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Multicopter-assisted acoustic surveys complement ground-based transects in assessing bat activity and species group composition

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We evaluated multicopter-based acoustic transects as a complement to traditional ground-based bat surveys, which cannot reach the airspace in which wind turbines operate. We compared species group composition and activity levels acoustically recorded along the same transect routes, surveyed simultaneously at ground level and at 104 m height with two multicopter types, across three habitat types (forest, meadow, and waterbody). Overall bat activity was almost eight times higher at ground level than at 104 m. Myotis species were virtually absent at 104 m, Pipistrelloid activity declined strongly with height, and Nyctaloid activity did not differ significantly between the two heights. Activity at 104 m was largely unrelated to the habitat structure at ground level. The two multicopter types did not differ in recorded activity when the recording device was positioned sufficiently below the multicopter and oriented away from it. Multicopter-based acoustic transects therefore extend the vertical reach of bat surveys into the risk area around wind turbine nacelles and can inform conservation and mitigation planning.

Keywords Transect survey, UAS, Bat, Multicopter

The continued expansion of wind energy infrastructure represents an increasing threat to bat populations, as documented by numerous mortality studies[1–5], and turbine-related fatalities may reduce population viability and elevate extinction risk[5]. Most bat species are insectivorous and prey on large numbers of insects[6,7]. Bats therefore play a substantial role in regulating insect populations and in maintaining ecosystem balance, and they also suppress agricultural pest species[7]. Bats have a low number of offspring[8], and all bat species in the European Union are listed in Annex IV of the Habitats Directive. In Germany, this strict protection is operationalised through the Federal Nature Conservation Act. Their protection status requires careful monitoring and consideration in impact assessment and project planning[9], which includes knowledge of how bats use the airspace in which wind turbines operate.

Bat conservation planning requires knowledge of site-specific species diversity, activity patterns and space use[10], which is obtained by combining several monitoring methods before wind turbines are constructed[9]. Mist netting is used to identify species[11], and tagging and telemetry are used to locate day and nursery roosts of specific species[12]. Mobile acoustic recordings along ground-based transects show activity levels, foraging habitats and species diversity[13], and stationary acoustic recording devices on the ground[14] or on meteorological masts[15] detect rare species and show activity patterns over longer time periods[16,17]. Mast monitoring before and nacelle monitoring after construction show which species might be threatened by wind turbines, but they cover only a small percentage of the rotor-swept area of large modern wind turbines[10]. All of these methods are tied to fixed locations or existing paths, and they therefore cannot adequately sample larger areas that are difficult to access[18] or located at greater heights, such as the airspace in which wind turbines operate.

Mobile acoustic transect surveys at ground level are particularly useful for identifying bat species and assessing their activity levels across large areas[16]. Because a single recording device passes through several potential foraging habitats, they also increase the likelihood of detecting species whose limited flight range confines them to small foraging habitats. When a vehicle travels at a minimum speed of 32 km/h to avoid repeated detections of the same individual, transect surveys can also be used to estimate population size[13]. However, such surveys depend on the availability of paths or roads, which makes some areas difficult or impossible to reach[18], and

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they are restricted to ground level and cannot sample the rotor-swept area of a wind turbine[16]. A cost-effective mobile approach capable of detecting bats in hard-to-reach areas and at greater heights is therefore needed, and Unmanned Aerial Systems (UAS) may represent a promising tool for this purpose.

The use of UAS for wildlife monitoring has increased gradually in recent years[19]. Several studies have explored the acoustic detection of bats using UAS. These studies focus on the associated technical and biological challenges[20–25]. Most of these studies have employed multicopter UAS, as they enable stable and stationary hovering and low-speed flight, which is advantageous for acoustic bat detection. A key technical challenge is the noise generated by the UAS, particularly by multicopters, which can interfere with the acoustic recording of the bat calls. This interference can be reduced by strategic positioning of the recording device[22,25]. Biological studies research the extent to which bats are frightened or attracted by the presence of UAS. The results of these studies indicate that quieter UAS are more suitable for recording bat calls, and that the Nyctaloid and sometimes Myotis echolocation groups are particularly adversely affected by the influence of the UAS emissions[20–22,26]. With appropriate recording device positioning, the bat calls recorded within the sampling area remain statistically unaffected, both technically and biologically by the operation of certain multicopters[22,23]. In addition to studies addressing the biological and technical challenges, a small number of studies has demonstrated the efficacy of UAS in detecting bat calls over heights of up to 60 m[23,27]. However, there remains a research gap, as the nacelle height of wind turbines typically ranges from approximately 80 m to over 200 m[28], placing the rotor-swept zone largely beyond the vertical coverage of existing UAS-based acoustic surveys. Consequently, mobile recording of bat calls within the risk zone for bats at wind turbines have not yet been collected, leaving this critical zone largely unexplored.

This study aims to assess the extent to which multicopter-based acoustic transect surveys can complement traditional ground-based transect methods, particularly in capturing vertical variation in bat activity and species group composition. Specifically, we compared traditional transect surveys with multicopter-based transect surveys conducted at the maximum permitted UAS flight altitude in Germany (120 m). Due to a 16 m separation between the recording device and the multicopter (see Methods), the effective recording height was 104 m. We then evaluated how habitat structure and multicopter type affected detection outcomes. Our first research question was: How do acoustically recorded bat activity levels and echolocation group composition differ between ground-based transect surveys and multicopter-based transect surveys conducted at 104 m height? We hypothesised that (1) echolocation group composition at 104 m height would predominantly consist of Nyctaloid and Pipistrelloid, and (2) that overall bat activity would be lower at 104 m than at ground level. This assumption is based on previous observations of vertical stratification in bat activity and strike records from wind turbines, which suggest that species from the Myotis echolocation group are less commonly detected at rotor height, whereas open-space foragers from the echolocation group of Nyctaloid or Pipistrelloid are more frequently observed aloft[12,29,30]. Our second research question examined: To what extent do ground-level habitat characteristics influence bat activity and species group composition at 104 m height? Given that several studies have reported highest bat activity levels in the vicinity of water bodies[31,32], we hypothesised that (3) bat activity at 104 m would likewise be highest over water, compared with forest or meadow, assuming that habitat effects extend vertically. The third research question was: To what extent does the type of multicopter affect the number of bat calls recorded, both at 104 m height and at ground level? Here, we hypothesised that (4) with sufficient distance and alignment of the recording devices from the multicopter, there would be no significant difference in the recorded activity values between the multicopter types, neither at a height of 104 m nor near the ground at a vertical distance of 120 m from the multicopter. This assumption is based on our pre studies findings that suggest that acoustic disturbances caused by multicopters can be effectively minimised through careful recording device positioning[22,26]. By addressing these research questions, we aimed to determine the extent to which multicopter-based acoustic transect surveys are suitable for generating robust data on bat activity patterns.

Results

A total of 87 transect surveys were conducted during the study period. Of these, 44 were carried out using the DJI Mavic 2 Pro and 43 using the ConVecDro multicopter. Of all surveys, 59 were carried out at Aileswasensee and 28 at Beutwangsee. The ambient temperature during the surveys ranged from a minimum of 16 C to a maximum of 24 C, with an average temperature of 21.3 C. In total, 14,549 one-second files were identified as containing bat calls from at least one bat species (Table 1). Altogether, 15 bat species belonging to three different echolocation groups were detected (Table 2).

