Accelerating Towards an Understanding of Foraging in Greater Noctule Bats (*Nyctalus lasiopterus*)

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Submitted to Swansea University in fulfilment of the requirements for the Degree of MRes Biosciences

Swansea University

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Declaration

This work has not previously been accepted in substance for any degree and is not being concurrently submitted in candidature for any degree.

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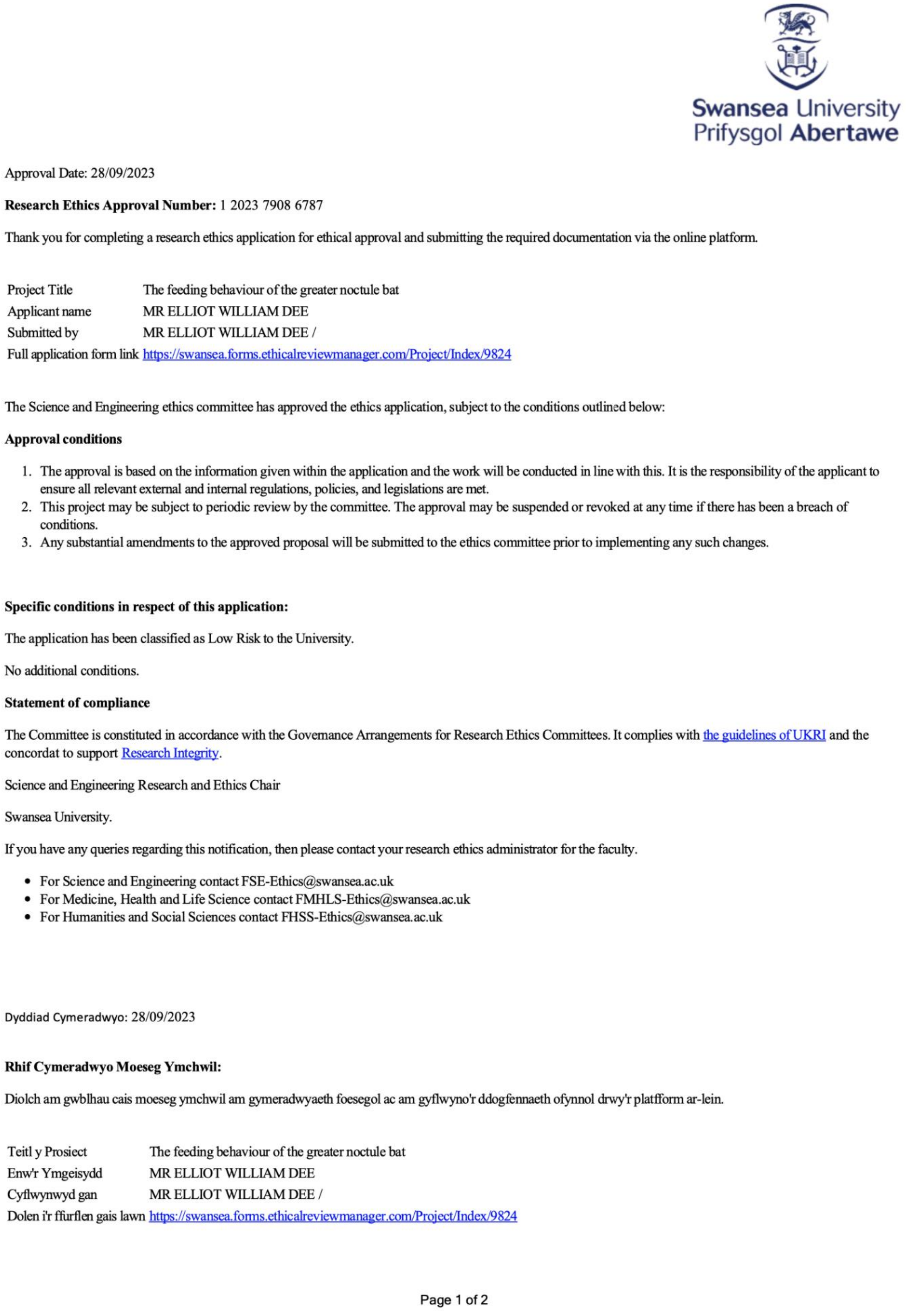
Research Ethics



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Prifysgol Abertawe

Approval Date: 28/09/2023

Research Ethics Approval Number: 1 2023 7908 6787

Thank you for completing a research ethics application for ethical approval and submitting the required documentation via the online platform.

Project Title	The feeding behaviour of the greater noctule bat
Applicant name	MR ELLIOT WILLIAM DEE
Submitted by	MR ELLIOT WILLIAM DEE /
Full application form link	https://swansea.forms.ethicalreviewmanager.com/Project/Index/9824

The Science and Engineering ethics committee has approved the ethics application, subject to the conditions outlined below:

Approval conditions

1. The approval is based on the information given within the application and the work will be conducted in line with this. It is the responsibility of the applicant to ensure all relevant external and internal regulations, policies, and legislations are met.
2. This project may be subject to periodic review by the committee. The approval may be suspended or revoked at any time if there has been a breach of conditions.
3. Any substantial amendments to the approved proposal will be submitted to the ethics committee prior to implementing any such changes.

Specific conditions in respect of this application:

The application has been classified as Low Risk to the University.

No additional conditions.

Statement of compliance

The Committee is constituted in accordance with the Governance Arrangements for Research Ethics Committees. It complies with the guidelines of UKRI and the concordat to support Research Integrity.

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Dyddiad Cymeradwyo: 28/09/2023

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Diolch am gwblhau cais moeseg ymchwil am gymeradwyaeth foesegol ac am gyflwyno'r ddogfennaeth ofynnol drwy'r platfform ar-lein.

Teitl y Prosiect	The feeding behaviour of the greater noctule bat
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Mae'r pwyllgor moeseg Science and Engineering wedi cymeradwyo'r cais moeseg ymchwil, yn amodol ar yr amodau a amlinellir isod:

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Definitions of Abbreviations

Abbreviation	Meaning	Definition
DDMT	Daily Diary Multiple Trace	Custom-built software for handling high resolution bio-logging data (including accelerometer, magnetometer, pressure, and temperature data).
Heave_{sm}; surge_{sm}; sway_{sm}	Smoothed acceleration in heave, surge, and sway axes, respectively	Running mean of acceleration in each axis, calculated over a specified time window ('smoothing window'), closely approximating static (gravitational) acceleration.
Heave_{dyn}; surge_{dyn}; sway_{dyn}	Dynamic acceleration in heave, surge, and sway axes, respectively	Residual acceleration in three axes after subtracting smoothed acceleration from raw data. Represents acceleration produced by body movements/ biomechanical forces.
VeDBA	Vectorial Dynamic Body Acceleration	Measure of absolute change in dynamic acceleration across the three axes of acceleration.
VeSBA	Vectorial Static Body Acceleration	Measure of absolute change in smoothed (static) acceleration across the three axes of acceleration.
PCA	Principal Component Analysis	Dimension-reduction technique, projecting datapoints into a series of lower dimensions which explain decreasing amounts of variance in the data.
KDE	Kernel Density Estimation	Technique for constructing smooth probability density functions approximating an underlying distribution. The sum of Gaussian kernel functions (with a given bandwidth) centred over each datapoint.
ICC	Intraclass Correlation Coefficient	Statistic describing the within-group similarity of a given variable.
FO	Frequency of Occurrence	Fraction of faecal samples collected from a given roost box containing a given prey type (taxon).
GLM	Generalised Linear Model	Linear regression models accommodating count, non-negative, binary, and proportional data through the specification of error distribution families and link functions.

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Abstract

Knowledge of foraging costs is important to understanding the drivers of animal movement, and can aid prediction of the energetic implications of environmental perturbation. Here, we characterise the feeding behaviour of greater noctule bats (*Nyctalus lasiopterus*) at the level of individual feeding events, with the aims of: (1) quantifying behavioural signatures corresponding with feeding; and, (2) examining differences in feeding attributable to prey type. Behavioural data were obtained from noctules equipped with accelerometers in Donaña National Park, Spain, along with faecal data collected from roosts. Stereotyped postures and movements indicating feeding were identified visually, using which thresholds in four metrics were selected for use in Boolean classification algorithms delineating individual feeds. The dimensionality of feed accelerometer metrics was reduced using Principal Component Analysis (PCA), and the metrics best characterising feeding retrieved using variable loadings. We calculated Intraclass Correlation Coefficients (ICCs) at the individual and roost levels to test for within-group correlation in feeding behaviour. Finally, binomial GLMs were fitted to predict the effect of PC1 on the frequency of occurrence (FO) of seven prey taxa in faeces. We identified 422 feeds, comprising significant departures in static and dynamic acceleration from normal flight. PCA loadings indicated six metrics characterising feeds, none of which showed evidence of clustering attributable to prey type. ICCs indicated individual- but not roost-level correlation in PC1, suggesting individual differences independent of proximity to prey fields. Additionally, GLMs yielded no evidence that FO varies with PC1. For the first time, we quantify feeding behaviour in *N. lasiopterus* - a threatened insectivorous bat - using accelerometers, with implications for reconstructing energy budgets across larger-scale movement trajectories. Disentangling the drivers of individual differences may be important to understanding demographic influences on bat foraging ecology. However, future studies linking diet and feeding behaviour would benefit from more refined behavioural algorithms.

Lay Summary

A better understanding of individual animal feeding behaviour, determinant in survival and reproduction, may inform population-level responses to resource variability, and therefore conservation. To achieve this, behavioural processes must be resolved across a range of relevant scales – from the seasonal patterns to its individual feeding events. This study examines fine scale feeding behaviour in an endangered bat species (greater noctule, *Nyctalus lasiopterus*), using animal-attached tags to quantify individual feeding attempts. Taking advantage of accelerometers that sense three-dimensional body movements at sub-second resolution, we identified presumed feeding events based on specific movements and postures known previously from foraging bats. Specifically, we developed an algorithm for defining presumed feeding behaviour based on rapid and substantial changes in body angle alongside high dynamic body acceleration. These elements capture characteristic transitions from level to inverted in-flight postures during prey capture, and the high biomechanical effort involved in feeding. We found differences in feeding behaviour at the level of individual noctules, perhaps associated with individual traits such as age and sex. A combination of our methods and existing larger-scale tracking (e.g. GPS/ satellite telemetry) may provide an opportunity to identify preferred feeding habitats in foraging bats. Such studies may pertain to questions of conservation interest, such as how changes in the distribution of resources as well as human perturbations (e.g. land-use, wind farms) are likely to influence noctule foraging movements.

