INTRODUCTION

In recent years, evidence for a dramatic regional or even global decline in insect abundance has emerged (Benton, Bryant, Cole, & Crick, 2002; Biesmeijer et al., 2006; Hallmann et al., 2017). Locally, decreases in insect biomass greater than 75% have been found, regardless of habitat type (Hallmann et al., 2017), which even exceeds the 58% decrease in wild vertebrate abundance (Ceballos & Ehrlich, 2018). This is of great...
consequence, not only for the conservation of arthropod diversity, but also because insects play an important role in ecosystem functioning as pollinators, herbivores, detritivores and by facilitating nutrient cycling (Hallmann et al., 2017; Mattson & Addy, 1975; Ollerton, Winfree, & Tarrant, 2011; Yang & Gratton, 2014). Insects are also an important food resource for both invertebrates and vertebrates including fish, amphibians, reptiles, birds and mammals (Baxter, Fausch, & Saunders, 2005; Clough et al., 2010; Losey & Vaughan, 2006). Insects impact the spatial distribution of nutrients between ecosystems by redistributing nutrients from one system to another during outbreaks and emergence events. For example, emerging adults of insects with aquatic larvae re-distribute nutrients from freshwater to terrestrial systems (reviewed in Prather et al., 2013). To understand the activity and abundance of flying insects, many factors such as life cycles, seasonality, swarming behaviour, mass emergences, weather conditions, habitat type or even moon phase (Nylin & Gotthard, 1998; Steinbauer, Haslem, & Edwards, 2012; Sumpter, 2006) have to be taken into consideration. This is important as the resulting variation in time and duration of insect occurrence in turn influences insectivorous predators.

Unfortunately the spatial and temporal distribution of flying insect abundance, especially of small species, remains poorly described. It is usually limited to the descriptions of spectacular mass appearances of insects over water bodies or carcasses (e.g. Oliveira & Vasconcelos, 2018; Walters, Fritz, & Otter, 2008). Even though a variety of sampling techniques exist for flying insects, most of them are aimed at identifying insect diversity and thus biased towards the insect taxa for which they were designed, restricted to sampling at small spatial scales, and often affect the distribution of the insects themselves. For example, traps that attract arthropods using light or pheromones are selective and lead to overrepresentations of specific groups of insects, which react to the lure (reviewed in Kunz, 1990). Non-attracting traps such as impaction, Malaise and sticky traps are less selective, but there is no temporal information about changes in abundance over the sampling period (Kunz, 1990). The same is true for suction, rotary, tow, or Johnson–Taylor suction traps, which, however are efficient at trapping flying insects and non-selective. Lidar and radar systems may provide precise information about the abundance especially of large insects, but the high costs of required equipment impede a broad scale use of these methods (Cant, Smith, Reynolds, & Osborne, 2005; Malmqvist, Adler, Kuusela, Merritt, & Wotton, 2004; Nansen & Elliott, 2016).

Current declines in insect availability and the correlated loss of their ecosystem services are alarming. Many insect-eating animals are highly specialized on clumped aggregations of insects, that is, swarms that are unevenly distributed in time and space and difficult to monitor. It is thus crucial to develop low-cost and maintenance-monitoring methods. Based on previous studies (Avila-Flores & Fenton, 2005; Blake, Hutson, Racey, Rydell, & Speakman, 1994; Collett & Fisher, 2017; Rydell, 1992), we have developed a non-invasive method estimating abundance of nocturnal flying insects using long-interval flash photography and applied it to measure spatio-temporal fluctuations in the abundance of nocturnal flying insects. This method allowed us to quantify but not identify insects. In order to evaluate the role insects play for ecosystem services, it is crucial to monitor overall insect abundance, changes in habitats and the importance of insects in predator–prey interactions and other ecosystem services (Kunz, 1990; Malmqvist et al., 2004; Prather et al., 2013; Rydell, 1992; Wickramasinghe, Harris, Jones, & Jennings, 2004). Particularly important is the monitoring of emerging aquatic insects as major prey for riparian consumers (Baxter et al., 2005).