	General activity level (n 1-second files)	
Echolocation group	Ground	104 m
Myotis	1,409	9
Nyctaloid	742	808
Pipistrelloid	10,770	811

Table 1. Distribution of bat activity by echolocation group and recording height, based on the number of one-second files with ≥1 call for the respective echolocation group.

Echolocation group	Myotis	Nyctaloid	Pipistrelloid
Bat species	*Myotis mystacinus/brandtii* *Myotis nattereri* *Myotis daubentonii* *Myotis bechsteinii* *Myotis myotis* *Plecotus auritus/austriacus*	*Nyctalus noctula* *Nyctalus leisleri* *Cnephaeus serotinus*	*Pipistrellus pygmaeus* *Pipistrellus nathusii/kuhlii* *Pipistrellus pipistrellus*

Table 2. Assignment of recorded bat species to echolocation groups based on acoustic call characteristics and foraging ecology.

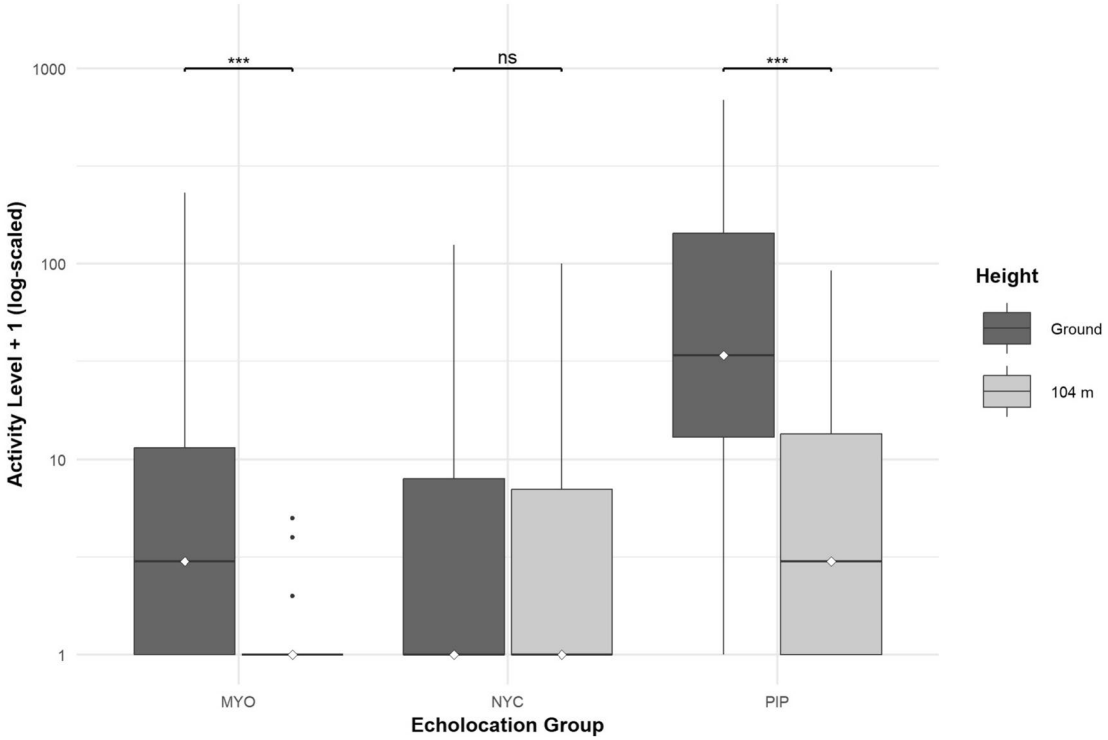


Fig. 1. Activity level (log-scaled number of one-second files containing echolocation calls) for each echolocation group (MYO = Myotis, NYC = Nyctaloid, PIP = Pipistrelloid) and recording height. Dark grey boxes represent ground-based recordings, and light grey boxes represent recordings at 104 m. Asterisks are used to indicate the significance levels of pairwise comparisons between heights within each echolocation group (*** $P < 0.001$; ns = not significant, $P \geq 0.05$). White diamonds mark the median of each box. In groups in which many surveys recorded no activity, the median lies on or close to the lower margin of the box.

Difference between bat activity levels at different recording height per echolocation groups

The generalised linear mixed-effects model (GLMM) (conditional $R^2 = 0.76$) showed a highly significant interaction between echolocation group and recording height ($P < 0.001$), indicating that the relationship between activity levels and height varies by echolocation group. Subsequent post hoc pairwise comparisons using the Tukey correction method showed that bat activity was significantly higher at ground level than at 104 m for the Myotis group ($P < 0.001$, Fig. 1, Supplementary Table 1) and the Pipistrelloid group ($P < 0.001$, Supplementary Table 1). For the Nyctaloid group, activity did not differ significantly between ground and multicopter-based recordings ($P \geq 0.05$).

Comparison between the recorded bat activity levels at different habitats

With regard to research question 2, which examined to what extent ground-level habitat characteristics influence bat activity at 104 m, the two separate GLMMs fitted to the ground-based and multicopter-based datasets showed different habitat-related activity patterns across echolocation groups. The ground-based GLMM indicated that bat activity differed among habitat types (forest, meadow, and waterbody) for most pairwise comparisons when analysed separately within each echolocation group (conditional $R^2 = 0.73$, $P < 0.001$) (Fig. 2, Supplementary Table 2). Post hoc Tukey-adjusted pairwise comparisons showed significant differences across all habitat types for the Myotis group, with activity being significantly higher in meadow than in forest ($P < 0.01$), significantly higher over waterbodies than in forest ($P < 0.001$), and significantly higher over waterbodies than in meadow ($P < 0.01$). Pipistrelloids exhibited highly significant differences between meadow and waterbody as well as