1. Introduction

Optimal foraging theory proposes that organisms seek to forage in a manner that maximises energetic profit from trophic resources while minimising the costs – with respect to both time and energy - of obtaining them (Pyke, 1978; 1984). Previous studies have used this framework as a basis for explaining the fitness implications of various foraging strategies, including consideration of diet (Waddington and Holden, 1977; Wells and Wells, 1983), foraging patch selection and residency (Charnov 1976; Pyke, Pulliam, and Charnov, 1977), and search trajectories (Humphries, Weimerskirch, and Sims, 2013; Pyke, 2015; Campeau, Simons, and Stevens, 2022). However, the costs-benefit trade-offs involved in foraging are modulated by inherent constraints associated with an organism's biology and environment (Stephens, Brown, and Ydenberg, 2007), and as such it can be difficult to reconcile the realised outcomes of foraging with predictions from optimal foraging theory. This is particularly true for organisms foraging in spatiotemporally heterogenous environments, which impose the additional metabolic and cognitive costs of searching for unpredictable resources given imperfect knowledge of patchy environments (MacArthur and Pianka, 1966; Bastos et al., 2020). In such cases, without detailed insights into the energetic demands of foraging, from the search phase to prey capture and processing, disentangling the cumulative fitness implications of all relevant processes, and how these may change in space and time, presents a significant challenge (Weimerskirch et al., 2003). The relevance of these considerations for many conservation issues is becoming increasingly obvious (Wilson et al., 2018).

Only recently, through the advent of bio-logging technology –animal-borne sensors that remotely measure a range of biomechanical, physiological, and environmental variables (Naito 2004)– has it been possible to monitor animal activity at very fine scales, and thus accurately approximate the energetic consequences of movement and foraging strategies (Wilmers et al., 2015). Indeed, advances in the miniaturisation of animal-attached loggers have facilitated the integration of increasingly large amounts of spatial and behavioural data through compact, multi-sensor systems (e.g. 'Daily Diary' tags; Wilson, Shepard, and Liebsch, 2008; Wild et al., 2022). This includes combinations of bio-logging and GPS telemetry data (Gunner et al., 2022), enabling the energetic strategies exhibited by various animals to be examined over a wide range of spatiotemporal scales up to and including resource encounter and consumption (Mori, 1998; Ropert-Coudert et al., 2004; Del Caño et al., 2021).

Triaxial accelerometers, inertial sensors capable of measuring body posture and movement with respect to gravity at sub-second resolution (Gunner et al., 2020), offer unprecedented insights into animal foraging behaviour and its associated energetic costs (Wilmers et al., 2015). Distinct behavioural states are often associated with stereotyped postural and dynamic elements, corresponding to quantifiable signatures in acceleration data (Shepard et al., 2008; Williams et al., 2015), enabling instances of particular behaviours to be identified across datasets spanning relatively long periods. In addition, the sensitivity of devices logging at high frequencies to changes in the dynamism of movement (Wilson et al., 2014), and the close adherence of such parameters to associated metabolic power requirements (Gómez-Laich et al., 2011; Qasem et al., 2012; Wilson et al., 2020) enables the near-continuous approximation of energy expenditure. Such capabilities present the opportunity to reliably quantify time and energy budgets over periods and at resolutions unfeasible for conventional studies utilising human observers in the field. For example, the concept of 'energy landscapes', which describe the heterogeneity in the energetic efficiency of locomotion through an environment (Shepard et al., 2013), has been advanced through the use of coupled accelerometers and magnetometers (measuring animal heading). This has generated fundamental insights into the strategies undertaken by animals to minimise the energetic cost of movement at the landscape scale: across variable terrain on land (Lempidakis et al., 2018; Redcliffe, 2021), through dynamic atmospheric conditions (Shepard, et al., 2011; Williams et al., 2020), and across depth gradients in the water column (Wilson, Quintana, and Hobson, 2011). Knowledge of such strategies is essential if a holistic understanding of foraging is to be reached, because the energetic profitability of trophic resources is relative to the costs of transport involved in obtaining them, meaning the overall fitness benefit accrued from foraging is contingent on all facets of this trade-off (Welham and Beauchamp, 1997; Weimerskirch et al., 2003).

Bats (Mammalia: Chiroptera, Blumenbach, 1799), and in particular small, insectivorous species, are underrepresented in bio-logging studies due to their small size, high mobility, and cryptic lifestyles (O'Mara, Wikelski, and Dechmann, 2014). The small size of insectivorous bats means that the excess weight of the tags may be critical in affecting their capacity (O'Mara, Wikelski, and Dechmann, 2014; Wilson et al., 2021). However, advances in the miniaturisation of biologgers offer increasing opportunities for tag deployments on small, volant species, making the study of insectivorous bat behaviour by this means more feasible (e.g. Stidsholt et al., 2019). This has facilitated an increased focus on understanding spatial patterns of bat behaviour in three-dimensional space, as informed by GPS telemetry, capable of measuring both geolocation and vertical position in the aerosphere (e.g. O'Mara et al., 2019; 2021). Understanding such facets of bat behaviour is compelling for many reasons, not least because they are significant predators of arthropods, consuming large numbers of insects including agricultural pests (Boyles et al., 2011), but are often threatened by human activities such as deforestation, urbanisation, and wind-energy development (Alcadé, Juste, and Paunović, 2016).

The greater noctule (*Nyctalus lasiopterus*) is a large, aerial-hawking bat occupying an extensive but discontinuous range in mainland Europe, from the Iberian Peninsula in the West to European Russia in the East (Paniccia et al., 2023). It is a species of conservation concern across its geographical range, a status largely driven by the loss of mature woodland habitat (Juste et al., 2016). The relatively large size of this species facilitates a broad and flexible diet, including a diverse array of taxa and body sizes (Smirnov and Vekhnik, 2013). Although primarily insectivorous, most frequently predating upon moths and beetles, it is one of few bat species outside of the neotropics believed to actively predate on vertebrates, in particular small migratory birds (Dondini and Vergari, 2000; Ibáñez et al., 2001; Smirnov and Vekhnik, 2013). The sensitivity of accelerometers to fine-scale changes in body posture and motion (Wilson et al., 2014) presents the possibility to apply this technology in an examination of prey selection in *N. lasiopterus*, an opportunity augmented by the wide range of prey sizes and taxa actively exploited by this species (Ibáñez et al., 2001). Indeed, differences in body posture and motion during foraging may be associated with variability in the behavioural and morphological traits of prey (Watanabe and Takahashi, 2012; Wilson et al., 2013). Therefore, the present study examines the possibility that systematic differences in feeding behaviour, as measured in multiple dimensions by accelerometers, may reflect prey selection at the level of individual feeding events in *N. lasiopterus.*

Limited knowledge of the foraging behaviour of insectivorous bats could impede their conservation, because energetic cost-benefit trade-offs associated with foraging may govern their interaction with extrinsic threats (e.g. wind turbines; O'Mara, 2023). In addition, knowledge of the energetic consequences of foraging could inform an understanding of how bat populations are likely to respond to habitat loss and altered prey communities (Rainho and Palmeirim, 2011). Accordingly, this study seeks to contribute to our understanding of feeding behaviour at the level of individual feeding events in *N. lasiopterus*, with the specific aims of: 1) characterising the body postures and movements (as measured by accelerometers) associated with *N. lasiopterus* feeding behaviour, thereby enhancing future attempts to identify feeding behaviour across bat movement trajectories; and 2) exploring the possible influence of prey selection on *N. lasiopterus* feeding behaviour, with the intention of providing a basis from which to quantify the energetic demands associated with given diet compositions. Following the identification of instances of feeding from accelerometer data, metrics characterising *N. lasiopterus* feeding behaviour are compared with diet data to explore patterns corresponding to prey selection. Individual dietary differences are expected to be associated with differences in feeding behaviour at the level of individual *N. lasiopterus.* In addition, spatial proximity to prey fields is expected to produce more similar feeding behaviour among bats from the same roost compared with those from different roosts.

2. Methods

2.1. Data Collection

Fieldwork was carried out in Donaña National Park Biological Reserve (Andalucía, southern Spain) by researchers from the Max Planck Institute for Animal Behaviour and Estación Biológica de Doñana, as part of a wider project studying the species' behaviour and ecology (E. Tena López, personal communication). The reserve comprises a mixture of habitats: pine forest, marshland, sand dunes, and Mediterranean shrubland. Fewer than 100 greater noctule bats (*Nyctalus lasiopterus*) occupy the reserve, inhabiting 28 bat roost boxes installed on trees (including stone pine, *Pinus pinea,* river red gum, *Eucatlyptus camaldulensis,* and white poplar, *Populus alba*; Popa-Lisseanu and Ibáñez, 2007; Santos et al., 2016). Bats were captured in April 2018 and October 2019 using mist nets erected outside of roost boxes, and equipped with compact GPS-triaxial accelerometer data loggers (Axytrek, Fleetronics tags). The tags measure acceleration (1 *g* = 9.81 m s^2) in three orthogonal axes (dorso-ventral or 'heave'; anterior-posterior or 'surge'; lateral or 'sway'; Figure 1) at a resolution of 100 Hz (100 data points s^{-1}), and barometric pressure at 1 Hz. The loggers were glued to the dorsal fur (O'Mara, Wikelski, and Dechmann, 2014) over the approximate centre of gravity during level flight, and in line with the longitudinal axis of the body. Loggers weighed 4.14±0.18 g, representing 8±0.15% of the bats' body masses. This is in excess of the commonly accepted 5 % threshold for animal-borne sensors (Wilson et al., 2021; implications of tag burden discussed further in section 4.3). After two to four days, the bats were recaptured directly from roost boxes and the tags were removed.