To test our method, we monitored nocturnal insect abundance in the field. Our aim was to document changes over the course of a summer and over the course of each night. We then calculated the influence of habitat type, temperature, wind and moon phase to show that the method is also sensitive to environmental effects. Specifically, we predicted (a) higher insect abundance and more frequent swarming events along rivers and near a lake than in forests and open areas in villages. We also predicted that (b) the abundance of insects should be patchy in time and space (both seasonally as well as during each night) as many insects hatch in simultaneous events, causing the short-term accumulation of swarms that later become scattered. We also performed tests to assess the reliability and repeatability of the method.

2 | MATERIALS AND METHODS

2.1 Camera settings and placement and setup of the study

To monitor insect occurrence, we installed cameras on a small platform on 2 m-high poles that were planted in the ground to avoid ground vegetation covering the lens and really focus on flying insects. The lenses of the cameras were directed towards the sky and took pictures with flash so insects were visible on the pictures as bright objects. Photos were taken at 5 min intervals from sunset to sunrise. We took and analysed a total of 63,180 photos. The cameras we used were programmable and waterproof (WG-5 Ricoh Imaging Company Ltd.). Photo size was 4,608 × 2,592 pixels, and the focus was set to infinity. Our study was carried out in North-eastern Poland near the village of Białowieża and the Białowieża National Park. We placed 18 cameras in three different habitats (six cameras in each habitat, Figure S1): (a) open forest clearings (Forest), (b) wetlands in river valleys (Wetland), and (c) open areas in villages in the Białowieża Forest (Open). We also placed ten cameras in 2015 and six in 2016 at the shore of Lake Siemianówka (Lake; Figure S1). Forest clearings were usually of small diameter, between 10 and 40 m, which allowed us to take photos devoid of tree crowns. Cameras were situated in mixed broad-leaved forests with small admixtures of spruce. In the Wetlands, we placed cameras in open places, near the small rivers Narewka and Łutownia. Distance to the nearest forest edge varied between 10 and 110 m. Alder and ash trees with admixture of spruce and to a smaller proportion oak, lime and hornbeam dominated in the vicinity. In the open areas, we placed the cameras near houses in protected parts of private properties. The distance to the nearest forest edge was highest in this habitat and ranged from 330 to 2,500 m. Finally, as insect abundances are known to be particularly high
around lakes, we placed cameras on a causeway, 1–20 m from the shore of Lake Siemianówka. The average distance between cameras (sites) in habitats was 250 m for Lake, 2,300 m for Open, 2,940 m for Forest and 3,000 m for Wetland habitats. We recorded insects with the cameras roughly once a week (Forest, Wetland, Open) and once every 2 weeks (Lake) from May till September in 2015 and 2016.

2.2 | Repeatability and reliability of observations

We conducted two experiments to verify the sensitivity of our method. We took photos of insects hanging on a thread at a height of 1–10 m above the cameras. From this, we estimated the distance from which insects were detectable. In the second experiment, we assessed the repeatability and reliability of our counts. We used white round paper spheres with a diameter of A—5.2 mm, B—9.4 mm and C—15.2 mm. We placed five paper spheres of size A, B and C each in a deep porcelain dish mounted at the end of a pipe protruding from a black photographic screen and blew them out with a compressor during experimental trials. A camera was installed on a tripod at increasing distance from the black screen. Photos with flash were taken immediately after paper spheres were blown out to be sure that spheres were in the camera’s field of vision. This procedure was repeated ten times at distances of 2, 4, 6, 8, 10 and 12 m from the screen in complete darkness. The person counting the paper spheres (ZH, the same person, who did all the counts of photographs from the field, too) did not know the experimental procedures and received the photos in randomized order.