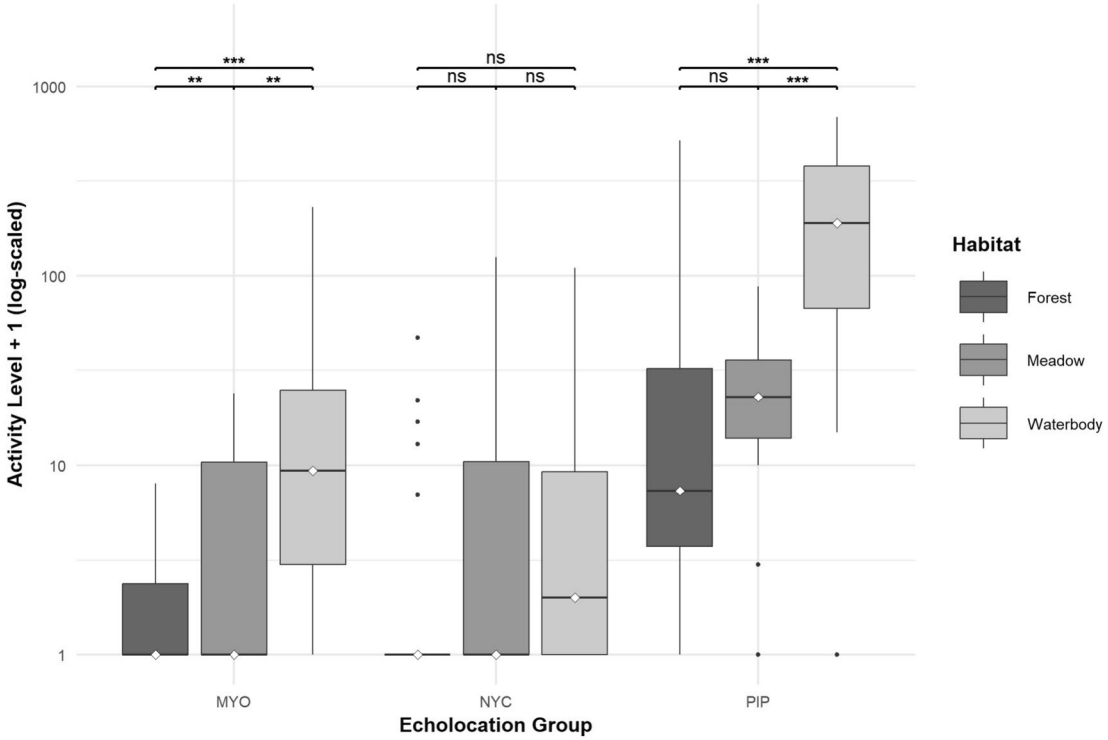


Fig. 2. Effect of habitat type on bat activity across echolocation groups (MYO = Myotis, NYC = Nyctaloid, PIP = Pipistrelloid) at ground level. Activity is log-scaled. Post hoc pairwise comparisons (Tukey-adjusted) are indicated (ns = not significant, $P \geq 0.05$; ** $P < 0.01$; *** $P < 0.001$). Each box is based on aggregated observations, with sample sizes per habitat of $n = 24$ for forest, $n = 27$ for meadow, and $n = 36$ for waterbody within each echolocation group. White diamonds mark the median of each box. In groups in which many surveys recorded no activity, the median lies on or close to the lower margin of the box.

between forest and waterbody, with activity being significantly higher over waterbodies in both cases ($P < 0.001$, respectively), but no significant difference between forest and meadow ($P \geq 0.05$). For the Nyctaloid group, no significant differences were found among habitat types at ground level ($P \geq 0.05$, respectively). In general, the activity levels of Myotis and Pipistrelloid echolocation groups on the ground were highest near waterbodies, particularly in the case of the Myotis group (Fig. 2). Nyctaloids showed a non-significant tendency towards lower activity in forest habitats, but habitat differences were not statistically significant for this group (Fig. 2).

At 104 m, Myotis activity was nearly absent across habitats and was therefore excluded from habitat-specific post hoc analyses. In the reduced GLMM for data at 104 m (conditional $R^2 = 0.63$), no significant habitat-related differences were detected for either the Nyctaloid or the Pipistrelloid group ($P \geq 0.05$, Fig. 3, Supplementary Table 2).

Comparison between the recorded bat activity levels from two multicopters

The third research question investigated potential disparities in bat activity levels between the two distinct multicopter types used during the acoustic monitoring flights for both recorded heights. The findings demonstrated no statistically significant differences in bat activity between the ConVecDro and the DJI Mavic 2 Pro at either height ($P \geq 0.05$, Fig. 4).

Discussion

Our results show that multicopter-assisted acoustic surveys recorded bat activity at 104 m, a height that ground-based transect surveys cannot sample, and that this activity consisted almost entirely of Nyctaloid and Pipistrelloid bats, whereas Myotis activity remained confined to ground level. Multicopter-assisted acoustic surveys therefore provide a valuable complementary method for detecting bats at greater heights and add value for sampling higher airspace that cannot be covered by conventional ground-based approaches.

Activity at 104 m was dominated by Nyctaloid and Pipistrelloid species and Myotis species were virtually absent, in line with assumption (1). This pattern aligns with previously described vertical stratification in bat communities, where Myotis species are known to forage near vegetation or close to the ground, reflecting their clutter-adapted foraging strategy[29,33]. In contrast, Nyctaloid bats are adapted to foraging in open airspaces and frequently use higher airspace[29]. Although pipistrelle bats are generally considered to be edge-space foragers, typically hunting along vegetation edges and other clutter boundaries, they are occasionally observed at higher heights[29,33]. However, their activity declines strongly with increasing height[30]. Nevertheless, their overall

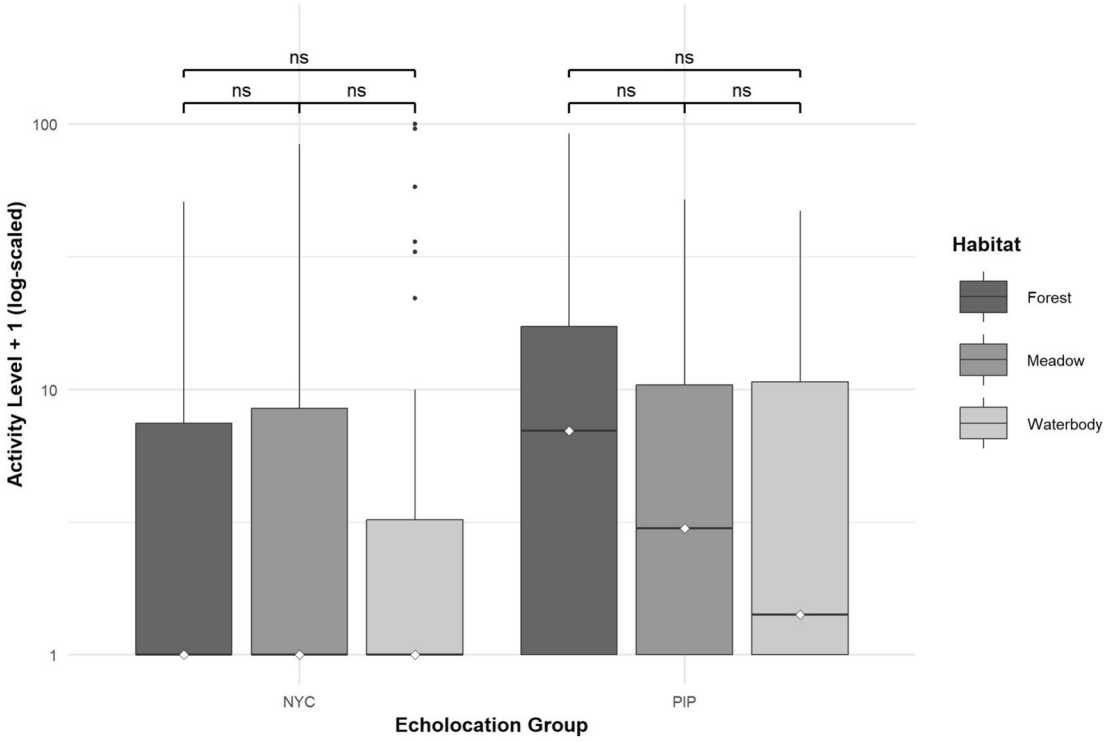


Fig. 3. Effect of habitat type on bat activity across echolocation groups (NYC = Nyctaloid, PIP = Pipistrelloid) at 104 m recording height. Activity is log-scaled. Post-hoc pairwise comparisons (Tukey-adjusted) are indicated (ns = not significant, $P \geq 0.05$). Each box is based on aggregated observations, with sample sizes per habitat of $n = 24$ for forest, $n = 27$ for meadow, and $n = 36$ for waterbody within each echolocation group. White diamonds mark the median of each box. In groups in which many surveys recorded no activity, the median lies on or close to the lower margin of the box.

numerical dominance in the bat community may explain why Pipistrelloid bats were still recorded regularly at 104 m.

