

## ORIGINAL RESEARCH

# Camera traps with white flash are a minimally invasive method for long-term bat monitoring

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## Keywords

Chiroptera, light barrier, long-term monitoring, mammals, *Myotis*, remote sensing, wildlife conservation

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## Abstract

Camera traps are an increasingly popular survey tool for ecological research and biodiversity conservation, but studies investigating their impact on focal individuals have been limited to only a few mammal species. In this context, echolocating bats are particularly interesting as they rely less on vision for navigation, yet show a strong negative reaction to constant illumination. At hibernacula, camera traps with white flash could offer an efficient alternative method for monitoring threatened bat species, but the potential negative impact of white flash on bat behavior is unknown. Here, we investigate the effect of camera traps emitting white flash at four hibernation sites fitted with infrared light barriers, infrared video cameras, and acoustic recorders over 16 weeks. At each site, the flash was turned off every second week. We quantified whether flash affected (1) nightly bat passes using generalized linear mixed models, (2) flight direction of entering bats using permutational multivariate analyses, and (3) latency of the first echolocation call after the camera trap trigger using randomization tests. Additionally, we quantified and corrected for the potential impact of confounding factors, such as weather and social interactions. Overall, white flash did not influence short- or long-term bat activity, flight direction or echolocation behavior. A decrease in nightly bat activity was observed with an increasing proportion of hours with rain. Moreover, flight direction was affected by the presence of other bats, likely due to chasing and avoidance behavior. Our findings highlight the potential of camera traps with white flash triggered by infrared light barriers as a minimally invasive method for long-term bat population monitoring and observation of species-specific phenology. Such automated monitoring technologies can improve our understanding of long-term population dynamics across a wide range of spatial-temporal scales and taxa and consequently, contribute to data-driven wildlife conservation and management.

## Introduction

Reliable and cost-effective population monitoring of bats is critical given their key role in ecosystem functioning and as effective ecological indicators of environmental changes (Jones et al., 2009). Moreover, monitoring of bat population trends is legally required in most European countries (Battersby, 2010). Nevertheless, obtaining accurate estimates of population trends is challenging due to

the cryptic nature of bats (i.e. small size, nocturnal habits, ability to fly and hide effectively in crevices), and sensitivity to disturbance. Traditional bat monitoring relies heavily on time-consuming and invasive techniques such as captures with mist-nets and visual counts at winter and summer roosts (Kunz et al., 2009). Over the last decades, several automated bat counting techniques have been developed, offering more accurate and less invasive alternatives to traditional bat surveying methods. For example,

thermal and infrared cameras combined with automated video processing methods have been used to accurately estimate population sizes during nocturnal emergence from roosting sites (Corcoran et al., 2021; Elliott et al., 2006; Frank et al., 2003; Sabol & Hudson, 1995), but due to high power and data storage requirements these methods remain unfeasible for widespread or long-term monitoring.

Remotely triggered cameras have become important survey tools for automated wildlife monitoring and their rapid improvement in recent years has transformed ecological research and biodiversity conservation (Wearn & Glover-Kapfer, 2019). Camera traps can be used to monitor population trends and community composition, which are fundamental requirements for efficient wildlife management and setting conservation priorities (Battersby, 2010). Although camera traps are often considered less invasive alternatives to traditional sampling methods that require capture or human presence (e.g. Sollmann et al., 2013), their novelty in an environment, as well as the light and sound they emit may also affect wildlife (Caravaggi et al., 2020; Meek et al., 2014). Several studies have found varying responses to camera traps among mammal species, including both avoidance behavior (e.g. coyotes, Séquin et al., 2003; kinkajous, Schipper, 2007; tigers, Wegge et al., 2004; wolves, Gibeau & McTavish, 2009) as well as curious visual exploration behavior (e.g. large felids, Kelly et al., 2012; apes, Kalan et al., 2019; feral cats, Meek et al., 2016; stoats, Glen et al., 2013). The use of infrared flash may constitute a less invasive alternative to white flash (Wearn & Kapfer, 2017), however, reliable and accurate identification of co-occurring species with similar characteristics is often more difficult (Burns et al., 2018). Improved understanding of how camera traps affect the behavior of focal individuals is necessary to minimize disturbance of automated monitoring methods.

Cameras with white flash automatically triggered by infrared motion detectors (Daan, 1970; Degn et al., 1995; Hope & Jones, 2013; Kugelschafter et al., 2014; Lubczyk & Nagel, 1995) and manually triggered cameras (Rydell & Russo, 2015) have been proposed as a viable method to monitor bat activity throughout the year. These studies either suggested that white flash has no negative impact on focal bats, or did not consider disturbance altogether. On the other hand, flash photography of bats emerging from roosts is banned at several touristic sites (e.g. Carlsbad Cavern, US) or permitted only with an appropriate license (e.g. United Kingdom), because the unexpected bright light might disturb the bats and may alter their emergence behavior. Similarly, Zukal et al. (2017) have asserted that the use of flash will negatively affect natural bat behavior. However, while the impact of light

pollution (i.e. continuous illumination) on bat roosting, commuting, and foraging activity has recently received increased attention (e.g. Barré et al., 2021; Russo et al., 2017; Spoelstra et al., 2018; Stone et al., 2015), to our best knowledge, the potential negative impact of white flash on bat behavior has never been systematically evaluated.