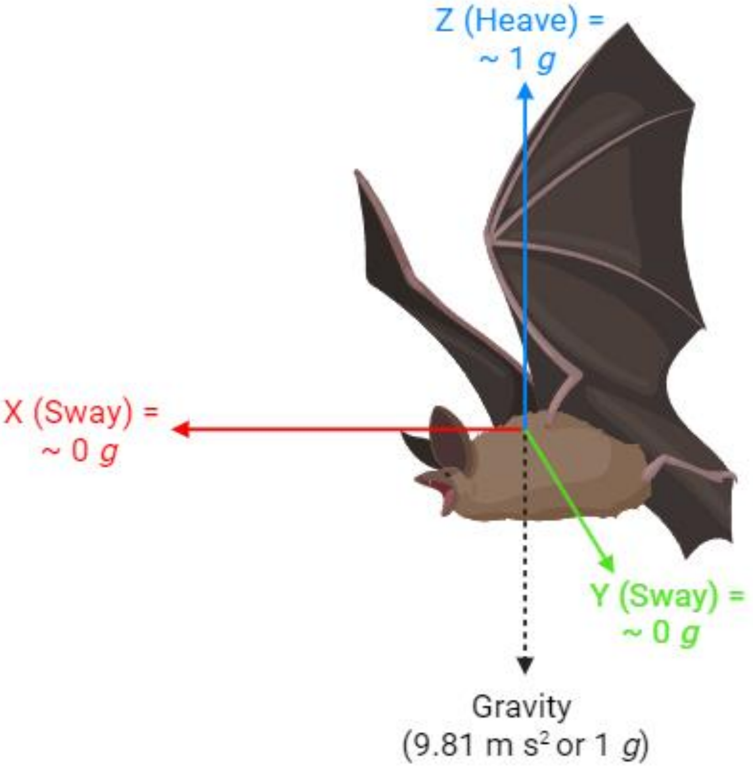

Figure 1: Schematic illustrating the orientation of the axes of accelerometer sensors on a back-mounted tag with respect to gravity (black dotted arrow) during level flight, superimposed on a diagram of a little brown bat (*Myotis lucifugus*). Smoothed acceleration in the Z (heave) axis closely approximates gravitational acceleration, being nearly parallel to the direction of gravity during level flight. The orientation shown reflects the logger orientation selected for deployments on *N. lasiopterus* (see section 2.1). Note that this configuration may not be representative of logger deployments in other studies, as the selection of logger orientation is species- and study-specific. Image created on www.BioRender.com (BioRender, 2023).

In addition to accelerometer data, faecal samples were collected from roost boxes every day that the bats equipped with loggers were active (indicated by the activation of GPS above an acceleration threshold of 1.25 *g*). Faecal pellets were retrieved from mesh guano collectors beneath the bottom entry holes of roost boxes. The samples were frozen at -20 °C or dried at room temperature in the laboratory. DNA was extracted from the faeces. Prey species in faecal samples were identified by amplifying prey DNA, following Ibáñez et al. (2016), and comparing the resulting sequences with the GenBank database (http://www.ncbi.nlm.nih.gov/GenBank). This yielded prey

ID to species level, and qualitative scores of their relative abundance ('High', 'Medium', 'Low') in samples from each roost box.

2.2. Acceleration Data

Acceleration and barometric pressure data were visualised as two-dimensional signals in 'Daily Diary Multiple Trace' (DDMT) – a custom-built software for handling animal behavioural data collected at sub-second resolution by accelerometers, magnetometers, and temperature and pressure sensors (Wildbyte Technologies, 2023).

Accelerometer data comprise static (gravitational) and dynamic acceleration components (Grundy et al., 2009). The static component (S) is derived for each orthogonal axis by averaging a sample (i) of raw acceleration over a moving window of size w ('smoothing window'; Bidder et al., 2015; Gunner et al., 2020):

$$S_i = \frac{1}{w}\sum_{j=i-\frac{w}{2}}^{i+\frac{w}{2}} S_j \tag{1}$$

In the present study, the width of the smoothing window, w, was selected to correspond with the approximate duration of two wingbeat cycles as observed in the raw heave acceleration (30 consecutive data points corresponding to 0.3 s of data at 100 Hz; Figure 2 – see section 3.1.2), following Shepard et al. (2008). Dynamic acceleration stems from actions undertaken by the tagged animal, and is calculated by subtracting the static acceleration from the raw data (Wilson et al., 2020).

In the absence of substantial biomechanical or inertial forces in excess of those experienced during linear motion (e.g. centripetal acceleration), 'smoothed' (static) acceleration closely approximates logger inclination (corresponding to body pitch and roll – equations 2 and 3) with respect to gravity (Bidder et al., 2015):

$$Pitch = \left(atan2\left(Heave_{sm}, \sqrt{Surge_{sm}sm^2 + \ Sway_{sm}sm^2}\right)\right) \times \frac{180}{\pi} \tag{2}$$

$$Roll = \left(atan2\left(Surge_{sm}, \sqrt{{Heave_{sm}}^{2} + \ {Sway_{sm}}^{2}} \right) \right) \times \frac{180}{\pi} \tag{3}$$

Where heave$_{sm}$, surge$_{sm}$, and sway$_{sm}$ represent smoothed acceleration (see equation 1) in the surge (X), sway (Y), and heave (Z) axes, respectively, and $180/\pi$ is an adjustment enabling the conversion of units from radians to degrees (°; Bidder et al., 2015; Gunner et al., 2020).

Various derivatives of acceleration were calculated to aid comprehension of both postural and dynamic elements of *N. lasiopterus* movement. Vectorial dynamic body acceleration (VeDBA), an indicator of changes in the dynamism of movement across all three axes of acceleration, was calculated as follows:

$$VeDBA \ = \ \sqrt{(Surge_{dyn})^2 + (Sway_{dyn})^2 + (Heave_{dyn})^2} \tag{4}$$

Where surge$_{dyn}$, sway$_{dyn}$, and heave$_{dyn}$ represent dynamic acceleration in the surge, sway, and heave axes, respectively (Qasem et al., 2011). By taking the square of each acceleration axis separately (equation 4), VeDBA captures both positive and negative changes in dynamic acceleration, increasing in response to any change across the three axes. Similarly, vectorial static body acceleration (VeSBA) varies in response to deviations from 1 *g* in smoothed acceleration (Surge$_{sm}$, Sway$_{sm}$, and Heave$_{sm}$):

$$VeSBA \ = \ \sqrt{(Surge_{sm})^2 + (Sway_{sm})^2 + (Heave_{sm})^2} \tag{5}$$

VeSBA is a measure of the static acceleration (equation 1) across all three axes, so remains close to 1 *g* when a body is static or in linear motion (assuming that velocity is constant). However, when a body 'pulls-*g*' – that is, experiences inertial forces in excess of gravity (centripetal acceleration) during circular motion – VeSBA increases, whereas it decreases to 0 *g* for bodies in freefall (Williams et al., 2015).

Deviations in logger placement from the centre of gravity were corrected by generating smoothed '*g*-spheres' (spherical scatter plots representing smoothed acceleration in three-dimensions; Wilson et al., 2016) for periods of level flight, and manually correcting the displacement of datapoints by centring them over the 'north pole' of the plot (i.e. 1 *g* in the heave axis an 0 *g* in the surge and sway axes). In general, the unprocessed data did not depart from 1 *g* to any significant degree, minimising possible source error associated with tag placement.

2.3. Behavioural Classification

N. lasiopterus feeding behaviour was first identified by visual inspection of acceleration traces in DDMT. The basic pattern of feeding was identified and classified based on the author's knowledge of accelerometry, cross-validated using peer-reviewed literature (Siemers and Schnitzler, 2000; Corcoran and Conner, 2017), high-speed videos of bats feeding found on the internet (Aaron Corcoran, 2013), and personal communication with experts in the field (R.P. Wilson and J. Redcliffe, personal communication, 27th March 2023). A Boolean-based classification algorithm (Wilson et al., 2018), outlining requisite criteria for identifying instances of feeding, was then defined based on consistent patterns in selected metrics (Table 1).

Table 1: Description of accelerometer metrics used to define instances of feeding behaviour using Boolean classification algorithms in DDMT.

Metric	Definition	Source(s)
Differential of smoothed heave acceleration	Rate of change in smoothed heave acceleration over 0.1 s window	Gunner et al. (2022)
Variance in surge acceleration	Deviation of raw surge acceleration from the mean calculated over a 0.5 s window	Wildbyte Technologies (2022)
Smoothed Heave	Running mean of raw heave acceleration over a 0.3s window	Shepard et al. (2008)
VeDBA Smoothed	Running mean of VeDBA (see equation 4) over a window of 0.3 s	Fehlmann et al. (2017)

Boolean-based algorithms recognise instances in which defined conditions, based on thresholds in the relevant metrics, are met, marking these instances as indicative of feeding behaviour (Wilson et al., 2018). Classification of a feeding event by the algorithm was conditional on each criterion being met in a specific sequence (Table 2), and within defined time windows following the fulfilment of the criterion at the previous step. Using this approach, instances of feeding could be delineated automatically over large datasets based on the presence of their basic postural and dynamic elements.

Table 2: Sequence of criteria required for the classification of feeding behaviour. The relevant channels are shown in the 'metric' column, and the corresponding thresholds required for the fulfilment of each criterion shown in the 'condition' column. 'IF' statements indicate that the condition must be fulfilled for a feed to be classified, while 'AND IF' indicate that the condition must be fulfilled in tandem with the previous 'IF' statement. For feeding behaviour to be classified, each condition must be met in-turn within a time window of 1 s from the previous step.

Step	**Metric**	**Condition**
1	**IF** Differential in Heave	< -0.2 *g*
	AND IF Variance in Surge	> 1 *g*
2	**IF** Smoothed Heave	> -0.8 *g*
3	**IF** VeDBA Smoothed	< 0.9 *g*
	AND IF Variance in Surge	< 1.5 *g*

The performance of feed classification was assessed by running the behavioural algorithm (Table 2) over a subset of accelerometer data, comprising a total of 107 feeding events across six bat nights, and comparing the feeding events retrieved by the algorithm to those identified visually. The recall, or true positive rate (Del Caño et al., 2021), was calculated as the fraction of all positive classifications considered to be true positives (in this case, the classifications representative of presumed feeding behaviour as defined by eye).

2.4. Data Analysis

All statistical analyses were carried out in R version 4.2.2 (R Core Team, 2022).

2.5.1. Principal Component Analysis

A subset of variables was selected from all available logger metrics, based on intuition regarding their relevance to *N. lasiopterus* feeding behaviour. Principal component analysis (PCA) (Bro and Smilde, 2014) was then used to reduce the dimensionality of the selected metrics. This method projects data onto new dimensions (principal components: hereafter 'PCs'), with each PC representing the minimum distance between the data and their projection, given the constraint that they must be uncorrelated with all previous PCs. Successive PCs thus encode decreasing amounts of variability in the data, such that the first PC (PC1) explains the most variability (Lever, Krzywinski, and Altman, 2017). The correlation between the original variables and each PC are represented by variable loadings. In the present study, variable loadings were used to determine the variables most strongly correlated with the first two PCs (PC1 and PC2), and these metrics were considered to be the most important in characterising differences in feeding behaviour.