Our assumption (2) of lower overall bat activity at 104 m was confirmed. Across all echolocation groups, we recorded 12,921 one-second files at ground level and 1,628 at 104 m, almost eight times as many at ground level (Table 1). While Myotis and Pipistrelloid activity declined strongly with height, Nyctaloid activity did not differ significantly between ground level and 104 m. This result can also be attributed to the differing foraging strategies and flight behaviours among echolocation groups. Nyctaloids are aerial hawkers specialised for fast, long-distance flight in uncluttered habitats and often use open airspace well above canopy height at 100 m and higher[34]. Myotis species, by contrast, exhibit gleaning behaviours and rely on cluttered habitats near the ground or water bodies, making high-height detection unlikely[29].

These patterns are also evident in call structure: Nyctaloids emit low-frequency, long-duration calls suited for long-range detection in open spaces, while Myotis species use high-frequency, short-duration calls ideal for cluttered environment[33,35]. Consequently, both habitat use and signal adaptation provide a comprehensive explanation for the stratified activity levels observed at varying heights.

These differences in call structure also affect how well each echolocation group is detected. The distance over which a call can be recorded depends on its peak frequency, its source level and its duration. Nyctaloids emit loud, long and low-frequency calls and are therefore detected over greater distances than Myotis species, whose calls are shorter and lower in intensity and whose broadband sweeps carry little energy in the lower part of the frequency range[10,16]. The three echolocation groups were consequently not sampled with the same detection space. All statistical comparisons reported here were computed within echolocation groups, so this difference does not affect the height- and habitat-related contrasts, and the recorded activity cannot be compared between the three echolocation groups. Detection space also differs between habitats and recording heights, because vegetation attenuates and masks calls at ground level, whereas the recording device at 104 m operated in open airspace. Correcting for this would require species-specific detection distances measured under field conditions, which we did not determine. The recorded activity is therefore not corrected for differences in detection space. The near-complete absence of the Myotis group at 104 m is nonetheless unlikely to be a detection artefact, because at this height the recording device operated without surrounding vegetation and thus under conditions that favour detection rather than reduce it.

The results obtained from this study demonstrate significant habitat-specific variation in bat activity at ground level for the Myotis and Pipistrelloid groups, which corresponded to the foraging strategies, flight behaviour and echolocation call structures described for these groups.

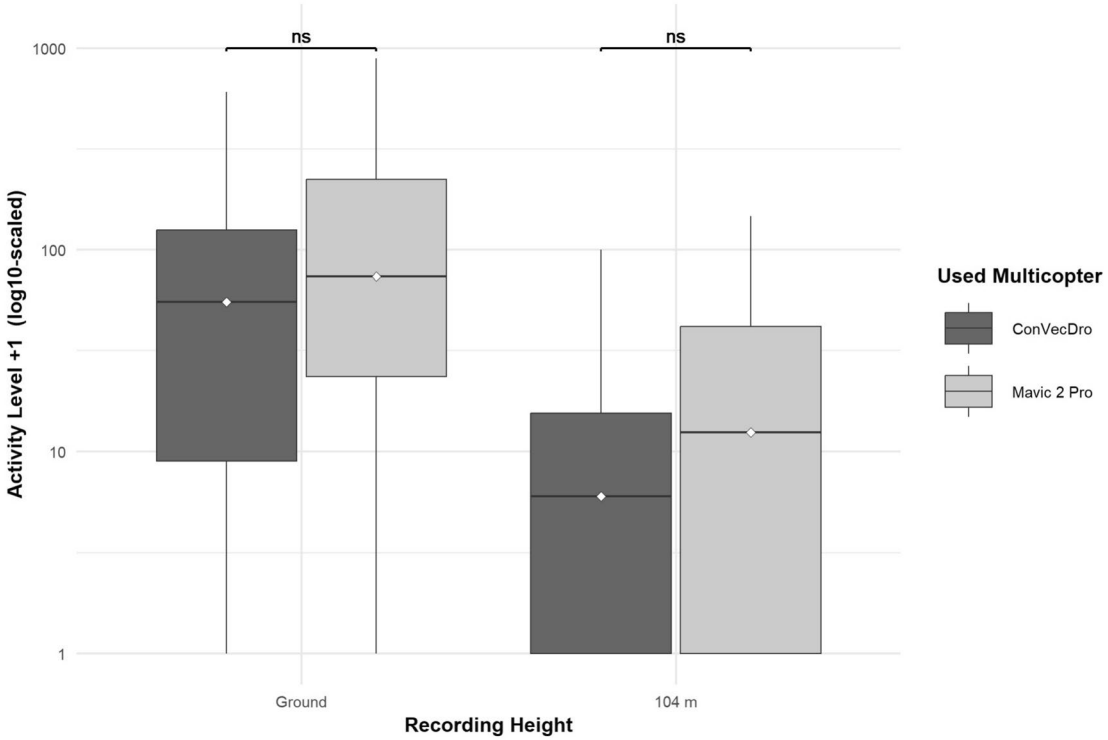


Fig. 4. Comparison of bat activity levels recorded by two different multicopter types (ConVecDro and DJI Mavic 2 Pro) at ground level (left) and at a height of 104 m (right). Each boxplot represents the distribution of acoustically detected bat activity (log-scaled number of one-second files containing echolocation calls) per flight. Sample sizes were $n = 43$ for ConVecDro and $n = 44$ for DJI Mavic 2 Pro at each recording height. No statistically significant differences were found between the two multicopter types at either height (ns = not significant, $P \geq 0.05$). White diamonds mark the median of each box. In groups in which many surveys recorded no activity, the median lies on or close to the lower margin of the box.

At ground level, Myotis activity differed significantly between all three habitat types. It was highest over waterbodies, intermediate in meadow, and lowest in forest. Myotis species are frequently categorised as forest specialists, but they have also been observed to forage along riparian corridors and water edges, particularly species such as *Myotis daubentonii*[12,31], which hunts low over the water surface. Aquatic insects such as chironomids emerge from the water and concentrate above it, so that waterbodies provide a reliable food supply for these species. The elevated activity levels observed in meadow habitats in the present study stand in contrast to the findings of several studies which describe *Myotis myotis* and *M. mystacinus* as predominantly forest-dwelling species[29,36]. A plausible explanation for the observed phenomenon can be found in the structure of the habitat. The meadow transects were situated in close proximity to both water and forest habitats, which may have functioned as transitional zones, thereby capturing spillover activity. Furthermore, the lower intensity and broader bandwidth of Myotis echolocation calls renders them more susceptible to acoustic attenuation and masking by vegetation, which may result in under-detection in forest interiors compared to more open meadows. The impact of acoustic attenuation and masking is found to be considerably less pronounced in the case of Pipistrelloid and Nyctaloid species.