Here, we comprehensively examine the effect of camera traps with white flash on bats in an experimental field study over 4 months at four hibernacula in Northern Germany. At each site, an infrared light barrier was installed to measure nightly bat activity and trigger the camera trap. Additionally, flight behavior was recorded using an infrared camera, and echolocation calls were recorded using a full-spectrum acoustic logger. We first evaluated whether the flash elicited any avoidance or attraction behavior using the light barrier data. We posit that if bat activity deviates on flash-on nights compared to flash-off nights, while correcting for weather and temporal effects, then data from camera traps with white flash may not be informative proxies of bat activity, and in the worst case may even cause a substantial disturbance and cause individuals to abandon the site. We subsequently categorized flight direction of bats and latency of the first echolocation call after the camera trigger to investigate whether bats are startled by the flash, even if this does not immediately lead to a reduction in the overall number of bat passes. We hypothesized that if entering bats are disturbed by the flash, this may either lead to a change in the relative abundance of specific flight directions observed within a site, or that bats might call earlier (i.e. surprise reaction) or later (i.e. shock reaction) as compared to flash-off nights. Finally, we investigated the long-term effects of a year-round camera trap installation at a fifth site where only one of two entrances has been monitored with a camera trap and flash for the past 6 years. We hypothesized that if the flash disturbs the entering bats, they should preferentially make use of the other entrance, or that the overall number of bats counted at the site in winter should decline.

## Methods and Materials

### Study site and experimental design

Infrared light barriers with camera traps (ChiroTEC, Lohra, Germany), self-built infrared video cameras, and Audio-Moth acoustic loggers were installed at the entrance of four hibernation sites in Northern Germany (Table 1; entrance schematics in Fig. S1). At each site, the white camera trap flash was turned on and off in a weekly alternating manner for 16 weeks between August and December 2020, with two sites exposed to 'flash-on' treatment and two to 'flash-off' during any given week (Table 1). The digital camera

was left turned on continuously, taking black images on flash-off weeks and thus the camera shutter emitted a detectable sound irrespective of flash treatment. The timing of the experiment coincided with the busiest activity period at the hibernacula, the autumn swarming phase and onset of hibernation. At two sites, Anklam and Peenemuende, the camera trap installation took place in autumn 2019, thus the adult bat population at these sites was exposed to flash for a whole year before the experiment. At the other two sites, Demmin and Friedland, camera trap installation occurred directly prior to this experiment, therefore bats were completely naive to the flash.

Light barriers consist of a sensor array with 4 (Liba-4) or 16 (Liba-16 and Liba-16k) pairs of infrared emitters and corresponding receivers. Adjacent sensors are 2.1 cm apart in the Liba-4 and Liba-16, and 1.1 cm apart in the Liba-16k model.

The camera trap consists of a Panasonic Lumix G5 digital mirrorless camera and a Metz 58 AF-2 digital white flash (aperture 5.6, power 1/16, zoom 70). The camera trap is connected to the light barrier, and it is triggered on each entry registered by the light barrier.

Self-built infrared video cameras were used to record the flight direction of bats entering the hibernacula. Each camera was built using a Raspberry Pi 3, an 8 MP camera, and an 850 nm infrared illuminator (see <https://gabik-bat.github.io/FlederCam/> for full construction details). Cameras were mounted on top of the camera traps and recorded continuously between sunset and sunrise (800 × 600 resolution, 25 frames per second). The video cameras were modified to additionally receive a signal from the light barrier for each registered event. Due to technical problems, infrared video recordings were unsuccessful on 8 of 64 deployments (Table 1).

Acoustic recordings were collected with AudioMoth acoustic loggers (v1.0.1, LabMaker; Hill et al., 2018). Each device recorded continuously every day between sunset and sunrise from week 3 onwards at a sample rate of 192 kHz on the medium gain setting. Devices were

encased in a protective case and mounted directly on top of the infrared video cameras, with the microphone facing the entrance of the hibernaculum.

Hourly air temperature (°C) and precipitation data (mm) for the study period were obtained from the German Meteorological Service (DWD) from the closest local weather stations to each hibernaculum: weather station in Anklam (Anklam), Tribsees (Demmin), Trollenhagen (Friedland), and Karlshagen (Peenemuende).

### Video analysis: flight direction and video-based bat activity

From the c. 5400 h of raw infrared video recording, 6-second-long video snips were isolated for each event registered by the light barrier. In total, 53 134 video snips were manually analyzed to quantify video-based bat activity. The camera flash was visible on the video snips as one or two overexposed frames. To reduce potential observers' bias in the video processing, these frames were detected based on white pixel threshold values and replaced by a merged image of the pre- and post-flash frames with 50% transparency. This pre-processing step ensured that when the videos were scored for flight direction, the observer was unable to tell whether the focal bat was exposed to the flash or not.

For each video snip of an entering bat, we categorized bat behavior based on the direction of its flight after the camera trap trigger. If a bat turned <180° during the time it remained in the field of view, it was scored based on the edge of the frame where it left the camera's field of view: **up**, **down**, **left**, **right**. If a bat turned more than 180° within the field of view of the camera but remained within the hibernacula, it was scored a **loop**. If a bat turned around and left the hibernacula, it was scored a **U-turn**. Finally, if the bat approached and triggered the light barrier while circling on the inside without leaving the hibernacula (i.e. inspection flight), it was scored an **innerloop**. Innerloops were excluded from the flight

**Table 1.** Description of the study sites, including location, light barrier model and its installation date, flash treatments on even and odd weeks, number of weeks with infrared video data per flash treatment (maximum number per treatment is eight; missing weeks due to video camera failure: Anklam week 4, 9, 10, 11; Friedland week 5, 6, 7; Peenemuende week 13), and species recorded at each site during the winter census in January 2020.

Location	LB model	LB installation	Even/odd weeks	Video weeks	Species composition
Anklam	Liba-4	18.10.19	On/off	6/6	<i>Myotis dasycneme</i> , <i>M. daubentonii</i> , <i>M. myotis</i> , <i>M. nattereri</i> , <i>Pipistrellus pipistrellus</i>
Demmin	Liba-16k	31.07.20	Off/on	8/8	<i>Myotis daubentonii</i> , <i>M. myotis</i> , <i>M. nattereri</i> , <i>Plecotus auritus</i>
Friedland	Liba-16	31.07.20	On/off	7/6	<i>Myotis daubentonii</i> , <i>M. myotis</i> , <i>M. nattereri</i> , <i>Plecotus auritus</i>
Peenemuende	Liba-4	18.10.19	Off/on	8/7	<i>Myotis brandtii</i> / <i>M. mystacinus</i> , <i>M. dasycneme</i> , <i>M. daubentonii</i> , <i>M. nattereri</i> , <i>M. myotis</i> , <i>Plecotus auritus</i>

direction comparisons to restrict the analysis to individuals entering the hibernacula from outside and from the video-based activity counts to avoid overestimating overall activity. In addition to the direction, we also categorized if an event was 'social' or not, based on whether any other bats were seen during the 6-second video snip.