A K-means clustering algorithm (Altman and Krzywinski, 2017) was applied to PCA scores to recover clusters of closely related datapoints. This calculates the Euclidean distance between each datapoint and k randomly selected datapoints (centroids), assigning each point to one of k clusters based on their similarity to each centroid. This is repeated using different randomly selected centroids within each cluster until the lowest within-cluster distance is reached (Altman and Krzywinski, 2017). The number of clusters (k) to be recovered by the K-means algorithm was selected initially to correspond with the number of taxonomic groups of prey recovered from faecal samples (see section 2.5.4), and the performance of this assessed using average silhouette scores (a measure of between-cluster similarity) for different values of k (Altman and Krzywinski, 2017).

2.5.2. Patterns in the Data

Probability density functions for PC1 and PC2 were constructed using Kernel Density Estimation (KDE), a method for computing smooth probability functions which approximate underlying distributions of data (Chen, 2017). This is achieved by summing Gaussian kernel functions with specified bandwidths (smoothing parameters), which are centred over each datapoint. Individual KDEs were also constructed for each of the logger metrics most strongly correlated with PC1 and PC2.

Generating smooth density estimates was considered more appropriate compared with frequency distributions for visualising structure of possible biological relevance in the data. This is because the inclusion of a smoothing parameter enables random noise in the data to be filtered, in favour of biologically interesting structure (Węglarczyk, 2018). Accordingly, the density estimates generated here were examined for evidence of multimodality – the presence of more than one distinct peak - indicative of concentrations of datapoints around multiple distinct values (Węglarczyk, 2018). Under the expectation that feeding events would differ predictably according to prey type, evidence of multimodal structure in each density estimate was thought to reflect multiple 'types' of feeding event corresponding to different prey types.

2.5.3. Differences in feeding behaviour

With the expectation that differences in diet would be reflected in individual- and roost-specific differences in feeding behaviour, group-level correlation in PC1 was calculated using intraclass correlation coefficients (ICCs; Altman and Krzywinski, 2015) for two grouping levels (individual and roost). GPS fixes corresponding to periods of inactivity (as shown by lack of flight behaviour in acceleration data) between successive nights, and corresponding to the locations of known roost boxes, were used to ascertain the roost boxes used by each individual *N. lasiopterus* on each night. The individuals associated with given faecal samples were therefore known. This enabled accelerometer data to be grouped according to the roost boxes associated with the corresponding nights of foraging activity. In each case, it was hypothesised that feeding behaviour would exhibit greater similarity within than between groups, on the assumptions that: (1) individual differences in diet would lead to individual differences in feeding behaviour; and (2) roost-mates would be exposed to the same proximal prey fields, so would differ less in their feeding behaviour compared with non-roost-mates (assuming that feeding behaviour is prey-specific). Based on previous animal behavioural studies (Fürtbauer et al., 2014), an ICC score greater than 0.5 with 95 % confidence intervals not overlapping zero was chosen as the threshold indicating significant within-group correlation.

2.5.4. Predicting diet from logger metrics

To test the association between selected metrics and *N. lasiopterus* prey selection, generalised linear models were fitted to predict the prevalence of each prey type in faecal samples from the characteristics of associated feeding events. Prey recovered from faecal samples from each box were first grouped by taxon. Taxonomic groups (hereafter, ‘prey type’) were determined to various levels of organisation, resulting in seven groupings: Carabidae (Carabid beetles), Dytiscidae (diving beetles), Culicidae (mosquitoes), Lepidoptera (moths), Tipulidae (marsh crane flies), Orthoptera (crickets), and birds.

The prevalence of each prey type in *N. lasiopterus* diet was then approximated by calculating their per-box frequency of occurrence (FO) as follows:

$$FO = \frac{Freq_{ij}}{N.Samples_j} \tag{6}$$

Where $Freq_{ij}$ is the number of samples recovered from box i containing prey type j, and $N.Samples_j$ is the total number of faecal samples recovered from box j. Qualitative scores of ‘high’, ‘medium’, and ‘low’, describing the density of remains of each prey type recovered from each box, were also available. However, this metric was found to be strongly correlated with FO (Pearson’s correlation = 0.91). Accordingly, only prey prevalence as measured by FO is considered here, as this metric was assumed to encapsulate information regarding both the frequency and density of prey in *N. lasiopterus* diet.

Calculating the exact FO of each species group is challenging in the absence of information regarding the identity of faecal samples from which each prey item was recovered. This is because multiple prey species belonging to the same group sometimes existed in samples from roost boxes housing multiple individuals. Therefore, it is unknown which samples share species from the same group. Accordingly, the FO of the most frequently occurring species from each group in a given box was taken as an estimate of the prevalence of its entire group, assuming that remains of this group occurred with at least the frequency of its most frequent constituent species. The group-level FOs calculated here should therefore be treated as conservative estimates of the prevalence of each prey type in *N. lasiopterus* diet, as this measure likely underestimates their real frequencies.

With the aim of approximating prey selection from acceleration data, the per-box FO of different prey types was modelled as a function of PC1 (see section 2.5.1). Given that FO is a proportional response (the fraction of faecal samples containing a given prey type), binomial GLMs with logit-links were fitted to predict the FO of each prey type from the PC1 scores of associated feeds (Bacallado and Shah, 2021). Models were fitted using the *glm()* function in the R package *stats.* This function also enabled prior weights corresponding to the total number of faecal samples collected from each box to be specified, which were intended to give increased weight to FO values derived from greater numbers of faecal samples (R Core Team, 2022).

3. Results

3.1. Presumed Feeding Behaviour

3.1.2. General pattern and classification

Presumed feeding behaviour (hereafter referred to as ‘feeding behaviour’ or ‘feeding’) was characterised by a departure from normal flight behaviour, with normal flight (Figure 2), consisting of periods with VeSBA persistently close to 1 *g*, negligible changes in altitude (as shown by barometric pressure), and regular wingbeats (repetitive oscillations of consistent amplitude and frequency in the heave axis).

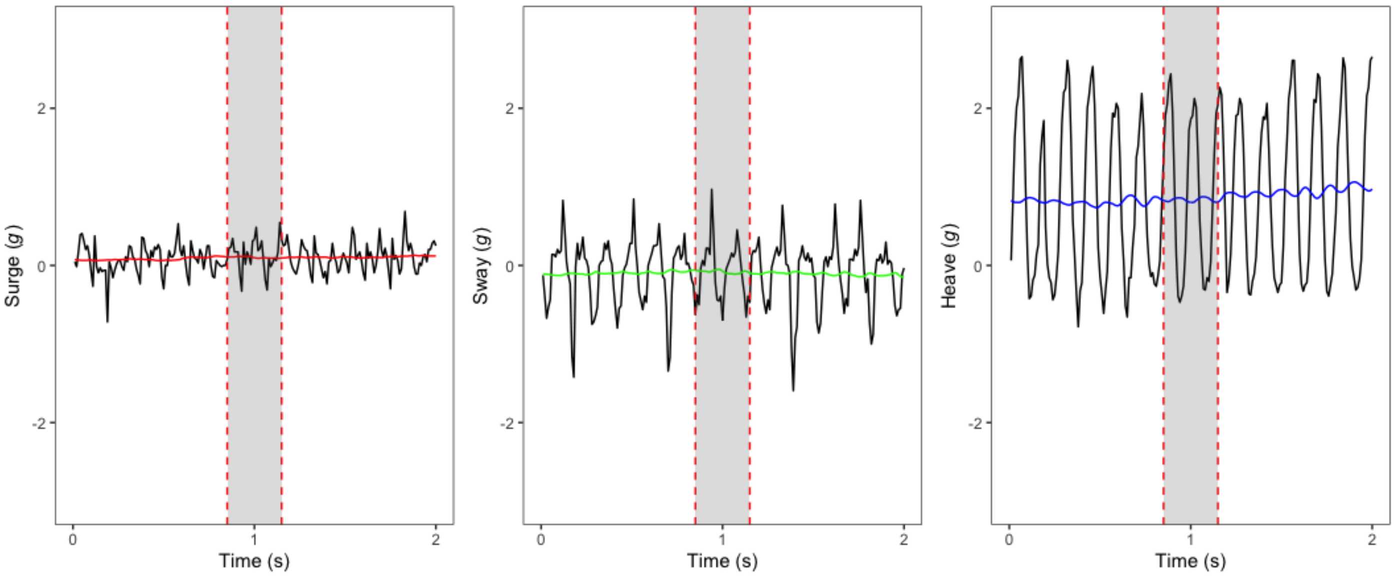

Figure 2: Acceleration in three orthogonal axes (surge, sway, and heave) over a 2 s period of level flight. Black lines represent raw acceleration, while coloured lines represent smoothed (static) acceleration calculated over a moving window of 0.3 s (window width shown by grey shaded area between red dotted lines). Note that smoothed acceleration in the heave axis is centred around 1 g (corresponding to the Earth's gravitational field), while smoothed surge and sway are close to 0 g. The oscillatory signal in the raw heave (black line, bottom plot) represents repeated vertical displacements of the logger caused by trunk movements during individual wingbeats, with wave troughs and peaks corresponding to the apex of wing upstrokes and downstrokes, respectively.

By contrast, during periods considered to be indicative of prey capture (or attempted prey capture) a distinctive sequence of postural and dynamic changes occurred. In particular, decreases in the smoothed heave were consistent across feeding events (Figure 3A) so were considered a prerequisite for this behaviour. Substantial changes in the dynamism of movement were also evident, reflected as a substantial increase in VeDBA (Figure 3B). Elevated VeDBA appeared to be driven primarily by erratic oscillations in the surge axis about 0 *g* (Figure 3C) and substantial decrease in heave below 0 *g*. Smoothed heave thus decreased considerably (to approximately -2 *g* in Figure 3A) relative to the value observed in level flight (1 *g*; Figure 2). The changes observed in smoothed heave contributed to a characteristic increase in VeSBA above 1 *g*, albeit often in a 'W' shape with short periods below 0 *g* directly preceding and following a central peak frequently exceeding 2 *g* (Figure 3E). Furthermore, feeding was often accompanied by considerable variability in pitch and roll, particularly at the start and end of a feeding event (Figure 3F), but the exact nature of these patterns varied on a feed-to-feed basis.