Our results for the Pipistrelloid group demonstrated a marked increase in activity at water bodies and intermediate levels in forest and meadow habitats. Whilst some studies describe Pipistrelloid bats as edge-space foragers utilising both woodland margins and aquatic habitats[37], our findings suggest that their activity is not significantly different between forest and meadow at ground level. The documented evidence, which is supported by empirical observation, indicates that Pipistrelloid bats exhibit a high degree of versatility in their utilisation of diverse structural elements, with a particular predilection for those in proximity to waterbodies.

For Nyctaloid bats, habitat differences at ground level were not statistically significant, although activity tended to be lowest in forest habitats. In line with previous studies, this pattern suggests that Nyctaloid bats such as *Nyctalus noctula* and *Nyctalus leisleri* are less associated with closed or densely structured forest habitats and, owing to their quasi-constant frequency echolocation calls, are better adapted to foraging in more open habitats[34,35,38]. It also shows that, unlike the Myotis and Pipistrelloid groups, Nyctaloids did not exhibit a clear preference for waterbodies over meadows at ground level. One possible explanation is that part of the recorded activity may be attributable to species such as *Cnephaeus serotinus* (formerly *Eptesicus serotinus*)[39], which are known to use open woodland and edge habitats and are not strongly associated with waterbodies[37].

In contrast to ground-based recordings, habitat-related differences in bat activity at 104 m were weak overall. Myotis activity was nearly absent across all habitats at this height and could therefore not be evaluated robustly

in the multicopter-based habitat model. This reinforces the classification of Myotis species as clutter-adapted forest foragers that do not use open airspace at high elevations[12,36]. For the Nyctaloid and the Pipistrelloid group, which were both recorded at 104 m, no significant habitat-related differences were detected. Activity at this height was therefore not related to the ground-level habitat.

The initial hypothesis proposed that bat activity would be most prevalent over waterbodies at ground level and at 104 m, with Nyctaloids predicted to predominate in high-height environments. Our results provide partial support. Pipistrelloid bats showed significantly higher activity in proximity to waterbodies at ground level, whereas Myotis species were notably absent from higher elevations. Nyctaloids, however, did not show a direct preference for waterbodies. At ground level their activity was significantly lower in forest than in meadow and waterbody habitats, which did not differ from each other, and at 104 m no habitat-related contrasts were detected for either group. We did not classify the recorded calls by function, for example as mating calls or feeding buzzes, and therefore report these patterns as associations rather than as evidence for a particular behaviour.

A limitation of the habitat comparison is that the three habitat transects within each study site were located in close proximity to one another. We therefore cannot exclude that bats of an adjacent habitat were recorded on a given transect, which does not require an individual to have moved between habitats. However, we quantified bat activity as an acoustic activity index, that is, the number of one-second files containing identified calls per echolocation group, rather than as a count of individuals, so that the analysis does not assume that recordings represent independent individuals. To account for the non-independence of the three habitat transects sampled within the same night and study site, we included habitat as a nested random effect within the combination of study site, survey night, and multicopter type. The habitat-related patterns for the Myotis and Pipistrelloid groups remained unchanged under this structure, which shows that they do not depend on how the transects surveyed within one night are treated in the model. Recording bats of a neighbouring habitat makes the recorded activity of the three habitat types more similar to one another, so this mechanism can weaken a habitat difference but cannot create one. The differences we detected for the Myotis and Pipistrelloid groups are therefore conservative, and transects placed further apart would be expected to produce larger rather than smaller contrasts. The habitat differences we detected for the Myotis and Pipistrelloid groups correspond to the foraging strategies, flight behaviour and echolocation call structures discussed above, which supports an ecological interpretation rather than an effect of the transect layout. Where we detected no habitat-related differences, as for the Nyctaloid group at ground level, the same mechanism may have masked a difference, and we therefore do not interpret this result as evidence that habitat use does not differ. We interpret the habitat-related results as patterns of recorded activity and habitat use rather than as estimates of independent abundance, and we recommend spatially more separated transects in future studies.

The surveys covered 18 nights between 6 June and 11 August 2024, that is, lactation and the post-lactation phase when juveniles become volant. They did not cover the spring period after hibernation or the autumn migration and mating period, during which the requirements of the species and the proportion of high-flying individuals may differ. Our results therefore describe this part of the activity season only.

In line with hypothesis 4), which stated that the two multicopter types would not differ in recorded activity as long as the recording device was mounted at sufficient distance and alignment from the multicopter, bat activity did not differ significantly between the DJI Mavic 2 Pro and the ConVecDro under optimised recording conditions, that is, with the recording device suspended 16 m below the multicopter on a nylon cord and oriented away from it. These findings suggest that, under these conditions, the two multicopter types did not differ detectably in their influence on acoustic bat detection.

Previous studies indicate that reduced acoustically detected bat activity occurs primarily when recording devices are placed too close to the multicopter and oriented towards it. Reduced activity relative to negative controls has been reported at 5–10 m[20], 15 m[21], and 20 m[22], depending on multicopter type and noise emission. In a companion study, we derived multicopter-specific minimum distances from the noise profile of each multicopter and from the sound levels at the peak frequencies of the echolocation calls. For a recording device oriented towards the multicopter, this yielded 20 m for the DJI Mavic 2 Pro and an extrapolated 36 m for the louder ConVecDro, and orienting the recording device away from the multicopter allowed shorter distances[26]. Together, these studies underline the importance of the recording device distance and orientation in minimising interference.

Our transect surveys did not include a negative control without a multicopter, so the absence of a difference between the two multicopter types cannot be interpreted as an absence of a multicopter effect on bat activity. Because a multicopter was in the air during every survey at 104 m height, we cannot exclude that its presence and noise affected bat activity itself. Two companion studies did include such a control at ground level, where the same positions were recorded with and without a multicopter present[22,26]. Multicopter presence reduced recorded bat activity, most strongly for the Nyctaloid group and more strongly for the louder ConVecDro, and the effect decreased with increasing distance and when the recording device faced away from the multicopter. We suspended the recording device 16 m below the multicopter and oriented it away from the noise source. This distance is shorter than the distances derived for a recording device facing towards the multicopter, and although the away-facing orientation permits a shorter distance, the corresponding value was not quantified, so a residual effect at 16 m cannot be ruled out. The comparison between the two multicopter types speaks against a pronounced effect, because the ConVecDro showed the stronger deterrence in the companion studies and recorded activity did not differ between the two multicopter types in our surveys. At ground level, the remaining effect can be quantified directly by surveying a transect without a multicopter and repeating it immediately afterwards with one. At 104 m height, a negative control is not attainable with a mobile survey, because the recording device can only be brought to that height by a multicopter, and it would require a stationary elevated platform such as a meteorological mast.