### Audio analysis: echolocation call latency

All audio files were processed in Python v3.7.3 to automatically identify each recorded camera trap trigger based on the audible shutter sound. We downsampled each audio file from the original 192 to 96 kHz and cut it into fragments, consisting of  $2^{17}$  datapoints. We computed the *short-time Fourier transform (STFT)* of each fragment using a Gaussian window with 256 data points. The normalized, squared magnitude of STFT was integrated between 450 and 550 Hz, to obtain the bandpower of the corresponding peak intensity range of the shutter sound. To detect the typical trimodal intensity peaks (see Fig. S3) of the camera trigger, we used the *find\_peaks* function (prominence 0.2, SciPy package, v1.6.3; Virtanen et al., 2020). The precise moment of the camera trigger was defined as the middle intensity peak, which also corresponds to the flash event on flash-on nights.

To measure the potential change in echolocation behavior of bats, we calculated the time from the camera trigger onset to the first echolocation pulse, which we refer to as the first echolocation call latency. We selected this measure as we hypothesized that bats may either react to the flash by calling faster ('surprise'), or slower ('shock'). Other measures such as call activity prior to entry or inter-call-interval after entry varied strongly in repetition rate and amplitude between sites due to large differences in hibernacula entrance dimensions and between flight directions and therefore could not be quantified reliably using automatic detection thresholds.

We created 2-second-long audio snips centered around the detected camera trigger signals. Based on the corresponding video snips, we excluded those scored as 'social', because the detected call may not have been produced by the entering bat, and additionally bats may modify their echolocation behavior in the presence of other bats. To detect echolocation calls, spectrograms were computed using STFT of the original 192 kHz audio data and bandpower was calculated between 35–65 kHz, representing the broad frequency range of species present at the study sites (Barataud et al., 2015). We identified all peaks corresponding to individual pulses after the camera trigger using the *find\_peaks* function (prominence 0.005) and calculated the time between the camera trigger and the first subsequent echolocation call. Spectrograms of all events, with marks denoting the timing of the

automatically detected camera trigger and echolocation pulses (see Fig. S3), were inspected manually. All events with failed detections or calls of multiple bats were excluded from the analysis, resulting in a total of 3272 events (1568 flash-on, 1704 flash-off).

### Long-term monitoring

At a fifth hibernaculum with two entrances (Eldena), the main entrance has been monitored using a camera trap with white flash and a light barrier (Liba-16), while the nearby side entrance ( $\pm 20$  m) has been monitored with only a light barrier (Liba-4) since autumn 2015. Annual hibernation surveys were carried out once per year in January.

### Statistical analyses

All statistical analyses were conducted in R (v3.6.1; R Core Team, 2019).

### Activity data

Light barrier-based bat activity was measured as the total number of bat passes registered each night by the light barrier. In addition, we quantified the video-based bat activity by counting the passes observed in the infrared video data. We investigated the impact of flash on nightly bat activity registered by the infrared light barrier using a generalized linear mixed model with negative binomial distribution (*glmer.nb* function, package lme4, v1.1-26; Bates et al., 2015). To account for temporal variation (e.g. higher activity in August than in December), weather variation (e.g. higher activity on warmer and dry nights), and variation across sites, we included study week, precipitation, and temperature in the full model as fixed effects and study site as random effect. However, study week was excluded from the final model due to collinearity with temperature (Pearson's correlation coefficient,  $r = -0.8$ ). Temperature was defined as the ambient temperature at sunset as Parsons et al. (2003) postulated that temperature at emergence may be the primary driver of swarming activity at underground hibernacula. Precipitation was defined as the proportion of hours with rain between sunset and sunrise, because we expected lower bat activity with longer duration of rain, irrespective of the amount of rainfall. We standardized both weather parameters prior to analysis. Model assumptions were examined using the DHARMA package (v0.4.1; Hartig, 2021). Odds ratios with 95% confidence intervals were calculated for each fixed effect with the *confint* function of the stats package (R Core Team, 2019). An additional model was run with identical model structure but using the video-based activity data to investigate whether

excluding innerloops could improve the strength of correlation between activity and weather parameters.

### Behavioral data

Possible flight directions were highly dependent on the layout of the hibernacula entrance and positioning of the video camera (Fig. S1), thus we performed only within site comparisons of flight directions. Social interactions often included chasing and avoidance behavior and are therefore likely to influence the flight direction categories. Thus, we compared the compositional similarity of flight directions between flash-on and flash-off nights, as well as social and non-social events using a non-parametric permutational ANOVA (PERMANOVA; Anderson, 2014) with the *adonis* function of the *vegan* package (v2.5-7; Oksanen et al., 2020). Pairwise comparisons were based on Bray–Curtis dissimilarity matrices with  $10^4$  random permutations and adjusted for multiple comparisons (*p.adjust* function, ‘*bonferroni*’ method, *stats* package; R Core Team, 2019). All calculations used flight direction totals per group as an abundance-based measure of dissimilarity to account for overall reduction of flight activity as a potential effect of disturbance.

Permutational multivariate analysis of variance is sensitive to heterogeneous group dispersions. The activity data showed that weekly flight direction totals had unequal variances due to temporal and weather effects. Therefore, we grouped nightly flight direction totals by day of the week, thereby pooling days (e.g. all flash-off Mondays) across the entire sampling period, to create samples with homogenous variance between flash treatments and social groups. Homogeneity of dispersion between compared groups (flash-on vs. flash-off, social vs. non-social) was tested using the *betadisper* function of the *vegan* package (v2.5-7; Oksanen et al., 2020).