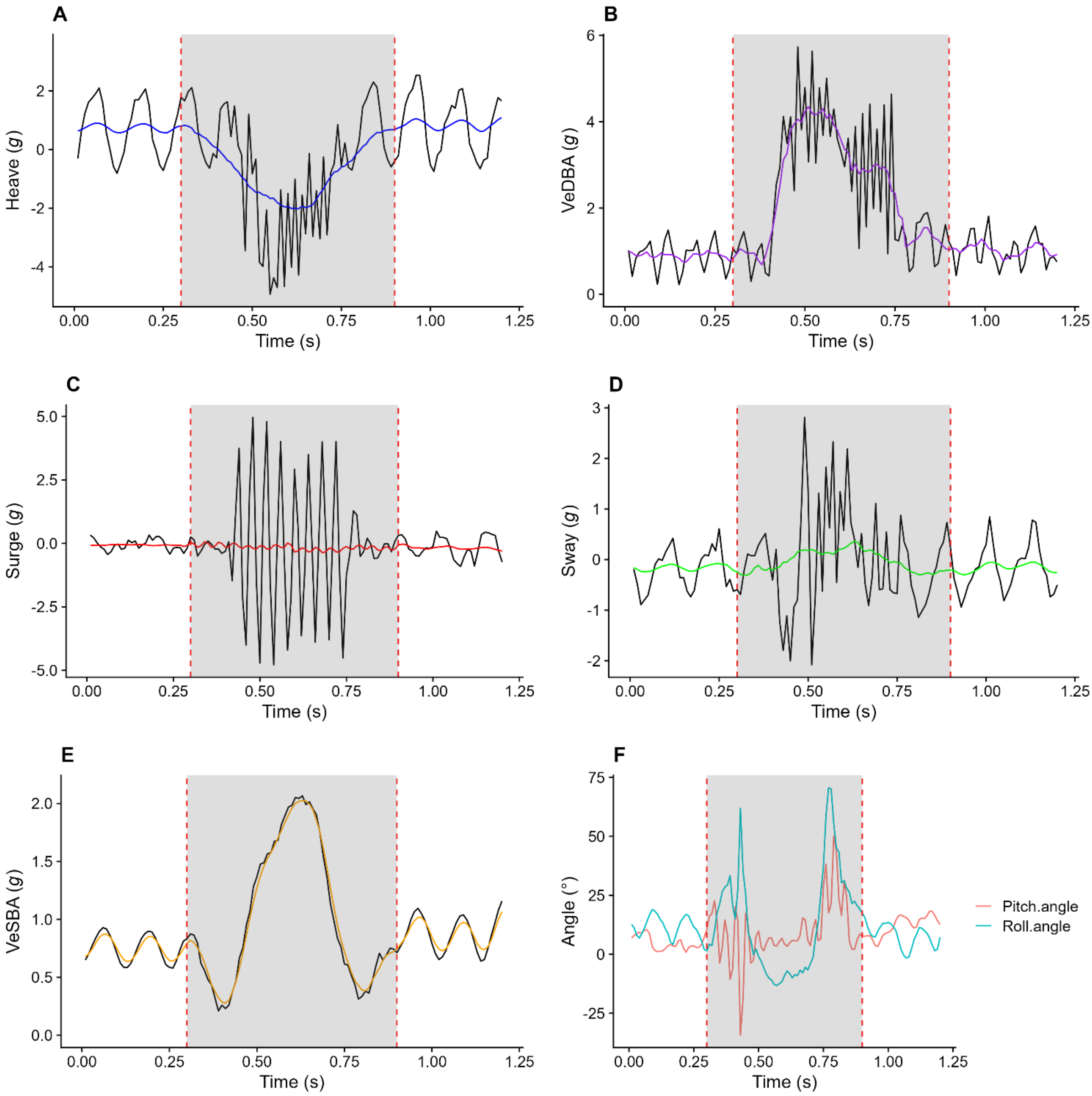

Figure 3: Example traces of various acceleration metrics across the duration (in seconds) of a single *N. lasiopterus* feeding event. In each case, the presence of postures/ movements indicative of feeding behaviour is highlighted by shaded areas between vertical dashed red lines, while non-shaded areas correspond to level flight preceding/ following the feed. For plots **A-E**, black lines represent raw values while coloured lines represent smoothed values (over 0.3 s). **(A)** heave; **(B)** VeDBA; **(C)** surge; **(D)** sway; **(E)** VeSBA; **(F)** pitch (red line) and roll angles (green line). Note that pitch and roll angles are realistic approximations of body posture even when the subject is ‘pulling-*g*’, because these metrics are derived from surge and sway, while distortions in smoothed acceleration caused by centripetal force are restricted to the heave axis, acting

perpendicular to the load-bearing surfaces of the bat (R. P. Wilson, personal communication, 20th September 2023).

Based on the patterns previously described, a Boolean classification algorithm capturing the changes most characteristic of feeding behaviour was constructed (Table 2). Here, a simultaneous decrease in the differential of heave and increase in the variance of surge demarcated the transition from normal flight to feeding behaviour. Low absolute values of smoothed heave, high smoothed VeDBA, and high variance in surge were maintained for the duration of the feeding event, so the return of these metrics towards the values observed in normal flight indicated the termination of the behaviour.

The feeding algorithms used here recalled 67.3% of presumed feeding events identified by eye during validation. However, false-positive classifications often resulted primarily from movements within the roost (representing 15 out of the 28 false-positives), as indicated by a concurrent lack of flight behaviour, meaning many misclassified feeds could be filtered by considering only those instances occurring during periods of activity between leaving and returning to the roost. This was considered a reasonable constraint given the primarily aerial-hawking hunting strategy of *N. lasiopterus* (Ibáñez et al., 2001; Pineda, 2023). Applying this constraint to feeding algorithms improved their recall rate to 78.3%. In addition, a total of seven false-negative classifications, representing a false-negative rate of 6.5%, were identified by eye.

3.2. Patterns in Feeding Behaviour

Using the algorithm described in Table 2, and after filtering for false-positive classifications, a total of 422 instances of feeding were identified across 17 individual *N. lasiopterus*, occurring on seven separate nights (49 bat nights). The mean number of feeding events identified per individual was 24.8±17.7, but the total number of feeds observed per bat ranged from two to 59. Foraging occurred at a range of times both before and after midnight, but never in the afternoon before 17:25 or in the morning after 03:46. Foraging time was highly variable throughout the night, showing two peaks around sunset and approximately three to four hours after sunset (Figure 4).

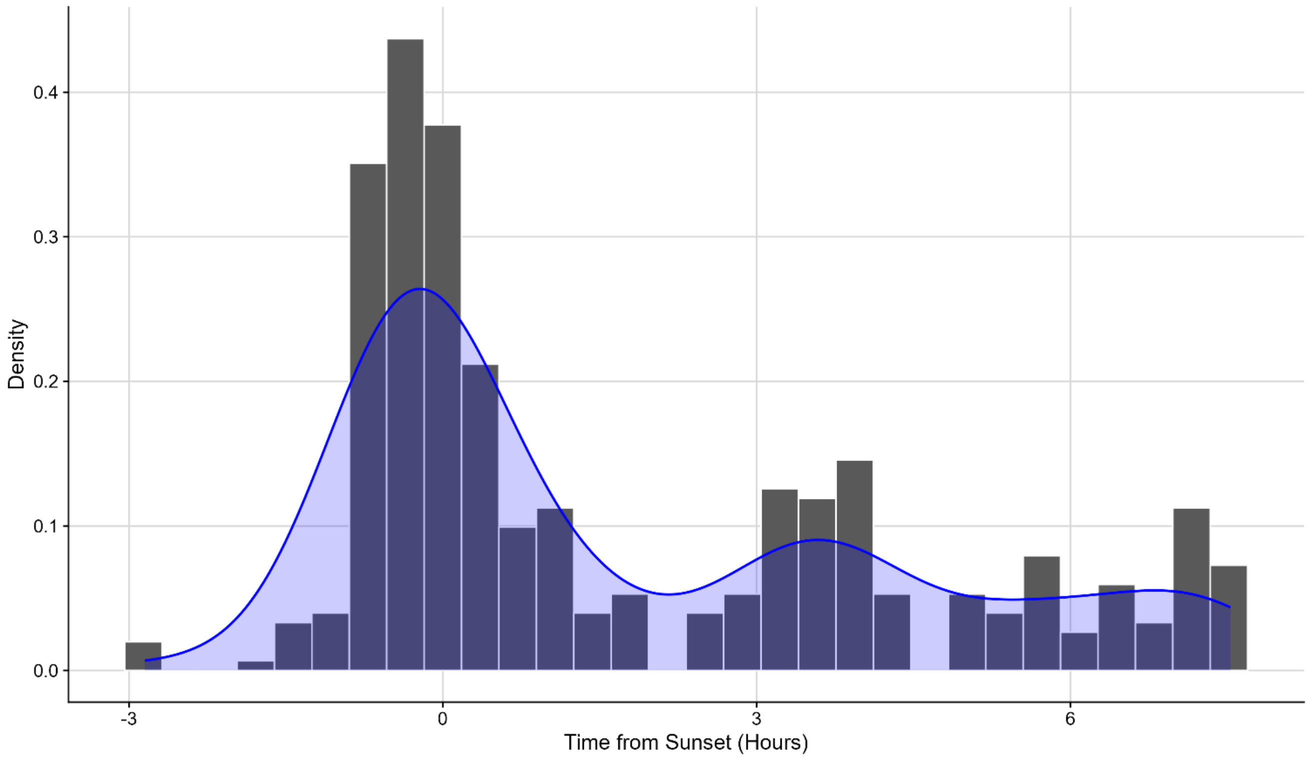

Figure 4: Distribution of feeding events in time relative to the time of sunset (0 hours on the x-axis), as shown by frequency (black bars) and continuous density distributions (blue line and shaded area). Time is represented over the course of a night, with the smallest values representing 17:24 (first feed observed after emergence from roost for a night's foraging) and the largest representing 03:46 (the last feed observed before return to roost from a night's foraging).

A total of 16 variables were included in PCA characterising variability in *N. lasiopterus* feeding behaviour (see Appendix: Table A1). Accordingly, PCA recovered 16 principal components explaining between 0.4 % (PC16) and 32.1 % (PC1) of this variability in, while PC2 accounted for 15.1% of variation in the data. Mean VeDBA was most strongly correlated with PC1, decreasing as PC1 increased (loading = -0.388). This was followed by variance in surge and mean VeSBA, which were also negatively correlated with PC1 (loadings = -0.385 and -0.377, respectively). In addition, mean smoothed heave was positively correlated with PC1 (loading = 0.373). Mean and maximum pitch angles (loadings = 0.538 and 0.513, respectively), and mean smoothed sway (0.487) were most strongly correlated with PC2, with no other variables displaying loadings greater than 0.3 in this axis (Figure 5).