2.3 | Insect counts

Insects were visible in the camera flash as bright objects on the dark background see also (Rydell, 1992). To make sure we correctly identified only the right objects as insects, we took reference photos of different objects (dust, rain, fog, insects). Based on this database, we extracted characteristic elements that help classify those objects. Usually insects were not perfectly round on the pictures due to the longitudinal shape of the wings, legs and antennas (Figure S2a,b). Dust and pollen were visible as spherical and less contrasting objects (Figure 2c). Drops of rain, which like insects reflect the flash, were strongly contrasting but more round (Figure S2d). Objects, which were far away from the lens and gave weaker reflections proved the most difficult for identification (Figure S2b). Consequently, we counted only objects that clearly reflected the flash in the analysis. Another impeding factor was limited visibility of insects due to fog (Figure S2b) and rain. All insects were counted blind to camera ID date, time and order by a single observer (ZH). To investigate the effect of insect size on the distance from which they can reliably be observed, we performed experiments with artificial objects of varying size. We pooled the number of insects on the photos by hourly intervals for modelling purposes as we generated large numbers of photos with no insects on them. Only intervals with at least eight photos per hour were included in the analyses.

2.4 | Insect ephemerality

To quantify the ephemerality, that is, the clumped distribution of insects in time and space, we considered the photos that showed ten or more insects on photos taken in each habitat during the sampling period. We analysed swarming intensity based on the number of photos with ten or more insects out of those photos with at least one insect.

2.5 | Temporal and environmental data

We calculated the time after sunset as a proportion of a given night’s length, which had elapsed since sunset. Ambient temperature (at 2 m above-ground) and wind speed were obtained from the local weather station in Białowieża at a resolution of 5 min, and air humidity at a resolution of 10 min.

2.6 | Statistical analyses

To test the effect of distance from the camera on the number of the observed paper spheres in the calibration experiment, we applied a generalized linear model (GLM) with a Poisson error structure. To calculate the likelihood of overlapping insects affecting the counts, we assessed the proportion of white (insects) and black pixels (without insects) on ten reference photos with 25 insects or more. To test the effect of distance from the camera on the number of insects, we used the negative binomial generalized additive model (GAM1; Wood, 2006). There was low multicollinearity between explanatory variables (R < 0.3); thus all variables were included in the modelling procedure. This model included main effects of the following explanatory variables: time (season), time after sunset, wind, temperature, air humidity and habitat. We added year as a covariate. We implemented the unique set of smoothers for each habitat type by adding a factor (habitat)–smooth interaction (Wood, 2006). For each smoother, we kept smoothing intensity (curvilinearity) at a relatively low level (5 df) in order to avoid model overfitting. We took pictures at several sites (one camera at each site) within each habitat. Therefore, we added the unique camera identification number as a random effect (as a penalized regression term; Wood, 2006). Finally, we optimized the negative binomial distribution for the global model by fitting the best dispersion parameter (theta). To choose theta, we ran global models ranging from 0.01 to 1, compared their AIC values and selected the model with the lowest AIC value for the best parameter.

We then fitted binomial a generalized additive model (GAM2; Wood, 2006) to analyse the effect of time (season), time after sunset (proportion of night), and habitat, on swarming intensity of insects. We set swarming probability as a binomial response: with ‘1’
attributed to photos containing 10 or more insects and ’0’ to photos with 1 to 9 insects. Explanatory variables were time (season), time after sunset and habitat. We kept year as a covariate. We used the same smoothing settings and random effect as in the GAM1.

For both datasets and global models, we applied model ranking on submodels containing all possible combinations of explanatory variables with the Akaike information criterion (AIC) (Burnham & Anderson, 2002). We assumed that a ΔAIC below 2 would suggest substantial evidence for the model. All statistical analyses were performed in R 3.5.2 (R Core Team, 2017).

3 | RESULTS

3.1 | General results

Insects were observed on 9.89% (n = 6,249) of 63,180 photos. The number of insects on one photo ranged from 0 to 600 (median: 0 for all photos and 2 for photos with insects). Based on the assumption that insects had wing length of 10–20 mm and were visible on the photos up to a distance of 8 m, we conservatively estimated the average number of insect per cubic meter to be 0.006, or one insect in 161 cubic meters.

We estimated the significance of predictors that explained overall insect abundance in time and space. The best model that predicted insect abundance after model selection included a whole set of considered variables, that is, time, time after sunset, wind, temperature, humidity and habitat (see also Table S1 for parameter estimates).