### Acoustic data

Mean first call latency, the mean time in milliseconds from the camera trigger to the first echolocation pulse, was compared between flash-on and flash-off nights using a randomization test with  $10^4$  permutations. Since the echolocation behavior of bats can be affected by the dimension of the hibernacula entrance, the analysis was restricted to within site comparisons.

## Results

### Activity data

Nightly bat activity did not differ between flash-on and flash-off nights (Fig. 1A, Table 2). Bat activity decreased with a higher proportion of hours with rain between

sunset and sunrise (Fig. 1B, Table 2), but ambient temperature at sunset did not uniformly impact bat activity (Fig. 1C, Table 2). Specifically, nightly bat activity increased in Demmin and Peenemuende, and decreased in Anklam and Friedland with higher temperature at sunset (Fig. 1C). Results were comparable when using the video-based activity data (Fig. S2, Table S1).

### Behavioral data

The composition of flight directions differed between sites, with up and down being the most common flight directions, and U-turns being the rarest events overall (Table S2). During non-social events, bats entering hibernacula with narrow entrances (i.e. Anklam and Peenemuende) most often left the frame at the bottom, presumably due to losing height after gliding through the entrance (in 74.84% and 62.95% of the non-social events, respectively; Table S2). In Demmin, where the entrance is slightly taller, and Friedland, where the camera was placed further away due to the entrance’s height above ground, bats primarily left the frame at the top (in 65.67% and 37.92% of the non-social events, respectively; Table S2).

Tests of the homogeneity of group dispersions indicated that variances of nightly flight direction totals were homogenous for both flash and social variables at all hibernacula, except in Peenemuende, where variance was non-homogenous between flash treatments (Table 3).

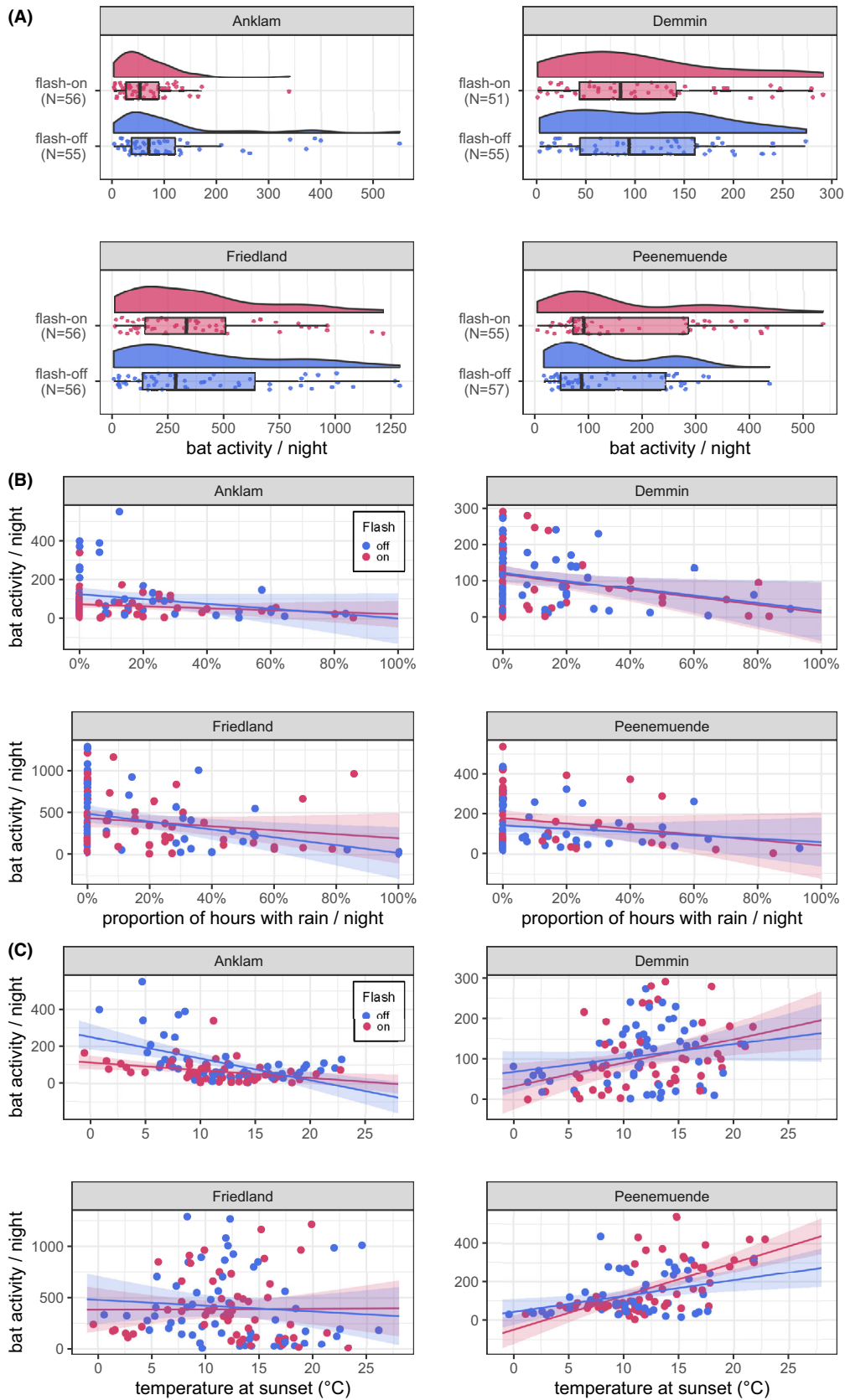
The composition of flight directions of bats entering the hibernacula was different between social and non-social events but did not differ between flash-on and flash-off nights (Fig. 2, Table 3). PERMANOVA results between flash treatments in Peenemuende trended toward significance, but this is likely the result of heterogeneous group dispersion (Table 3). Social events reduced the number of bats entering in the ‘default’ direction (Fig. 2), and chasing (i.e. both bats leaving the frame in the same direction in close succession) or avoidance (i.e. flying away from the other bat observed in the frame without the other bat pursuing) behaviors were frequently observed.