According to average silhouette scores of PC values grouped into different numbers of K-means clusters (k), the best number of clusters was lower ($k = 2$; silhouette = 0.16; Figure 5B) than would be expected if the similarity between datapoints was consistent with grouping by prey taxon

($k = 7$; silhouette = 0.11; Figure 5A). Examination of PC loadings suggest that maximum smoothed acceleration in the sway and heave axes, mean VeDBA, mean VeSBA, and the duration of feeding events are potentially good descriptors of the grouping of datapoints when $k = 2$ (Figure 5B).

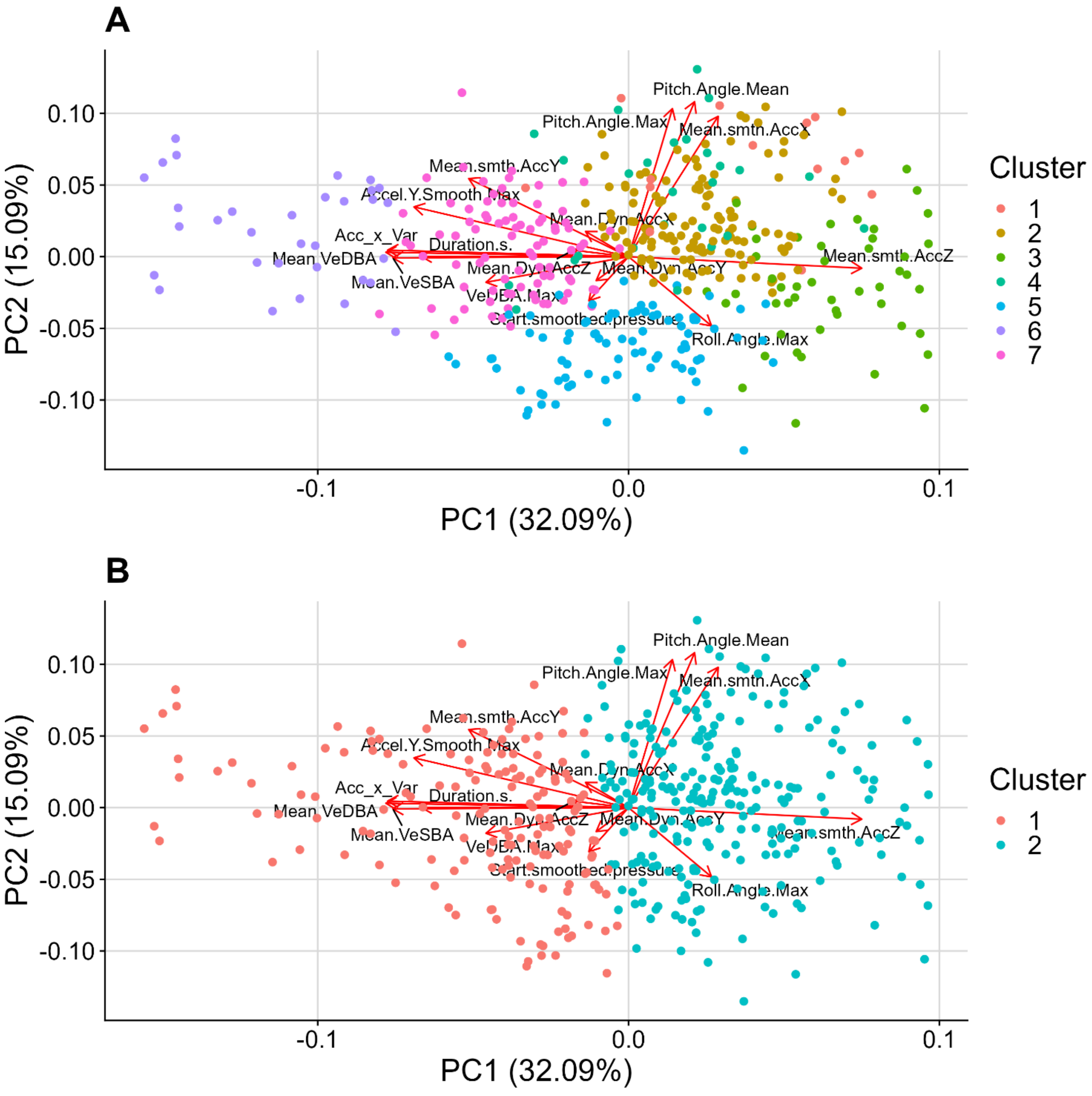

Figure 5: Values of the first (PC1) *versus* the second principal component (PC2) from PCA conducted on 17 logger metrics characterising *N. lasiopterus* feeding behaviour. Each datapoint represents one of 422 feeds observed across 17 individual *N. lasiopterus* on seven separate nights. Datapoints grouped into k clusters (see section 2.5.2) are separated by colour: **(A)** k = 7, and **(B)** k = 2. Eigenvectors corresponding to each variable (labelled) are represented by red arrows and indicate the direction and strength of correlation with

PC1 and PC2. The percentages of variance explained by PC1 and PC2 are shown in brackets on the x and y axis, respectively.

None of the Kernal Density Estimates (KDEs) generated for the metrics most strongly correlated with PC1 showed evidence of multimodality: mean VeDBA (mean = 0.34; SD = 0.38), mean smoothed heave (mean = 0.2; SD = 0.22) and mean VeSBA (mean = 0.28; SD = 0.28; Figure 6A). The same was true for KDEs generated for PC1 and PC2 scores (mean = 0.002; SD = 0.001; Figure 6B), as well as the duration of feeding events (mean = 0.67; SD = 0.15).

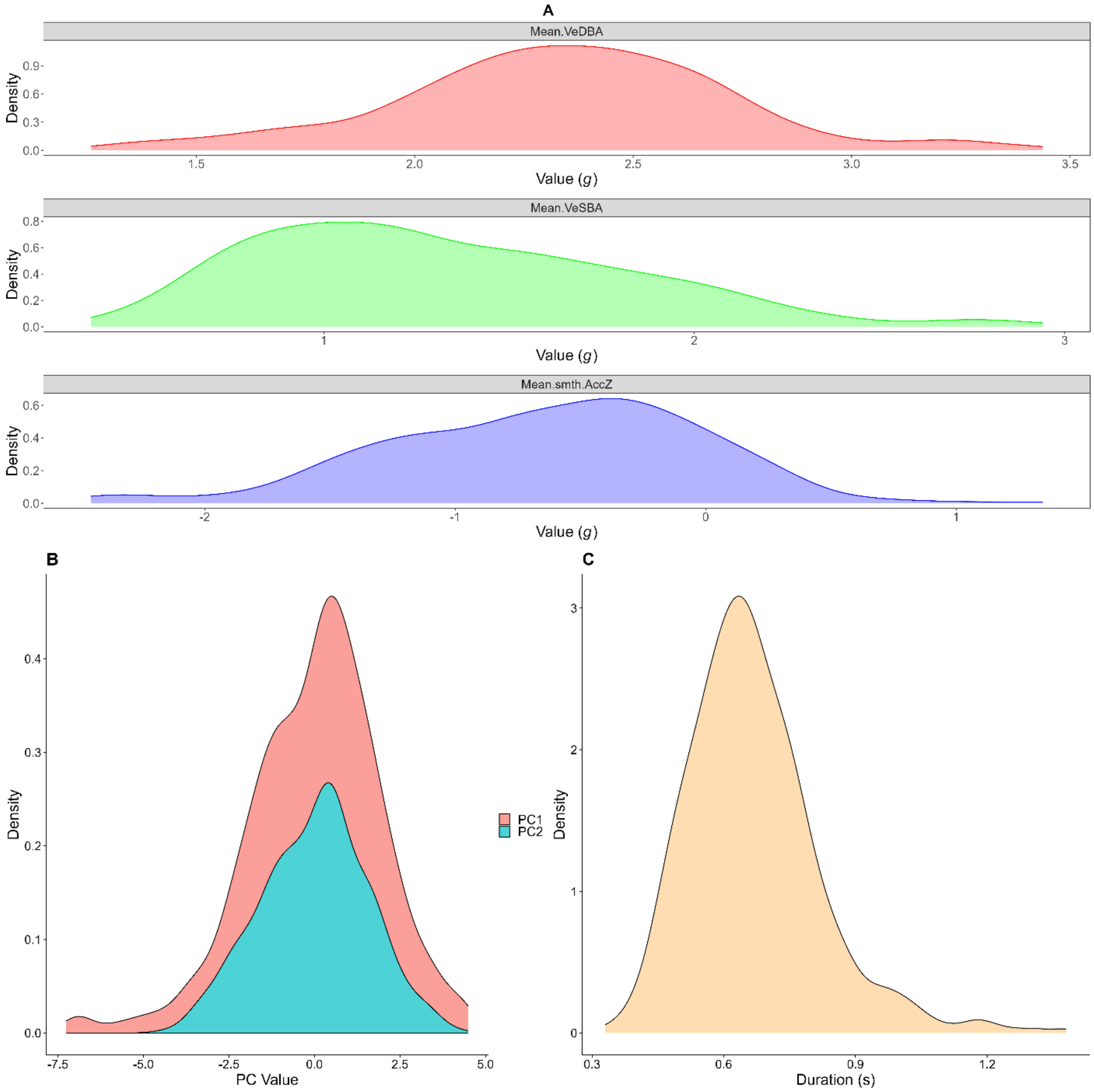

Figure 6: Continuous probability distributions of: **(A)** three logger metrics describing feeding behaviour; top to bottom: mean VeDBA, mean VeSBA, and mean smoothed heave; **(B)** values of the first (PC1; in red) and

second principal components (PC2; in blue) from PCA conducted on 16 variables; **(C)** the duration in seconds of feeding events. Estimates were constructed using Kernal Density Estimation (KDE).

PC1 scores were correlated within individual *N. lasiopterus* (ICC = 0.51; lower CI = 0.2; upper CI = 0.81), suggesting individual differences in feeding behaviour (Figure 7A). However, PC1 was not similarly correlated with roost-box ID (ICC = 0.08; lower CI = -0.07; upper CI = 0.23; Figure 7B), contrary to the assumption that proximity to the same prey fields would be manifested in roost-specific differences in feeding behaviour.