Our surveys covered a height of 104 m, which lies within the rotor-swept zone of tall wind turbines, reported to extend from about 50 m to 150 m above ground level[40]. We therefore sampled the lower to middle part of the zone in which bats are at risk, but not its upper part. In the open category, EU and German regulations limit UAS operations to 120 m above ground level, and this limit may be exceeded only within a horizontal distance of 50 m from an artificial obstacle taller than 105 m and with the consent of the entity responsible for it[41]. This exception does not apply to surveys carried out before construction, which is the stage at which activity data are needed for siting decisions. Partial vertical coverage is not unusual in this field, because nacelle-based acoustic monitoring also samples only a part of the rotor-swept zone and estimates activity in the remaining part from reference studies that covered the entire zone[42]. The same principle could be applied to our data in combination with studies conducted at greater heights. Direct recordings in the upper rotor-swept zone would nonetheless provide a more complete picture, and we therefore argue that exemptions from the 120 m limit should be made accessible for wildlife monitoring, particularly as turbine dimensions continue to increase.

This study demonstrated that multicopter-based acoustic surveys provide a valuable complement to traditional ground-based transect methods. In particular, they allow access to elevated airspace, in which bat activity was largely unrelated to ground-level habitat structure, such as forests, meadows, or waterbodies, and which cannot be assessed using traditional ground-based surveys. Our results show that this upper airspace is primarily used by Nyctaloid and Pipistrelloid bat species. This finding underscores the increased vulnerability of species belonging to these groups to wind energy infrastructure operating at similar heights. In contrast, Myotis activity remains confined to near-ground habitats. Furthermore, the recorded bat activity did not differ between the two multicopter types when the recording device was positioned sufficiently below the multicopter and oriented away from it. As such, multicopter-assisted acoustic bat monitoring offers a practical and reliable tool complementing bat transect surveys at different heights and above hard-to-access habitat, especially in bat conservation at wind energy projects. Additonally, it enables acoustic sampling directly above forest canopies, which is currently not feasible with conventional monitoring methods. As wind energy continues to expand in response to the increasing demand for renewable energy, monitoring that also covers the airspace in which turbines operate will become more important for reconciling this expansion with bat conservation.i

Methods

Approval

The study was approved by Ethics Committee of the University of Applied Sciences Hamburg prior to the start. Each flight was operated in the open category and was supervised throughout by a licensed pilot (e-ID = DEU48hakpl6va5su), who monitored the programmed flight and was able to take over manual control at any time. All flights were conducted at or below 120 m above ground level (AGL), which is the general maximum 'open' category in the EU and in Germany. Study sites were public and unprotected areas for which the survey was agreed without the need of any permits by the respective town (City of Nürtingen, municipalities of Neckartailfingen). Furthermore, we considered the national animal and nature protection law and involved the relevant nature conservation authority, in this case the Nature Conservation Authority of the Esslingen District, which gave its unreserved approval. All surveys took place after sunset. Operations at night are permitted in the open category without a separate authorisation[41], and the approval of the nature conservation authority covered the possible disturbance of animals during these flights.

General information

We conducted the study in southern Germany in 2024. We used April and May to establish the technical setup and the survey protocol. The transect surveys that entered the analysis were carried out on 18 survey nights between 6 June and 11 August 2024. Field surveys began approximately 30 minutes after sunset and lasted up to a maximum of four hours after sunset. We carried out all surveys under bat-friendly conditions: wind speeds below 10 km/h, temperatures above 10 C, and no rain.

Selection of study sites

To select appropriate study sites, we identified two sites that had shown high bat activity and species richness in previous years. In addition, we ensured that each site provided access to three nearby transects representing different habitat types: waterbodies, meadow, and forest. Forest transects were selected within structurally rich woodland, including canopy gaps, natural clearings and forest edges, with the aim of facilitating ground-based acoustic surveys on foot. Based on these criteria, we selected the areas Aileswasensee (48 36'N, 9 15'E; Fig. 5A) and Beutwangsee (48 36'N, 9 18'E; Fig. 5B). Previous studies[22] had already documented high bat activity at these locations, which made them suitable for our research objectives.

Each study site contained three fixed transects representing different habitat types – meadow, forest, and water bodies. Each transect was surveyed repeatedly at a walking speed of 0.7 m/s for 15 minutes, so that every survey covered 630 m. Where the mapped path was shorter, we turned at its end and walked back, so starting points varied between surveys. The multicopter followed the same transect route directly above the surveyor on the ground. We planned each route in advance as a sequence of waypoints and uploaded it to the multicopter, which then flew the route automatically at a speed of 0.7 m/s. This speed corresponds to a slow walking pace and matched the speed of the ground-based transect survey, so that the multicopter-based and the ground-based survey covered an identical route of 630 m over the same 15 minutes. We used the same waypoint procedure for both multicopter types. We started both acoustic recording devices at the same time and stopped them simultaneously when the multicopter landed at the end of the route, which corresponded to the flight endurance of one battery charge. Survey duration was therefore identical for the ground-based and the multicopter-based recording of every transect.