### Acoustic data

Mean first call latency did not differ on flash-on and flash-off nights at each site based on randomization tests (Anklam  $P = 0.092$ , Demmin  $P = 0.258$ , Friedland  $P = 0.955$ , Peenemuende  $P = 0.562$ ), with a maximum difference of  $4.61 \pm 1.7$  ms in Demmin (Fig. 3).

### Long-term monitoring

The proportional use of the main entrance (with camera trap) and side entrance (without camera trap) did not



**Figure 1.** Comparison of light barrier-based (A) nightly bat activity on flash-on and flash-off nights, and the relationship between bat activity and (B) proportion of hours with rain per night between sunset and sunrise, and (C) ambient temperature at sunset. Each point corresponds to the total number of bat passes recorded per night using infrared light barriers. Data points are colored based on flash treatments for illustrative purpose only, as no differences were found between flash-on and flash-off nights. Solid lines with shading represent the regression line and 95% confidence interval.

**Table 2.** Results of the generalized linear mixed model showing the effect of the proportion of hours with rain between sunset and sunrise, ambient temperature at sunset and flash on light barrier-based nightly bat activity.

Fixed effects							
Variable	Estimate	SE	z-value	Odds ratio	LCL	UCL	P-value
(Intercept)	5.12	0.33	15.74	166.63	75.16	370.59	<b>&lt;0.001</b>
Proportion rain	-0.30	0.05	-6.28	0.74	0.67	0.81	<b>&lt;0.001</b>
$T_{\text{sunset}}$	0.09	0.11	0.85	1.10	0.89	1.36	0.394
Flash	-0.08	0.08	-0.95	0.93	0.79	1.08	0.341
Random effect							
Variable	N	Variance		SD	Observations		
Site	4	0.37		0.61	441		

When the 95% confidence interval (between lower – LCL – and upper – UCL – confidence level) of the odds ratio (OR) contains 1, the variable is considered to have no measurable effect. An interval above 1 indicates a positive, and below 1 a negative effect of the predictor. Bold values indicate statistical significance at  $P < 0.05$  level.

change substantially over the past 6 years. On average 67% of the bats entered the hibernacula via the main entrance (Fig. 4), suggesting that this is the preferred entrance, despite bats being exposed to the white flash upon entrance. Moreover, the number of hibernating individuals counted during the winter census increased from *c.* 250 in the year prior the installation of the monitoring system, to over 300 individuals in recent years.

## Discussion

In several mammal species, distinct startle and attraction responses elicited by the white flash of camera traps have been observed (Séquin et al., 2003; Wegge et al., 2004, e.g. Gibeau & McTavish, 2009; Schipper, 2007), potentially biasing population monitoring. In this experimental field study investigating the reaction of bats to white flash at the entrance to four hibernacula, we did not observe an effect of flash on bat activity, flight direction, or echolocation behavior.

Successful conservation of threatened species relies on accurate assessment of long-term population trends. In temperate-zone bats, monitoring of hibernacula has the distinct advantage that many species make use of these sites, thereby bundling monitoring efforts. However, traditional winter counts only yield a single population estimate per

year. Automated monitoring methods, such as light barriers that measure activity and camera traps that allow for species identification, have the potential to vastly improve monitoring via accurate, year-round sampling of nearly all entering bats. The system is particularly applicable to situations where several hundred to several thousand bats hibernate in a site with a comparatively narrow entrance, but where traditional winter counts are impossible for safety reasons or ineffective due to uncountable sections or crevices (e.g. bunker complexes, tunnels, shale mines).

Activity models accounting for temporal and weather parameters showed no negative impact of flash on nightly bat passes. Unsurprisingly, bat activity was negatively affected by precipitation that corresponded to findings of previous studies (e.g. Parsons et al., 2003). Visual inspections suggested that higher temperature at sunset increased or decreased nightly bat activity depending on the site, which can be partially explained by differences in species-specific behavior. For example, a highly synchronized winter arrival of *Pipistrellus* was observed during the last and coldest study week in Anklam, thereby shifting the overall correlation. In addition, due to the collinearity between temperature and study week, the correlation between activity and temperature may also encompass temporal effects. It should be noted that given the lack of an independent temporal variable in the