3.2 | Repeatability and reliability of observations

Tests with dead insects showed that our cameras detected insects in more than 200 m³ of air depending on insect size (Figure 1). Small insects, such as Culex (wing length—5 mm) and Ephemeroptera (wing length—4 mm) were detected at a distance of up to 4 m from the camera. Larger ones, such as Tipulidae (wing length—20 mm), Coleoptera (wing length—10 mm) or Vespa sp. (wing length—17 mm) were detected from a distance of up to 7–8 m, and Heterocera (wing length—15 mm), from more than 10 m. The cubature on the photo thus varied from at least 18 m³ for small insects (distance of 4 m) up to more than 282 m³ for large insects (distance of 10 m; Figure 1).

In the second experiment determining sensitivity of the method, we found a linear decrease in the number of detected paper spheres with distance, but this relationship was repeatable and consistent (slope = −0.09 ± 0.01, z = −7.2, p < .001, R² = .82; Figure 2). Results for different paper sphere sizes were pooled.

Insects visible on ten randomly selected photos with more than >25 insects covered from 0.0003% to 1.6% of photo area (27–135 insects on each photo). The average insect covered 0.006% (±0.003) of the photographed area. The probability that one insect masks one or several other insects is extremely low and thus negligible.

3.3 | Variation of insect abundance over the season and during each night

There was a strong effect of time (month) and time after sunset (Tables S1 and S2). Insect abundance increased from May to late June/early July and then gradually decreased in Open habitats, Forest and Lake (Figure 3a). The insect peak in habitat Wetland occurred at the beginning of May, after which numbers decreased until the beginning of June. Then they increased and peaked again in mid-July. Over the course of each night, the highest number of insects was observed just after sunset in Lake habitats, Wetland and Open, however, the dynamic of changes differed between habitats (Figure 3b). The most profound decrease as well as increase in insect numbers occurred in the Lake habitat. Insect numbers were most stable throughout the night in the Forest habitat (Figure 3b).
Habitats differed greatly in insect abundance. Insects were observed most frequently on photos taken at the Lake (22.9%), followed by Forest (9.5%), Wetlands (7.9%) and Open (5.5%). The model confirmed these clear differences in insect abundance (i.e. the cumulative number of insects) between habitats (Tables S1 and S3).

### 3.4 Habitat differences in insect abundance

Habitats differed greatly in insect abundance. Insects were observed most frequently on photos taken at the Lake (22.9%), followed by Forest (9.5%), Wetlands (7.9%) and Open (5.5%). The model confirmed these clear differences in insect abundance (i.e. the cumulative number of insects) between habitats (Tables S1 and S3).

### 3.5 Influence of environmental variables on insect abundance

Higher temperatures were correlated with higher insect abundance in all habitats, although this relationship was very weak on the Lake.
(Figure 4a; Table S1). Increasing humidity had a weak but positive effect on the number of insects (Figure 4b, Table S1). We observed a negative influence of higher wind speeds on insect numbers, which was most pronounced in the Lake and Open habitat (Figure 4c; Table S1).

3.6 | Insect ephemerality

Insect swarming (i.e. pictures with 10 insects or more on them) was rare. We observed swarming only on 1.48% of all photos. The number of insects on these photos varied from 10 to 600 (median 21, n = 938, Figure S3). The frequency of swarming events was the highest on the Lake (8.16% of photos from this habitat) and very rare in Wetlands (0.74%), Forest (0.18%) and in Open habitats (0.08%). The duration of night varied from 7:03 to 10:28 hr, but swarming occurred mainly during the first two hours after sunset (93.1% of all photos with swarming).

There was thus a strong difference in swarming intensity among habitats and in response to temporal variables. The best model retained time, time after sunset, habitat and year (Tables S2 and S4). Swarming probability was the highest in the Lake in June/July, shortly after sunset and before sunrise. However, swarming probability then decreased again just before sunrise (Figure 5a–c). Swarming was observed mainly during warm nights (16.3°C ± 3.8°C) but also at a temperature of only 6.1°C.