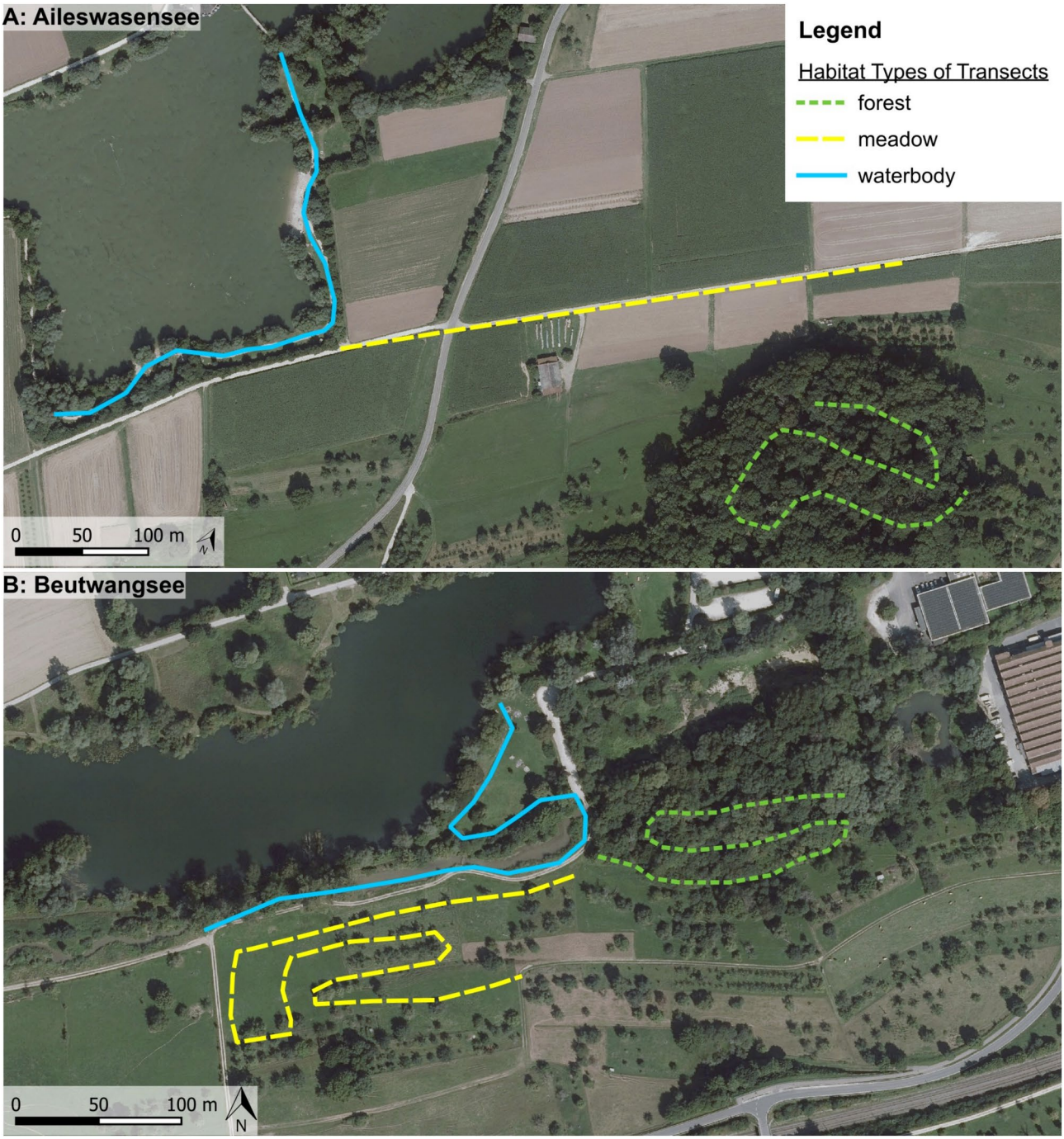


Fig. 5. Overview of the study sites at Aileswasensee (**A**) and Beutwangsee (**B**). Transects are coloured by habitat type: blue for waterbodies, yellow for meadow, and green for forest. We created the map with QGIS 3.44.13 (https://qgis.org). Data source of the aerial imagery: LGL Baden-Württemberg, www.lgl-bw.de, licensed under the Data licence Germany – attribution – version 2.0, dl-de/by-2-0 (https://www.govdata.de/dl-de/by-2-0).

In previous studies, we were able to detect almost all species native to Germany at these sites: whiskered/brandt's bat (*Myotis mystacinus/brandtii*), natterer's bat (*Myotis nattereri*), serotine bat (*Cnephaeus serotinus*), common noctule (*Nyctalus noctula*), leisler's bat (*Nyctalus leisleri*), brown/grey long-eared bat (*Plecotus auritus/austriacus*), soprano pipistrelle (*Pipistrellus pygmaeus*), nathusius'/kuhl's pipistrelle (*Pipistrellus nathusii/kuhlii*), daubenton's bat (*Myotis daubentonii*), and common pipistrelle (*Pipistrellus pipistrellus*).

In accordance with previous studies[22], we grouped recorded bat species into three echolocation groups, Myotis, Nyctaloid, and Pipistrelloid, based on their call characteristics and foraging strategies (Table 2). In this way, we minimised misclassification errors that are common in acoustic surveys while ensuring sufficient

sample sizes for robust analysis. These group names denote acoustic groups and not taxonomic units. The Myotis group also included the two *Plecotus* species, which we pooled with *Myotis* because of their similar low-intensity broadband calls, and the Pipistrelloid group included only species of the genus *Pipistrellus*, because *Hypsugo savii* was not recorded at our study sites. Species whose ordinary echolocation calls overlap too strongly to be separated reliably were treated as a single category throughout the analysis[16,35]. This applied to *Pipistrellus nathusii* and *P. kuhlii*, to *Myotis mystacinus* and *M. brandtii*, and to the two *Plecotus* species, for which a species-level assignment would have required diagnostic social calls. Because we carried out all analyses at the level of the echolocation group, this pooling did not affect the results. Throughout the manuscript we set the genus name in italics where we refer to the genus *Myotis*, and upright where we refer to the acoustic group of that name.

Multicopter selection and used materials

We used two multicopters for our surveys: the ConVecDro (Third Element Aviation GmbH[43]) and the DJI Mavic 2 Pro (SZ DJI Technology Co., Ltd.[44]; full specifications in Table 3). The ConVecDro was fitted with light- and noise-reducing modifications and operated with EN4709-004-compliant lighting (green beacon plus red/green position lights), whereas the Mavic 2 Pro used its integrated navigation lights and auxiliary light. Under the study payload, typical endurance was 20 minutes for the ConVecDro and 15 minutes for the Mavic 2 Pro.

Both multicopters had been tested in previous studies and showed promising results with regard to potential deterrent effects[21,22]. Both multicopters were expected to have only a limited effect on bat behaviour in the recording zone 16 m below, with the recording direction oriented away from the multicopter.

Test setup and data collection

In line with previous studies regarding recommendations to minimise the impact of recorded bat activity, we positioned the ultrasonic acoustic recording device 16 m below the multicopter using a nylon cord, orienting the acoustic recording device away from the multicopter (Fig. 6). This distance was a compromise between two requirements. A larger separation moves the recording area further away from the multicopter and thereby reduces its influence on the recorded bat activity, which decreases with distance and is smaller again when the recording device faces away from the multicopter[20–22]. Suspending the recording device further below the multicopter on a cord, however, impaired flight stability in internal tests. We therefore selected the largest separation that still allowed stable flight. We used an Echo Meter Touch 2 Pro acoustic recording device connected to an Android smartphone to record bat calls from the multicopter at 104 m height and during ground-based transect surveys, owing to its favourable recording characteristics at low mass, which has supported its use in prior multicopter-based bat acoustic studies[20,21]. We selected the Caterpillar S62 Pro smartphone as the multicopter payload due to its robustness. Additionally, we protected the smartphone with a silicone case and securely attached the Echo Meter Touch 2 Pro to the smartphone using adhesive tape.

Data analysis and statistics

All recording data were split into files with a length of one second and analysed manually on species level using Kaleidoscope Pro (Wildlife Acoustics) and assigned to the respective echolocation group. We used one-second files as the unit of bat activity, as in our previous studies on multicopter-based bat recordings[22,26]. Counting individual calls instead would give more weight to species and situations with high call rates. Bats foraging close to vegetation, such as Myotis species, emit short calls at short intervals, whereas open-space foragers such as Nyctaloid bats emit longer calls at longer intervals[33,35]. A call count would therefore inflate activity near vegetation and at ground level relative to open airspace and 104 m. A one-second file is counted once, regardless of how many calls it contains, which reduces this bias. We calculated bat activity by summarising one-second files recorded for every echolocation group per habitat type, day, recording height and study site. Because the ground-based and the multicopter-based survey of a given transect ran simultaneously and over the same fixed duration, survey effort was constant across recording heights, habitat types and study sites. Bat activity therefore represents the activity recorded per standardised transect survey, and we did not include survey duration as an offset or covariate in the models.

