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Diverse behavioural responses of vampire bats to human disturbance revealed by state-space modelling of sparse GPS data.

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ABSTRACT

1. Human activities can alter animal movement, having unexpected consequences for disease transmission. In Latin America, culls of common vampire bats (*Desmodus rotundus*) for rabies control have been indicated to raise viral spatial spread by increasing long-range movement and inter-colony mixing among surviving bats, but behavioural responses to disturbance have not been quantified.
2. We used Global Positioning System (GPS) tags to track the movements of 93 vampire bats from 5 roosts in the Peruvian Andes over 9 nights after human disturbance (capture, handling and tag attachment). Responses to disturbance were modelled under a Bayesian state-space framework that estimated bat departure time, activity duration, and travel distances while accounting for the sparse GPS data obtainable in a topographically complex landscape where vampire bats occur.
3. A large fraction of bats (43%, 39/90) abandoned the study area on the night of disturbance, with more abandonment observed in groups expected to have greater dispersal capacity (males and bats with longer forearms). Among the remaining bats, we observed high individual heterogeneity on the night of disturbance, with some bats staying atypically close to the roost and others travelling unusually long distances. With increasing time post-disturbance, bats tended to remain closer to the roost.
4. Analysis of inferred flight histories showed that bats travelled >5 km on most nights, with high variability both within individuals across nights and between individuals in the same roost.
5. By inferring movement from irregular and error-prone data, our model extends the utility of animal-borne GPS tracking to landscapes with poor satellite visibility,

revealing greater complexity in vampire bat movement than previously recognised. Vampire bat disturbance was associated with three distinct behavioural responses: roost abandonment, increased flight distances and extreme individual heterogeneity on the night of disturbance. In the context of vampire bat management, such perturbations would be expected to exacerbate the spatial spread of rabies and potentially undermine the efficacy of culling activities which are currently practiced by most Latin American governments.

Key words: Bayesian integrated model, disease control measures, JAGS, perturbation effect, travel distance, wildlife management, wildlife telemetry, zoonoses

1| INTRODUCTION

Human-induced changes in animal movement can influence disease dynamics and increase spillover risk to humans or domestic animals by forcing the mixing of infected and uninfected populations, potentially increasing the incidence and spatial extent of pathogens (Blackwood et al., 2013). For example, in Brazil, urbanization and habitat loss forced non-human primates into cities potentially increasing human exposure to yellow fever virus (Couto-Lima et al., 2017). In Europe, badger culling for managing bovine tuberculosis increased survivors' ranging and dispersal behaviours, likely explaining increased tuberculosis risk in cattle outside of culled areas (Ham et al., 2019). Independently, disturbance may induce chronic stressors that diminish immunity and increase infection rate and intensity (Becker et al., 2018; Seltmann et al., 2017).

Bats are important reservoirs of zoonotic viruses including Nipah virus (Paramyxoviridae, *Henipavirus nipahense*), Hendra virus (Paramyxoviridae,

125 *Henipavirus hendraense*), Marburg virus (Filoviridae, Orthomarburgvirus), and
126 various Lyssaviruses (Calisher et al., 2006). The high mobility of bats arising from
127 their capacity for flight, together with their high sensitivity to human
128 disturbance - including occasional, deliberate human persecution - may
129 inadvertently increase human disease risk (O'Shea et al., 2016). Indeed, bat
130 disturbance has been linked to increases in the spread or incidence of both
131 rabies virus and Marburg virus (Amman et al., 2014; Streicker et al., 2012).
132 Despite the potential links between zoonotic risk and bat movement, few
133 studies have quantified how human disturbance affects bat movement, likely
134 due to challenges posed by bats' cryptic lifestyles and small size, which
135 restricts available tracking technologies (O'Mara et al., 2014). One study using
136 radiotelemetry revealed that disturbance from removal of big brown bats
137 (*Eptesicus fuscus*) from houses induced roost switching, potentially
138 exacerbating rabies virus transmission (Streicker et al., 2013). Another study
139 using Global Positioning System (GPS) tags in straw-coloured fruit bats
140 (*Eidolon helvum*) showed that disturbance from human capture led to
141 increased daytime movements (Costa et al., 2020). While these studies
142 suggest that human disturbance can affect bat behaviour, reactions and
143 intensity of responses may vary across species and types of disturbance.
144 In Latin America, *Desmodus rotundus* (the common vampire bat) is the
145 main reservoir of rabies virus (Rhabdoviridae, Lyssavirus), which causes
146 sporadic lethal outbreaks in humans and a sustained agricultural burden
147 through livestock mortality (Schneider et al., 2009). This species is routinely
148 disturbed during campaigns aimed at controlling vampire bat-transmitted
149 rabies (VBR). Sanctioned population control (culling) uses anticoagulant