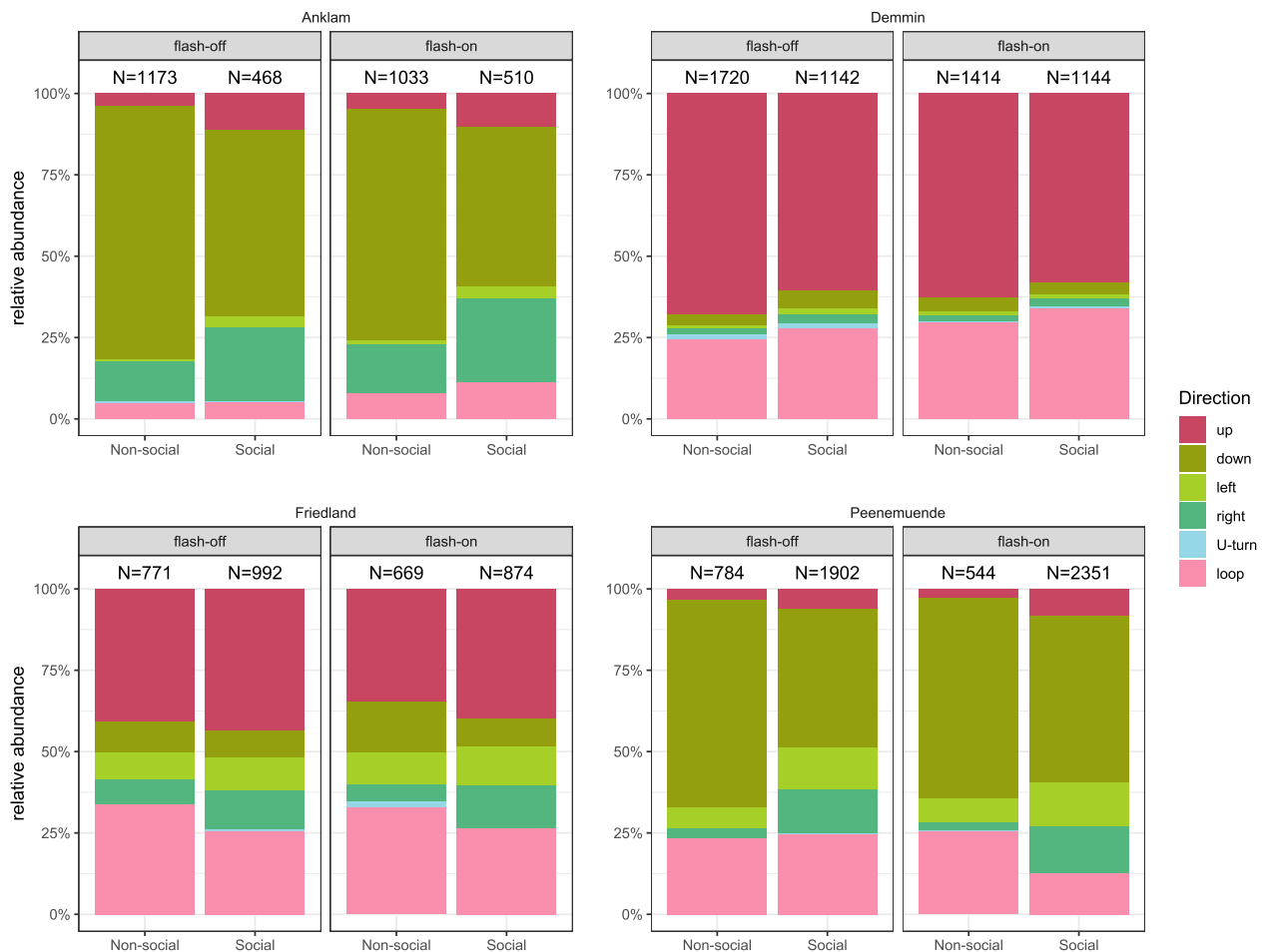
**Table 3.** Homogeneity of group dispersions of nightly flight direction totals (top) and non-parametric permutational ANOVA using Bray–Curtis dissimilarity matrices of nightly flight direction totals (bottom) between flash-on versus flash-off nights and social versus non-social events.

BETADISPERSION	Social		Flash	
	F-value	P-value	F-value	P-value
Site				
Anklam	0.02	0.896	2.79	0.107
Demmin	1.10	0.304	0.09	0.765
Friedland	0.76	0.391	0.02	0.896
Peenemuende	0.02	0.903	18.69	<b>&lt;0.001</b>

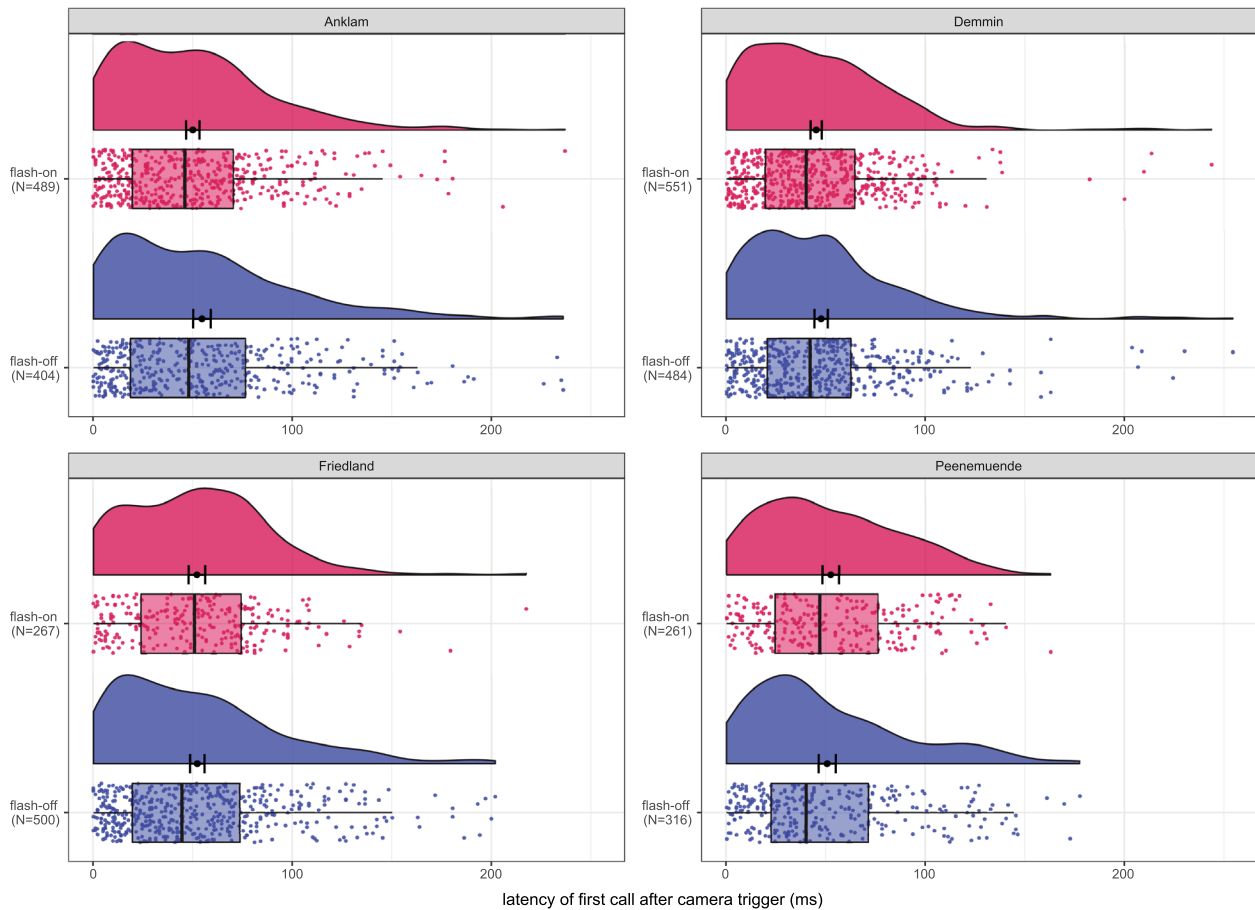
PERMANOVA	Social		Flash	
	R <sup>2</sup>	P-value	R <sup>2</sup>	P-value
Site				
Anklam	67.72	<b>&lt;0.001</b>	3.10	0.363
Demmin	24.55	<b>0.004</b>	5.60	0.530
Friedland	24.24	<b>0.003</b>	4.85	0.659
Peenemuende	78.12	<b>&lt;0.001</b>	4.24	0.068