All statistical analyses were conducted in R 4.6.1. To address the first research question on how bat activity levels and species group composition differ between ground-based and multicopter-based acoustic transect surveys at 104 m height, we modelled the acoustically recorded bat activity using a generalised linear mixed-effects model (GLMM) with a negative binomial distribution (nbinom2) and a log-link function, fitted with the glmmTMB package version 1.1.14[45]. We used a negative binomial rather than a Poisson distribution because the activity counts were strongly overdispersed, which renders Poisson-based inference anti-conservative[46]. Fixed effects included the interaction between bat echolocation group (three levels: Myotis, Nyctaloid, Pipistrelloid), recording height (two levels: ground, 104 m), and the type of multicopter used (two levels: ConVecDro, DJI Mavic 2 Pro). A composite identifier, combining study sites, survey night, multicopter type, and habitat, was included as a random intercept to account for repeated measurements and nested data structure. Where the same habitat was surveyed more than once within a night, each survey was treated as a separate unit. Significant main effects and interactions were assessed using estimated marginal means (via the emmeans package version

Multicopter model	Mass [g]	Dimensions (L × W × H) [mm]	Max flight time (without payload) [min]	Max wind resistance [m/s]
DJI Mavic 2 Pro	907	322 × 232 × 84	24	8–10.5
ConVecDro	5000	1430 × 1430 × 530	30	15

Table 3. Technical data for the multicopters used.

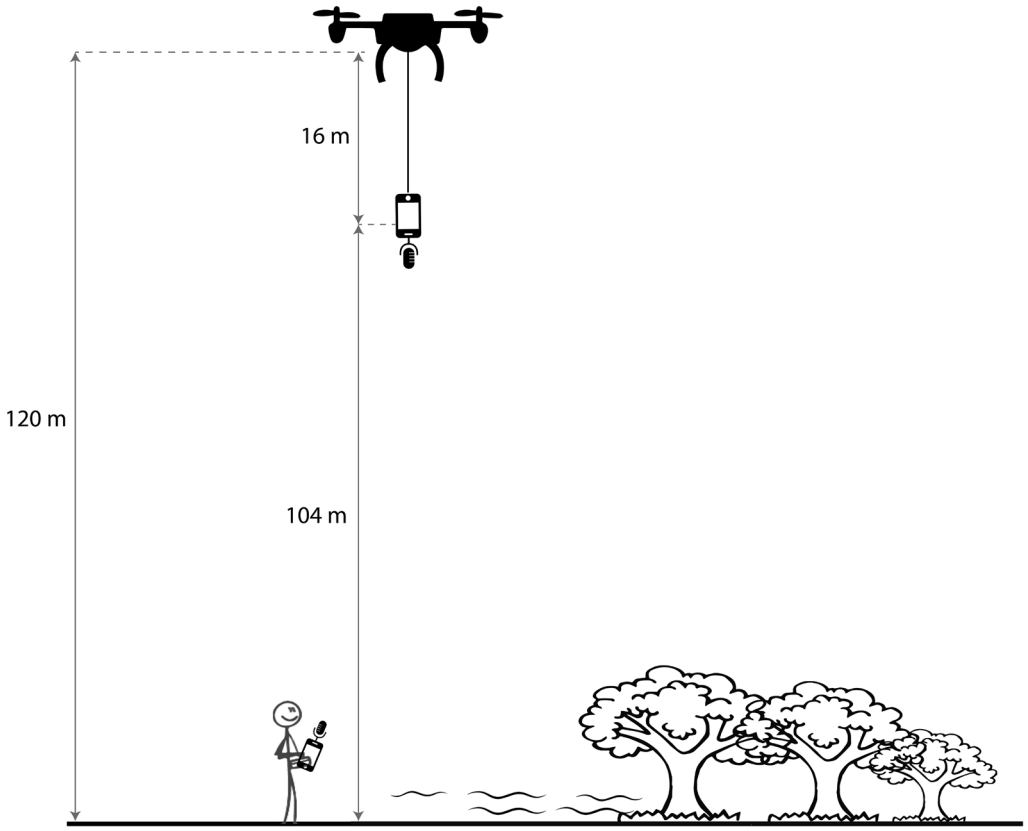


Fig. 6. Schematic test setup: Recording with a multicopter (flight at 120 m height) and an ultrasonic acoustic recording device (Echo Meter Touch 2 Pro) 16 m downfacing under the multicopter. Leads to a recording height of 104 m. Simultaneously recording by walking with an acoustic recording device (Echo Meter Touch 2 Pro) on the ground.

2.0.4), with Tukey's correction applied for multiple comparisons. Marginal and conditional R^2 values were calculated for all fitted GLMMs to assess model fit.

To address the second research question – to what extent ground-level habitat characteristics influence bat activity levels and species group composition at a height of 104 m – we fitted separate generalised linear mixed-effects models (GLMMs) with a negative binomial distribution (nbinom2) and a log-link function (glmmTMB package) for ground-based and multicopter-based recordings separately. For the ground-based dataset, the model included echolocation group, habitat type, multicopter type, and their three-way interaction as fixed effects. For the multicopter-based dataset at 104 m, the Myotis group was excluded from the habitat-specific analysis because activity of this group was nearly absent at that height, resulting in sparse data and unstable model estimates in the full model. The multicopter-based model therefore included only Nyctaloid and Pipistrelloid groups, with echolocation group, habitat type, multicopter type, and their interaction terms as fixed effects. In both models, habitat was included as a nested random intercept within the combination of study site, survey night, and multicopter type. This structure accounts for the non-independence of the three habitat transects sampled within the same night and study site, which were located in close spatial proximity. Estimated marginal means (EMMs) were computed for each combination of echolocation group and habitat, followed by Tukey-adjusted pairwise comparisons of habitat types within each echolocation group.

To address the third research question regarding whether bat activity levels differ between two types of multicopters for both recorded heights, we extracted the relevant pairwise contrast from the previously fitted models for multicopter-based recordings and separate ground recordings. We took this contrast from these models because their nested random intercept accounts for the non-independence of the habitat transects sampled within the same night, which a comparison across individual surveys would treat as independent replicates. We used estimated marginal means (emmeans) to compare the two multicopter types at 104 m and ground levels separately, applying Tukey correction for multiple testing. A comparison of bat activity data recorded at a height of 104 m (i.e. 16 m below the multicopter) with data recorded at a vertical distance of 120 m from the multicopter was undertaken in order to ascertain whether any acoustic or behavioural effects of the multicopter's presence could still be detected.

Data availability

The analysis dataset ist available in the HAW Hamburg repository at https://doi.org/10.48441/41201.3385.2

Code availability

The R script that reproduces Table 1 and the three generalised linear mixed-effects models is deposited together with the analysis dataset under the same DOI (https://doi.org/10.48441/41201.3385.2).

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Author contributions

Marc Huamán Roswag = M.H.R.; Joanna Fietz = J.F.; Anna Roswag = A.R.; Tessa Touridocht Taefi = T.T.T. M.H.R., A. R., J.F. and T.T.T. conceived and designed the study. M.H.R. collected the data. M.H.R. analysed the data and drafted the manuscript. M.H.R., J.F. and A.R. contributed to the interpretation of the results. All authors reviewed and approved the final manuscript

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Declarations

Competing interests

The authors declare no competing interests.

Additional information

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