4 | DISCUSSION

Our results demonstrate that camera transects are a useful tool for monitoring changes in the abundance of nocturnal, flying insects. The method detected and thus confirmed a strong influence of weather conditions (especially ambient temperature and wind) on insect abundance. We found profound differences in insect abundance among the studied habitats with the highest abundances in lake, followed by the wetlands along rivers. We also documented high ephemerality of insect occurrence. Our method allowed us to describe the temporal patterns of occurrence of insect swarms, which were altogether rare, but occurred predominantly in June/July, shortly after sunset and before sunrise but not during the brightest part of sunset and sunrise. This emphasizes the importance of quantifying the dynamics of flying insects with a high spatial and temporal resolution, because it allows for monitoring the presence of short-lived phenomena such as insect swarming.

Our experiments with artificial objects of varying size show that our method is predictable and repeatable. However, calibrations will be necessary for future studies. It is extremely difficult to assess background insect abundance, which is why we developed this method. But, this means that insect size and distance from the cameras will always introduce a bias. This can partially be overcome with back-up experiments like ours, which could also be performed with dead insects of variable size. Perhaps also setting the camera focus to a short distance will restrict the range, but give reliable counts. Nonetheless, our method gives a good approximation of insect abundance even of very small size within several meters of the camera and is thus useful for the detection of patterns and comparison of sites and habitats.

Measuring insect abundance with the camera transects we describe is relatively unbiased, non-invasive and straightforward. While camera transects can also be used to identify insects, especially non-flying ones, if the camera focus is set to a close focus (Collett & Fisher, 2017), our method allows a larger-scale, but less
specific census. Some experience interpreting the images is required, but quickly achieved using and comparing calibrated images containing insects, dust, rain or fog. The main disadvantage of the method is the time-consuming manual image analysis, as well as the lack of insect species identification and sizing. Larger insects are depicted from longer distances, which may also have affected our results. An important factor is that we do not think our method influenced insect distribution patterns. Even though we use flash and thus light, this was at such low intervals that it is unlikely that it made insects remain near the camera. Supporting this, we did not observe any accumulation of insects over time or an effect of the interval between pictures on insect abundances. The method can be used as a good alternative for monitoring insect abundance and especially insect swarming. This method could be improved by developing code for the automated identification of objects in the photos (Aguzzi et al., 2011), allowing for monitoring of long- and short-term changes in insect abundance even at continental scales. Developing automatic classification will be helpful at least to pre-select those photos that have insects on them as large numbers of pictures are easily collected but most will be empty. However, the distinction between insects, dust particles and water droplets was less trivial than anticipated and thus the development of this is still in progress. Nonetheless, even now our results, as well as equally promising ones using cameras to monitor terrestrial arthropods as an alternative to pitfall traps (Collett & Fisher, 2017), show that the use of camera transects might develop into a method for insect monitoring similar to methods for monitoring populations of terrestrial vertebrates with camera traps (Kuijper et al., 2014; Rovero & Marshall, 2009). This is especially important in the context of insect, bat, and bird declines observed in recent decades (Butchart et al., 2010; Hallmann, Foppen, Turnhout, Kroon, & Jongejans, 2014; Safi & Kerth, 2004).

Beyond the method, a striking result of our study was the low number of images that contained any insects. Clearly, the density of flying, nocturnal insects is extremely low even in the most insect-rich habitats such as the eutrophic lake included in our study. Similar to previous studies (Hallmann et al., 2017; Salvarina, Gravier, & Rothhaupt, 2018) we found a strong seasonal effect on insect abundance, but now we were able to discern differences in insect dynamics between habitats as well. Insect numbers peaked during the warmer months from about mid-June to early July and then started to decrease, dropping off dramatically in August. Higher insect abundance during the warmer months in the temperate zone is a result of the favourable environmental conditions that allow insects to complete their life cycle (Bale et al., 2002). However, our data also indicate that ambient temperature does not influence insect abundance in the Lake as much as in other habitats. We also observed a peak in insect availability early in the night, just after sunset and a lesser one just before sunrise. This is in line with many other studies (Malmqvist et al., 2004; Rydell, Entwistle, & Racey, 1996), but now we were also able to show differences between habitats, for example, low but stable number of insects in Forest and very dynamic changes in Lakes.