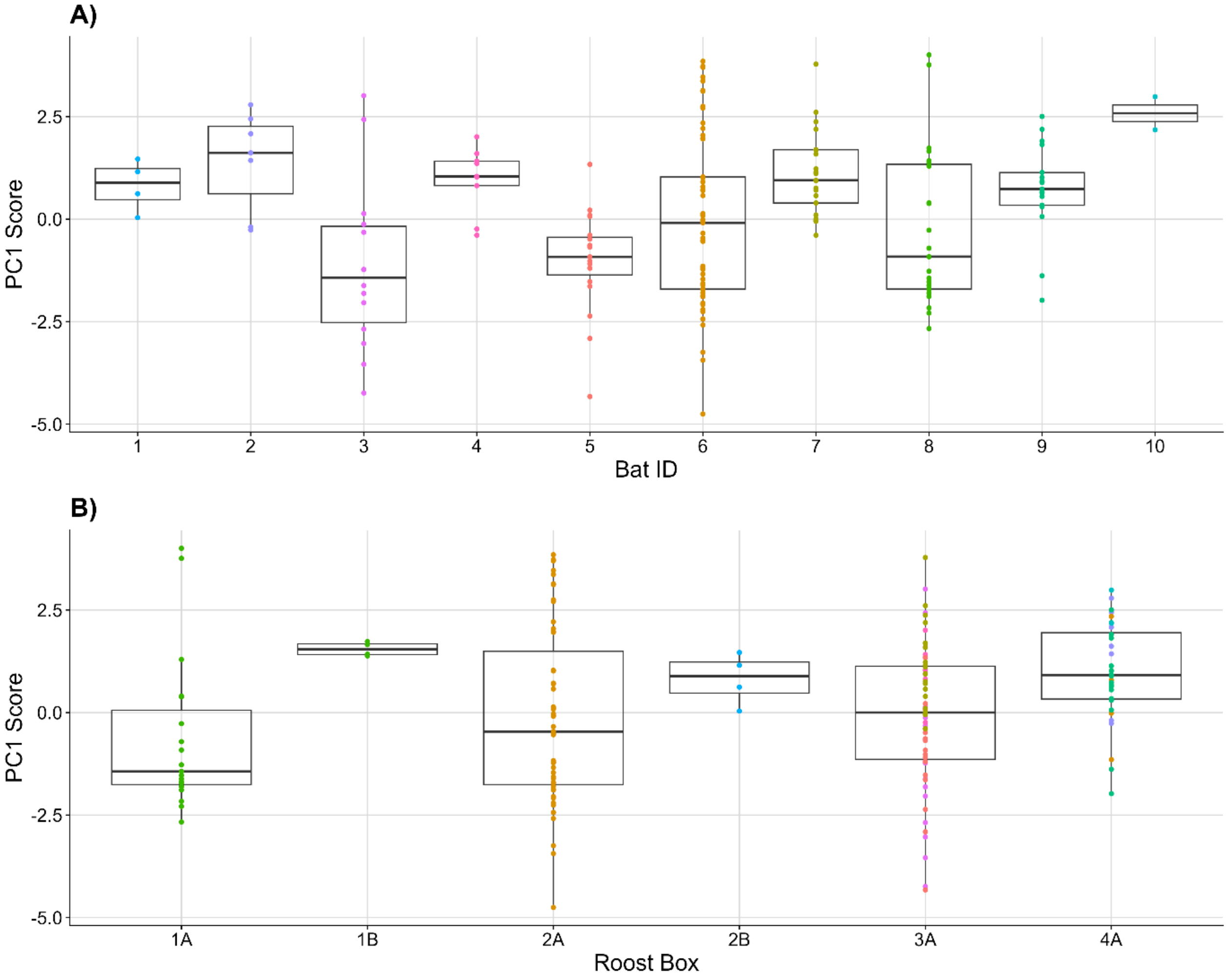

Figure 7: Comparison of PC1 values of **(A)** ten individual *N. lasiopterus* for which associated faecal data exists (bat ID is represented by integers 1-10), and **(B)** different roost boxes, with alphanumeric codes corresponding to four boxes (1-4) observed across two time periods (A-B). Datapoints in both plots are coloured by individual bat ID (note in plot B that some individuals share the same roost box, and that different individuals may occupy a given box across time periods).

3.3. Feeding behaviour and diet

PC1 was not a significant predictor of the per-box FO of any of the prey types recovered in faecal samples (Table 3).

Table 3: Summary of outputs from binomial GLMs predicting the per-box frequency of occurrence (FO) of each prey type (divided into seven taxa listed in the 'response' column) from PC1 of associated feeding events. In each model, PC1 was not found to be a significant predictor of prey FO, as shown by the estimate, standard error, confidence intervals, and p-value columns.

Response	Intercept	Estimate	Standard Error	95% Confidence Intervals		P-value
				Lower	Upper	
Carabidae	1.51	-0.02	0.06	0.88	1.09	0.73
Culicidae	2.58	0.13	0.07	0.98	1.31	0.09
Dytiscidae	1.92	-0.05	0.05	0.86	1.06	0.381
Lepidoptera	-0.25	0.07	0.04	0.99	1.17	0.09
Birds	0.02	-0.04	0.04	0.9	1.04	0.316
Tipulidae	-0.64	-0.02	0.04	0.9	1.07	0.64
Orthoptera	-0.81	0.04	0.05	0.95	1.15	0.35

4. Discussion

This study is a first step to understanding the fine scale feeding behaviour of a cryptic species of conservation concern: the greater noctule bat (*Nyctaulus lasiopterus*; Juste et al., 2016). This represents one of only a small number of attempts utilising accelerometers to examine feeding behaviour at the level of individual prey captures in insectivorous bats (see Stidsholt et al., 2018). Specifically, the stereotyped pattern of feeding in *N. lasiopterus* was documented, enabling the quantification of the inertial (i.e. VeSBA, smoothed heave) and biomechanical forces (i.e. VeDBA) associated with feeding behaviour (Gleiss et al., 2011). A biological interpretation of the accelerometer signals observed during presumed feeding events is given in the following sections. Systematic differences in feeding behaviour at the level of individual *N. lasiopterus* were also observed. By contrast, the lack of evidence for roost-specific foraging behaviour was unexpected, given the assumption that individuals sharing the same roost would be exposed to similar prey fields, and thus exhibit similarities in feeding behaviour compared with individuals from other roosts. The possible drivers of inter-individual differences in feeding behaviour are discussed, along with the implications of this for understanding prey selection in *N. lasiopterus.*

4.1. Presumed feeding behaviour

The present study takes advantage of the multi-dimensionality of accelerometer data to examine possible sources of variability in *N. lasiopterus* feeding behaviour, and underlines the importance of several key metrics as possible descriptors of prey type. That mean VeDBA was the main source of variability in *N. lasiopterus* feeding behaviour is not surprising. Measures of dynamic body acceleration (DBA), including VeDBA, are considered robust proxies for the metabolic power associated with various body movements (Fahlman et al., 2008; Gómez-Laich et al., 2011; Qasem et al., 2012; Wilson et al., 2020), and as such would be expected to vary with prey capture and handling effort. The concurrent importance of variance in X-axis acceleration attests to the fact that dynamic acceleration in the surge axis is instrumental in driving increased VeDBA during feeding (see equation 4). This is perhaps the result of rapid head and neck movements associated with prey handling and mastication following capture in the interfemoral membrane, leading simultaneously to appreciable but highly variable changes in body attitude, as supported by the secondary importance of pitch metrics as descriptors of feeding (postures described in aerial hawking *Myotis* *nattererii* by Siemers and Schnitzler, 2000, and shown by high-speed video in *Corynorhinus townsendii* by Corcoran and Conner, 2017). Rapid and erratic wingbeats performed to maintain altitude while the body is orientated away from the normal flight posture (Aaron Corcoran, 2013), leading the body to rock back and forth, may also explain oscillations in surge. Important variations in mean VeSBA and smoothed heave with PC1 are similarly intuitive: the subject pulls-*g* as it rapidly inverts its body preceding and during an attempted prey capture (Siemers and Schnitzler, 2000; Aaron Corcoran, 2013), inducing inertial forces in the direction of the heave axis while simultaneously reversing its sign (because the heave axis has been inverted with respect to gravity). The stooping courtship displays of Anna's hummingbirds (*Calypte anna*) are analogous to this phenomenon, with this species experiencing centripetal acceleration well in excess of the Earth's gravity (close to 10 *g*) when pulling out of rapid vertical dives (Clark, 2009). Accordingly, decreases in smoothed heave substantially below 0 *g* (negative by virtue of the directionality of inertia during inversion *c.f.* turning/circling in level flight: see Williams et al., 2015) were found to be a consistent feature of feeding behaviour in the present study. The dependence of VeSBA on the square of smoothed acceleration (see equation 5, section 2.2) dictates that it changes concurrently with smoothed heave acceleration, although with opposite sign, explaining why both metrics were correlated with PC1 with similar magnitudes but opposing directions.

4.2. Variation in feeding behaviour with respect to diet

Despite the importance of parameters with intuitive links to stereotyped patterns in feeding behaviour, and the expectation that these should vary in response to prey type, the present study detected no evidence of multiple types of feeding event. This is unexpected given the sensitivity of acceleration sensors sampling at 100 Hz to small changes in posture and dynamism (Wilson et al., 2014), combined with the range of prey sizes taken by *N. lasiopterus* (Smirnov and Vehknik, 2013), which should theoretically be associated with systematic differences in handling. Previous studies have documented discernible differences in accelerometer metrics according to prey type. For example, Wilson et al. (2013) described prey species-specific chase strategies in cheetahs (*Acinonyx jubatus*) based on variation in VeSBA over the course of a hunt. Specifically, sudden changes in direction, as indicated by the accumulation of static forces, become important to capture success relative to maximum velocity when chasing prey prone to highly angular escape trajectories. Similarly, Watanabe and Takahashi (2012) were able to detect Adélie penguin (*Pygoscelis adeliae*) prey capture events corresponding separately to krill and fish captures (verified using animal-borne video) using differences in the vectorial sum of acceleration derived from head-mounted accelerometers. Despite the apparent utility of accelerometry to this end, the present study was unable to generalise about how the multidimensional configuration of feeding events might relate to prey type.