All PERMANOVA were performed with 10<sup>4</sup> random permutations; a ‘*bonferroni*’ correction was applied to adjust P-values for multiple comparisons. Bold values indicate statistical significance at P < 0.05 level.



**Figure 2.** Proportion of social and non-social flight directions of bats entering four hibernation sites on flash-on and flash-off nights. Social events indicate the presence of other bats in the scored 6-second-long infrared video snips.





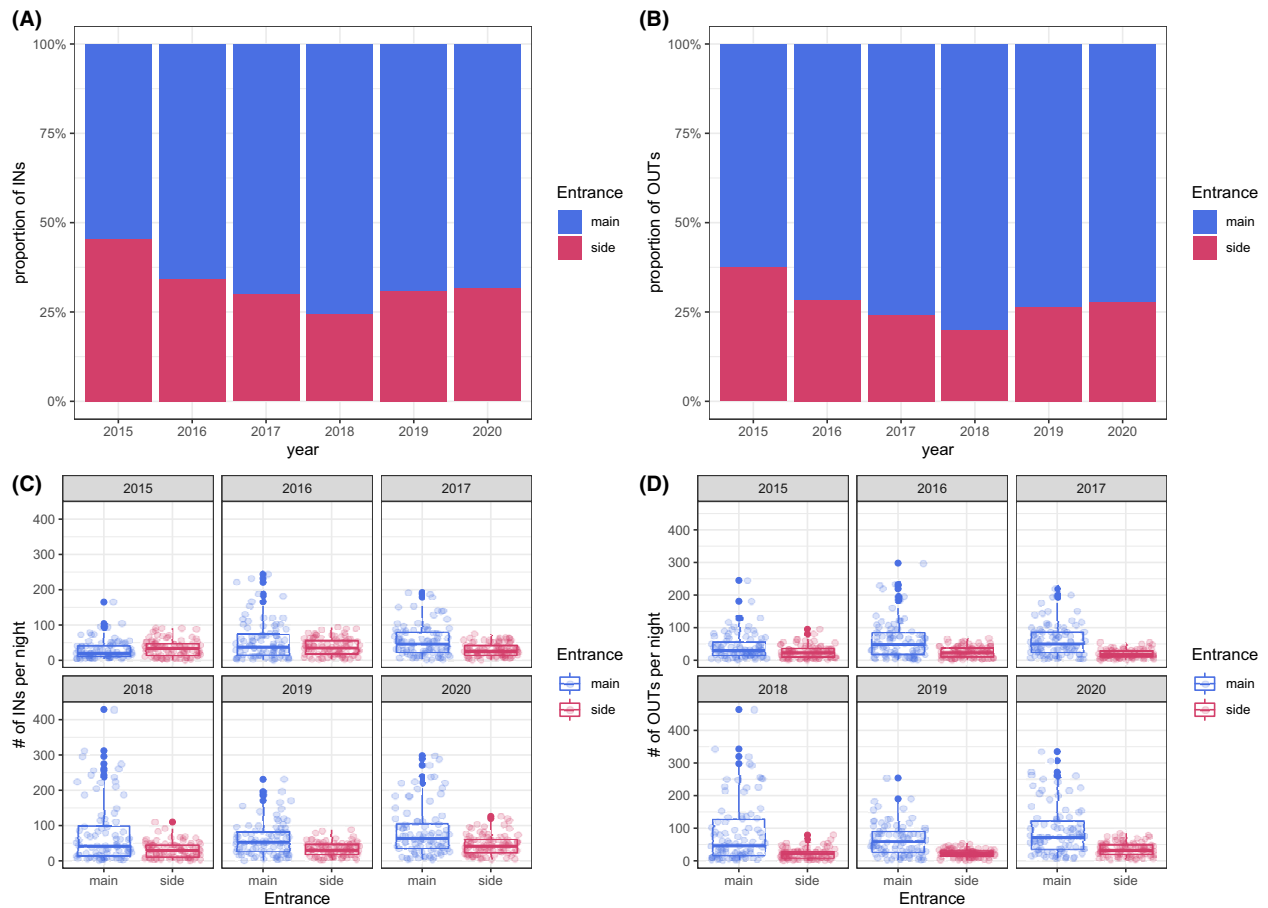
**Figure 3.** Comparison of latency of the first echolocation call after camera trigger in milliseconds between flash-on and flash-off nights. Mean values with 95% confidence intervals are indicated by black points and error bars.

activity model, we cannot exclude possible habituation effects, but critically, if individuals were to habituate, this would nevertheless yield reliable monitoring results.