It is intuitive that insect abundance is influenced by environmental variables, even within habitats (Malmqvist et al., 2004; Rydell et al., 1996). Flying insects are poikilothermic and small and their activity depends on suitable conditions. Variables such as temperature, wind, or the amount of light simultaneously influence insect activity, often with contradictory effects, which makes precise predictions about where and when high insect densities will occur difficult. We found that the influence of environmental factors on insect abundance differed between habitats, for example, wind negatively influenced insect abundance mainly on the lake and in villages. Insect abundance increased with rising ambient temperature in all habitats, but less so on the lake. Here, too, the high temporal resolution of our method is advantageous, as temperature, wind and rain (even though we could not test this due to dry weather during the study period) can change insect abundance within minutes.

Insects provide essential ecosystem services that can even be translated into monetary value (Losey & Vaughan, 2006). Benthic communities in freshwater ecosystems containing many insects are key to nutrient cycling, water quality and trophic cascades. However, their distribution is patchy and difficult to sample (Covich, Palmer, & Crowl, 1999). Indirectly monitoring numbers of aquatic insects as they emerge, often in mass events, may prove a useful tool for the assessment of ecosystem health. Importantly, we need to monitor not only single keystone species, but entire communities: an estimated 20,000 species of Diptera develop in freshwater bodies many of them important in food webs (Hutchinson, 1993). Monitoring insect numbers is also a valuable method for the success of remediation measures. The resurgence of mayflies, which could be easily monitored with our method as they mass emerge from the water, can be an indicator that nutrients are being cycled again instead of accumulating in the sediment (Kolar, Hudson, & Savino, 1997).

Our most important finding was to illustrate the extremely dynamic changes of insect abundance in time and space. The spatial and temporal ephemeral nature of nocturnal insects resulted in the complicated picture of a pulsating resource. Swarms, even when arbitrarily set at a very low threshold value of ten insects per picture or more, were extremely rare (938 pictures out of 63,180). Insect swarming at the lake exceeded insect swarming in the other habitats by several magnitudes as we documented with our method.

As papers on climate change and ecosystem services accumulate, studies on the effect of many specific taxonomic groups and especially insects remain scarce often due to the difficulty of sampling populations (Prather et al., 2013). Our method may help to monitor the state of habitats via assessing insect numbers. Especially in the diverse and crucial aquatic communities number of insect larvae can be difficult to assess directly. Instead, our method allows counting them as adults. In light of the ongoing
changes in climate and landscape structure and the correlated decline in insect numbers, we believe that simple but non-invasive and highly informative methods like the one we present here are warranted to monitor these changes and inform conservation policy makers.

ACKNOWLEDGEMENTS

We thank our friends, students and volunteers for the much appreciated help in the field: Marianna Wróbel, Laura Contreras Peinado, Jur Metselaar, Dirk Oosterholt, Ewa Komar, Mariusz Tulejko, Marzena Zlobrowska, Ewa Łękowska, Bob Jansen, Daan van Kalsbeek, Magdalena Dziwisz, Sofía Pantoja López, Laura Jiménez Martín, Ewa Przepiórka, Łukasz Ruczyński and Michael Kroeeze. Teague O’Mara, Jenna Kohles and four anonymous reviewers gave feedback about the manuscript. This work was funded by the Polish National Science Centre Grant DEC-2013/10/E/NZ8/00725

AUTHORS’ CONTRIBUTIONS

I.R. and D.K.N.D. conceived the idea and designed methodology; Z.H., M.Z. and I.R. collected the data; T.B and Z.H. analysed the data, Z.H. counted insects; I.R and D.K.N.D. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

Data deposited in the Dryad Repository: https://doi.org/10.5061/dryad.5dv41ns2s (Ruczyński, Hałat, Zegarek, Borowik, & Dechmann, 2019)

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**SUPPORTING INFORMATION**

Additional supporting information may be found online in the Supporting Information section.

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**How to cite this article:** Ruczyński I, Hałat Z, Zegarek M, Borowik T, Dechmann DKN. Camera transects as a method to monitor high temporal and spatial ephemerality of flying nocturnal insects. *Methods Ecol Evol*. 2020;11:294–302. https://doi.org/10.1111/2041-210X.13339