in (2) but without attaching a transponder (15 releases, 15 individuals; median flight duration: 1.6 min) and 4) were released without a transponder and experienced no handling procedure at all (20 releases, 19 individuals; median flight duration: 2.1 min) by just storing them below tins as in experiment (1). Thus, the same set of males was tested in all four experiments, but not necessarily every individual went through all four experiments. Neither the arrival frequency (Binomial glm: estimate = 0.0024, $P = 0.99$, $df = 57$), nor the time successful males needed to reach the females located 105 m away differed significantly between the four groups (negative binomial glm: estimate = 0.11, $P = 0.26$, $df = 33$). In accordance with our former results acquired for honeybees (71), we can therefore be confident that the flight behavior was not significantly affected by the tracking technique in our experiments.

Data Analysis. All tested individuals already showed a positive phototactic response, either to the light trap or the car beam we used to collect the experimental animals. Thus, for the analysis of the last recorded signals and the proximity to any of the six introduced streetlights during flight (Fig. 1), we neither distinguished between individuals on the family nor on the species level. However, only the sample size of hawk moths and lappet moths (*SI Appendix, Table S1*) were sufficient for a detailed analysis of flight behavior (Figs. 2 and 3). Flights with a total flight distance below 85 m that could not have reached a streetlight or with less than five recorded waypoints were not included in this dataset. To investigate the local impact of the streetlights we added to the experimental field, we analyzed flight trajectories up to a distance of 270 m from the release site as this was the maximal possible tracking range in the direction of the village Großseelheim for safety reasons. For the evaluation of the main flight direction displayed with arrows in Fig. 3, we determined the mean cardinal direction from the release site for every flight (72). Hawk moths and lappet moths were not analyzed together because they are native to different habitats and therefore perform different kinds of flights. Since hawk moths were not native to the experimental field, they should perform oriented and therefore rather straight flights to reach a more favorable habitat as fast as possible while lappet moths that are native to the experimental field should perform search flights to localize resources (e.g. females). This is especially relevant for the calculation of the tortuosity (Fig. 2), because a search path for local resources (lappet moths) differs from oriented flights to other landscape patches (hawk moths). According to Benhamou (41), tortuosity was therefore analyzed by calculating a sinuosity index for lappet moths and the straightness for hawk moths. The calculation of the sinuosity was implemented in R using the “TrajSinuosity2” function from the “trajr” package (73). Since this calculation follows the exact equation provided by Benhamou (41) and is implemented directly via the R package, we do not present the equation here. The straightness index was calculated as the distance between the release site and the last waypoint (d_i), if it was less than 270 m, or 270 m for all individuals that left the analysis radius, minus the distance between the release site and the first waypoint (d_1), divided by the total flight distance (d_t): straightness = $(d_i - d_1) / d_t$. The total flight distance is the sum of the individual path segments between waypoints from the release site to the last waypoint or the point where the individuals left the radius of analysis. Although some waypoints might be missing, which is important for analyzing flight tortuosity, these omissions appear to be random, as we could not identify systematic issues in the missing waypoints (*SI Appendix, Fig. S8*). This suggests that the data are robust for further analysis.

The software Sky Quality Camera (latest version 1.8.1, Euromix, Ljubljana, Slovenia) was used to calculate luminance values of 12 sectors spanning 30° each for the all-sky images (*SI Appendix, Fig. S9*). Since light conditions varied considerably between different nights, luminance values were normalized to compare light distribution patterns of different nights (Fig. 3). To normalize the values of the sectors, the mean luminance of the entire image was used:

$$\left(\frac{\text{meanluminancesector}}{\text{meanluminancewholeimage}} \right) / 12.$$

Consequently, normalized values reflect the contribution of each sector to the mean overall luminance. Thus, the sum of all 12 sectors equals the total contribution (100%) to the mean overall luminance of an all-sky image.

Statistics. All statistical tests specified below have been conducted with R (74). Because movement characterization as well as corresponding hypotheses were different for the tortuosity analysis of the two genera, we carried out statistical models separately for hawk moths and lappet moths. Assuming beta distributed errors for tortuosity response variables (bounded between 0 and 1) we utilized generalized linear models in response to light on/off, "moon below/above horizon," and their potential interaction (R package glmTMB 1.0.2.1)(75). Structurally identical models were adopted for the barrier analysis, however, with binomial error distribution accounting for binary data of the response variable indicating whether individuals left the circle of lights or not. To account for small and unbalanced sample size here, we replaced conventional logistic regression by exact logistic regression [implemented as glm in R package elm (76) by Markov Chain Monte Carlo simulation]. To analyze differences between lights on and off conditions for the distance of the last recorded waypoint to the closest light source as well as for the closest distance to any light during flights we applied linear regression to the pooled dataset of all individuals assuming normally distributed errors.

To test for differences in the four control experiments carried out with *S. ligustri*, we used a generalized linear regression model with binomial error distribution for arrival frequency and a negative binomial model to analyze flight duration. Bayesian projected normal regression models for circular data allowed identification of directional preferences [R packages circular (77) and bpnreg (78)].

Exact model specifications are provided with the tables or figures showing corresponding results.

Ethical Note. Our study involved individuals of several moth species (SI Appendix, Table S1) that were trapped in the wild. We obtained permission

for capture and release from the Regional Council of Giessen, Germany. All moths were carefully handled during experiments and maintained under appropriate conditions.

Data, Materials, and Software Availability. Raw data have been deposited in Dryad (79).

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