As in the overall activity, flash had no effect on the flight direction of bats entering the hibernacula, but we did observe changes based on social context. The presence of other bats is expected to alter the flight behavior of bats, particularly during the swarming season when chasing behavior is common (Parsons et al., 2003). Although bats circling inside the hibernacula were excluded from the behavioral analyses, flash did not deter bats from doing innerloop ‘inspections’ prior leaving the hibernacula, indicating no substantial impact of flash on their natural behavior. All analyses were performed at the population level, and therefore rare individual reactions or aversions could go undetected. In this context, it is worth noting that the number of U-turns, expected to be the most extreme behavioral reaction of an individual, were exceptionally rare on flash-on nights at all sites (in total 30 U-turns out of 14 920 events across all sites).

Likewise, we observed no difference in first call latency after a camera trigger between flash-on and flash-off nights. Bats are capable of extremely fast reaction as echolocation allows for very short reaction times due to higher temporal processing of the auditory system. In fact, a behavioral startle response to a sudden acoustic cue can only take 20 ms (Geberl et al., 2015). Therefore, although we only measured latency of the first call, we expect that most bats entering the hibernacula had enough time to process the visual information of the flash before emitting their first echolocation call.

While vision may be more important for bats than previously supposed (Voigt et al., 2018), they certainly do not rely on it as heavily as other nocturnal mammals. Nevertheless, light stimuli can be highly disturbing to bats. For example, evidence from summer roosts suggest that constant illumination during emergence may cause bats to use alternative entrances if available, or in the worst case, bats may abandon the site (Stone et al., 2015). Although this experimental study was limited to a single



**Figure 4.** Proportion of bats (A) entering and (B) exiting the hibernaculum through the main entrance (with camera trap) and side entrance (without camera trap), and the total number of (C) 'in' events and (D) 'out' events per night registered by light barriers at the two entrances in Eldena between August and December from 2015 to 2020.

season, long-term winter census data from Eldena, where one entrance is monitored with a camera trap and the other only with a light barrier, showed no increasing preference for the entrance without flash, or decreasing trend in overall light barrier activity or hibernation census counts over the past 6 years. In addition, it is notable that the investigated hibernacula were dominated by *Myotis* species that are considered particularly light-averse (Voigt et al., 2018) and even low levels of constant light can disrupt their natural behavior (Azam et al., 2018; Zeale et al., 2018).

The discrepancy between these findings and the lack of an effect observed here can likely be explained by the comparatively weak (power 1/16) and short duration (1/5500 sec according to manufacturer specifications) of the flash. Similarly, white camera flash had no negative effect on other light-sensitive mammals (Heaslip & Hooker, 2008), in contrary with the negative impact of continuous illumination observed in several mammals. In this context,

it is important to note that our results may not be directly applicable to professional photography, where the use of full illumination or several synchronized flashes arranged around the camera should be carefully evaluated.

Finally, this study additionally highlights the potential of low-cost video cameras, built with off-the-shelf components, as a powerful monitoring tool (Droissart et al., 2021; Klemens et al., 2021; Wilkinson et al., 2021), particularly in conservation projects with limited budget. The self-built, Raspberry Pi-based infrared cameras used in this study can be adapted to a wide range of contexts with minimal technical and programming skills. Further technological improvements, combined with recent computer vision technologies for automated data processing, are expected to support the more widespread application of camera traps in monitoring and applied conservation of other threatened mammals (McCallum, 2013), particularly during times with restrictions on fieldwork activity (Blount et al., 2021).

## Conclusion

Our multi-faceted experimental design showed no change in overall bat activity, flight, or acoustic behavior when exposed to white camera trap flash. Thus, camera traps are a promising minimally invasive tool to monitor bat populations. While in rare cases individuals may still react adversely, the overall effect of the monitoring technique appears to be minimal at most, certainly when compared to the alternative of winter hibernation counts. To optimally take advantage of these new techniques, the accuracy of the species-specific monitoring achieved by the camera traps should be evaluated and compared to the data obtained through traditional techniques. The development and application of camera traps and other automated monitoring technologies can help advance our understanding of changing population trends, species composition, and phenology across a wide range of spatial-temporal scales and taxa. Understanding long-term population dynamics can inform conservation decision making, contribute to data-driven wildlife conservation and management, and help to better understand and tackle the global biodiversity crisis.

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## Data Availability Statement

Detailed instructions regarding the construction and configuration of the self-built infrared video cameras can be found at: <https://gabik-bat.github.io/FlederCam/>. All data and scripts used for statistical analyses are available at: <https://github.com/GabiK-bat/BatFlash>.

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## Supporting Information

Additional Supporting Information may be found online in the Supporting Information section at the end of the article.

**Figure S1.** Layout of the entrance and monitoring setup at four hibernation sites in (A) Anklam, (B) Demmin, (C) Friedland and (D) Peenemuende, indicating the light barrier model, width (W), height (H) and height above ground of the light barrier, height of the camera trap above ground and the width and height of the infrared video camera's field of view (FOV).

**Figure S2.** Comparison of infrared video-based (A) nightly bat activity on flash-on and flash-off nights, and the relationship between bat activity and (B) proportion of hours with rain per night between sunset and sunrise and (C) ambient temperature at sunset.

**Figure S3.** Power spectrum of the broad frequency range of species present at the study sites (35–65 kHz) and zoomed in view of the normalized amplitude of the typical trimodal intensity peaks of the camera trigger (red dashed lines) between 450 and 550 Hz (top).

**Table S1.** Results of the generalized linear mixed model showing the effect of the proportion of hours with rain between sunset and sunrise, ambient temperature at sunset and flash on infrared video-based nightly bat activity recorded at four hibernation sites in Northern Germany between August and December 2020.

**Table S2.** Social and non-social flight direction totals of bats entering hibernation sites on flash-on and flash-off nights based on infrared video snips.