The inability to discern variation in feeding events attributable to prey type raises questions about the validity of the behavioural algorithms outlined here to describing feeding behaviour. Confidence that the data analysed herein accurately reflect the behaviour of study subjects is high, owing to the fact that loggers attached using glue adhere closely to the body and thus minimise logger displacement (and subsequent noise in the data) independent of the subject's own body movements (*c.f.* collar-mounted accelerometers; Redcliffe, 2021; Wilson et al., 2021; Gunner et al., 2022). Careful deployment protocols and post-processing of data (see section 2.2) also ensured that the data were centred over each subject's centre of mass, and thus offered biologically meaningful insights into deviations in logger, and therefore bat, orientation with respect to gravity (Gunner et al., 2020). However, the difficulty of observing nocturnal volant study subjects in the field meant that the behavioural algorithm used to define feeding could not be subject to rigorous ground-truthing in the manner of studies focusing on (semi-) captive, habituated, or more sedentary and diurnal species (e.g. livestock: Riaboff et al., 2022; zoo animals: English et al., 2023; habituated meerkats; Chakravarty et al., 2019) for which real-time observational data is readily available. The attempt to characterise feeding behaviour in the present study therefore represents a 'best-guess', in need of validation. Future enquiries pertaining to this may seek to compare the behavioural signals defined here with accelerometer data collected alongside real-time footage from wind tunnels (Hedenström and Johansson, 2015), from high-speed video in the field (Corcoran and Conner, 2017), or from animal-borne biosonar detectors (Stidsholt et al., 2018; Hurme et al., 2019). Subject to miniaturisation and testing on insectivorous bats, the use of mandibular sensors (e.g. IMASEN) may provide a potential avenue to this end (Ropert-Coudert et al., 2004; Iwata et al., 2011).

Nevertheless, the choice of algorithm used here is justified to an extent by the biological intuition discussed previously. It is possible, however, that the present study neglects feeding behaviour atypical of the perceived 'stereotype', and is thus overly conservative in its estimation of feeding. Indeed, previous studies of aerial insectivores using high-speed video assumed any sudden change in heading to be associated with feeding (e.g. barn swallows, *Hirundo rustica;* Warrick et al., 2016), in contrast to the somewhat stricter classification used here. Furthermore, feeding buzzes recorded by Stidsholt et al. (2023) indicated a much higher prey attack rate in greater mouse-eared bats (*Myotis myotis*) than was observed in the present study, albeit in an opportunistic species which forages flexibly using both gleaning and hawking strategies (*c.f.* aerial hawking in *N. lasiopterus;* Russo, Jones, and Arlettaz, 2007). This may suggest that the feeding behaviour as defined herein fails to encapsulate all manners of prey capture in *N. lasiopterus.* In support of this, rapid increases in VeSBA and decreases in altitude, indicating sharp turning behaviour and rapid vertical transits, respectively, were observed incidentally in the data analysed here. While these behaviours were not considered to be consistently associated with feeding according to the behavioural algorithm defined, it is possible that they represent decisions in response to prey encounter (as in Warrick et al., 2016). Indeed, it is thought that deviations from a relatively straight movement trajectories are the product of decisions based on environmental stimuli (Potts et al., 2018; Munden et al., 2021), and optimal foraging theory posits that accepting the increased transport cost of turning should be associated with some energetic or fitness benefit (Wilson et al., 2021). Based on this rationale, it is feasible that the present study overlooks some facets of *N. lasiopterus* feeding behaviour, and it would therefore be beneficial to account for this shortcoming in future studies of the species' foraging ecology.

It is also possible that variability in feeding behaviour is not driven by prey selection to the extent previously hypothesised. Interestingly, the subjects studied here showed individual differences in feeding behaviour, but these similarities did not extend to the level of roost boxes. Differences in feeding behaviour attributable to prey type were expected to be reflected in similarities in feeding behaviour within roost boxes, on the basis that roost-mates should experience more similar prey fields than individuals occurring in different, more distant roosts. In addition, social foraging, including passive gathering of information from conspecific echolocation, has been recorded in other bat species (Dechmann et al., 2009; O'Mara and Dechmann, 2023), suggesting that proximal conspecifics may be instrumental in individual foraging decisions. That this was not reflected by roost-level differences in feeding behaviour suggests that individual variation may be governed more strongly by individual factors such as size, sex, and age. Niche partitioning is thought to mediate intraspecific competition in colonial species, and indeed sexual segregation in diet has been recorded in marine central-place foragers (Breed et al., 2006; Quintana et al., 2010), as well as

European free-tailed bats (*T. teniotis;* Mata et al., 2016). However, the details of the mechanisms by which this occurs have yet to be fully disentangled in bats. Naďo et al. (2019) postulated altitudinal partitioning of foraging habitat between male and female *N. lasiopterus,* but overall, too few tagging studies have examined sex-dependent foraging strategies in this species to be confident in the generality of patterns observed to-date. Future studies would therefore benefit from considering explicitly the role of demography and individual morphology in determining feeding behaviour, as well as the role of conspecifics in individual foraging decisions (i.e. social avoidance or facilitation). These recommendations are underpinned by the findings of the present study, which suggest that processes occurring at the individual level may be more important than spatial proximity to resources in shaping feeding behaviour.

4.3. Limitations

Compact sensors such as those employed here, while granting access to unprecedented insights into the behavioural ecology of a wide range of organisms, are limited by the ethical implications of tagging, and indeed by the impact of logger deployments on the behaviour of free-ranging study subjects (Vandenabeele, Wilson, and Grogan, 2011; McIntyre, 2015). Live trapping and handling can have implications for the physical welfare, stress, and survival of tagged individuals, not to mention the validity of scientific inference from organisms with disrupted behavioural regimens (Wilson et al., 2019; Lennox et al., 2022; Lobato-Bailón et al., 2023). Furthermore, the energetic cost of locomotion increases when animals carry an additional load, which is especially the case for small, volant species such as bats, where increased weight leads to higher wing loadings and lower flight speeds (Hughes and Rayner, 1991).

Given the difficulty of comparing tagged and unconstrained subjects outside of laboratory settings, conventionally accepted upper limits for the weight burden of loggers – quoted variably to be between 2-5% of the subject’s body mass (Rerucha et al., 2017; Hurme et al., 2019; Wilson et al., 2021) - must be evaluated critically on a study-to-study and species-to-species basis. In the present study, data were derived from tags weighing in excess of 5 % of *N. lasiopterus* body mass. In addition, the high mobility/ manoeuvrability of *N. lasiopterus* may necessitate that the behavioural inferences presented here are treated with caution, because acceptable weight thresholds are likely reduced in species with highly ‘athletic’ forms of locomotion (Wilson et al., 2021). Increases in *N. lasiopterus* body mass of up to 40% during a single night’s foraging may also complicate the choice of appropriate weight thresholds for this species (Vasenkov et al., 2020), as the burden of loggers may increase relative to the level of satiation and could therefore fluctuate drastically over short periods (Hughes and Rayner, 1991).

While not explicitly carried out here, validation of the choice of logger weight would benefit future studies of this nature. Some biologging studies attempt to validate the soundness of their tag deployments, both before (e.g. by observing the movement of tagged subjects under semi-restrained conditions) and after data collection (e.g. by evaluating body condition; see Hurme et al., 2019), but such approaches may be limited by survivorship bias resulting from unpredictable logger recovery (Rushing et al., 2021). Some dedicated studies have examined the effects of tagging outside of laboratory conditions (e.g. Chivers, Hatch, and Elliott, 2015; Wilson et al., 2019), but to the author's knowledge, no such analyses exist for insectivorous bats. Given the highly specialised manoeuvrable flight, relatively small size, and high metabolic requirements of these species (Norberg, 1994), examining the effects of bat-borne sensors is a crucial avenue for future research. Such research must also take into account the diverse spectrum of foraging strategies (e.g. gleaning, aerial hawking, trawling) and corresponding specialisations in wing morphology (e.g. wing loading and aspect ratio) exhibited by insectivorous bats (Altringham, 2011), which likely dictate species-specific tolerances to excess burden.

5. Conclusion

The present study makes a tentative step towards an understanding of feeding behaviour at the level of individual prey captures in *Nyctalus lasiopterus*: a cryptic bat species whose capacity for long, fast, high-altitude locomotion is only just beginning to be understood. For the first time in this species, or indeed across most insectivorous bats, the details of the physical and biomechanical processes occurring during individual feeding events are outlined. The paucity of such information, however, attests to the difficulty in interpreting behavioural states at high resolution, so the present study should be considered a starting point from which to validate and expand the behavioural inference presented herein. Attempts to do so will be facilitated by recent advances in tagging technology, enabling the integration of increasingly large amounts of spatial and behavioural data, including lightweight on-board ultrasonic sensors. Furthermore, in future, an approach combining the methods of the present study with detailed spatial analyses using GPS telemetry will foreseeably advance our ability to bridge the gap between bat foraging behaviour at small and relatively large scales, and thus build a thorough understanding of the mechanistic basis of bat movement patterns. Overall, such information could be instrumental in efforts to protect populations of *N. lasiopterus* – a species of conservation concern across Europe – from extrinsic threats such as collisions with wind turbines, urbanisation, and agricultural intensification, as indeed it will be relevant to similar efforts in other aerial insectivores.

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Appendix A

Table A1: Names and definitions of 16 accelerometer metrics derived from *N. lasiopterus* feeding events and used in Principal Component Analysis (PCA; see section 2.5.1).

Metric name	Definition
Smoothed Pressure (start)	Barometric pressure (averaged over a window of 0.3 s) at the start of a feeding event, indicative of altitude.
Mean VeDBA*	Mean vectorial dynamic body acceleration (VeDBA; see equation 4) across a feeding event.
Max VeDBA	Maximum vectorial dynamic body acceleration (VeDBA; see equation 4) measured during a feeding event.
Mean Pitch Angle**	Mean angle of logger inclination in the anterior-posterior axis (pitch; see equation 2) across a feeding event.
Max Pitch Angle**	Maximum pitch angle (see above; equation 2) measured during a feeding event.
Max Roll Angle	Maximum angle of logger inclination in the lateral axis (roll; see equation 3) measured during a feeding event.
Max Smoothed Sway	Maximum value measured in the Y (sway) axis, averaged over a window of 0.3 s (see equation 1), during a feeding event.
Mean Smoothed Heave	Mean acceleration in the Z (heave) axis, averaged over a window of 0.3 s (see equation 1), during a feeding event.
Mean Smoothed Surge	Mean acceleration in the X (surge) axis, averaged over a window of 0.3 s (see equation 1), during a feeding event.
Mean Dynamic Heave	Mean residual acceleration after subtracting smoothed from raw acceleration in the Z (heave) axis.
Mean Dynamic Sway	Mean residual acceleration after subtracting smoothed from raw acceleration in the Y (sway) axis.
Mean Dynamic Surge	Mean residual acceleration after subtracting smoothed from raw acceleration in the X (surge) axis.
Mean VeSBA *	Mean vectorial static body acceleration (VeSBA; see equation 5) across a feeding event.
Duration*	Total duration in seconds from the beginning to the end of a feeding event.
Variance in Surge*	Deviation of acceleration in the X (surge) axis from the mean calculated over a moving window of 0.3 s.

***Correlated with PC1, as shown by variable loadings (see Figure 5, section 3.2)**

****Correlated with PC2, as shown by variable loadings (see Figure 5, section 3.2)**