150 poisons (‘vampiricides’) that can be topically applied to bats or injected into livestock
151 for later consumption by bats during blood feeding (World Health Organization,
152 2018). However, unsanctioned efforts to reduce vampire bat populations are
153 common and include direct killing of captured bats and destruction, sealing or
154 burning of roosts (O’Shea et al., 2016). Despite decades of culling, high VBR
155 burdens persist in enzootic areas and spatiotemporal analyses show viral
156 expansions into historically rabies-free regions of Latin America (Benavides et al.,
157 2016; Rojas-Sereno et al., 2022). Epidemiological models explaining the limited
158 efficacy of culls indicated that increased bat mixing after disturbance could raise
159 VBR incidence and local spillovers (Blackwood et al., 2013). Consistent with this
160 idea, evaluation of a large culling campaign in Peru showed that culling did not limit
161 rabies spillover to livestock, and culling in response to livestock rabies cases
162 (reactive culling) increased viral spatial spread, an effect that was hypothesized to
163 arise from increased movement of rabies-incubating bats (Viana et al., 2023). While
164 these observational studies suggest that culling affects bat movement with
165 downstream repercussions for rabies transmission, the behavioural responses of
166 vampire bats to disturbance remains unexplored.
167 Directly measuring the fine-scale behavioural response of vampire bats to
168 human disturbances is hampered by technical and ecological challenges. In mark-
169 recapture studies, low between-roost recapture rates limit inference on movement
170 (Britzke et al., 2014). Very High Frequency (VHF)-radio tracking has also been
171 applied, but it is labour-intensive, error-prone and only detects animal presence in
172 close proximity to antennas (Thomas et al., 2011). Use in vampire bats has thus
173 been limited to coarse-scale studies at foraging sites and identification of unknown
174 roosts (Rocha et al., 2020; Streicker et al., 2012). Recent advances in GPS allow for

the monitoring of animal movements at high spatial and temporal resolutions with lightweight tags equipped for remote data recovery, making them suitable for small animals such as bats (Kays et al., 2015). However, the reliance of GPS on satellite visibility introduces challenges in complex landscapes, including highly mountainous or densely forested areas. Indeed, to our knowledge, no GPS study on vampire bats has been reported.

Here, we used lightweight GPS tags to assess fine-scale movement of vampire bats in the Peruvian Andes in response to human disturbance, developing a new method to reconstruct movement despite the sparse and error-prone data expected from the obstructive local topography. We jointly reconstructed and identified ecological correlates of two fundamental metrics of movement: nightly departure time and distance from the roost at different times of the night. We hypothesised that bats would leave the roost under conditions of darkness at night, and that disturbance from capture, handling, and tagging, would induce roost abandonment and longer flights.

2| MATERIALS AND METHODS

2.1| Study area and design

The study was conducted between April 2022 and June 2023 in 5 vampire bat roosts, located >51.6 km apart (range 51.6-186 km). Roosts are in a region in southern Peru (departments of Ayacucho, Apurimac, and Cusco, AAC), that is characterised by rugged topography, with altitudes ranging from 1200 to 6000 meters (Fig. 1a). AAC is a hotspot of rabies in Peru, accounting for 60.2% of all reported livestock cases between 2003 and 2019, and this region is subjected to regular bat culls (Viana et al., 2023).

Vampire bats live below 3600 meters, roosting predominantly in natural caves, abandoned houses, mines, and irrigation canals (Benavides et al., 2016, 2020).

2.2| Data collection

Vampire bats were captured and handled under approved ethics protocols (University of Glasgow, EA28a/21) and permits from local authorities, including SERFOR (Servicio Nacional Forestal y de Fauna Silvestre, Nos. D000024-2022, D000107-2022, D000103-2024 and D000188-2024-MIDAGRI-SERFOR-DGGSPFFS-DGSPFS) and SERNANP (Servicio Nacional de Áreas Naturales Protegidas por el Estado, N° 021-2023-SERNANP-SHM/J).

Two capture and tagging sessions per roost were carried out from April to October (the Peruvian dry season), with at least three months between sessions. Roost 2 (Fig. 1c) had only one tagging session due to data recovery challenges. Each session aimed to tag 10 adult vampire bats (5 males, 5 females). All capture sessions began after dusk, except the first capture in April 2022, when due to logistical constraints, captures began in the morning. Vampire bats were captured using mist and butterfly nets. Captured bats were fit with a 3.5 mm wing ring (Porzana, UK), and weight (g), sex, reproductive status (non-reproductive, scrotal male, pregnant, or lactating female), age (adult, subadult, or juvenile), and forearm length (mm) were recorded. We applied lightweight GPS tags (2.8 g, 8 cm length [including a 5 cm antenna]; nanoFix®, PathTrack, UK) to bats that met specific inclusion criteria (see below). After light sedation using intramuscular (pectoral) injection (29-gauge needle, 1.0 mL syringe) of Ketamine (20–25 mg/kg) diluted in saline (NaCl) at a 50/50 volume ratio or Midazolam (0.25 mg/kg, used in 2023 to allow faster recovery times), GPS tags were attached to the skin of the dorsal side of

each bat using an absorbable suture (Monosyn®, B Braun), threaded through custom tag loops (Castle et al., 2015). According to the manufacturer, the absorbable sutures lose 50% of their strength after 14 days, allowing natural tag detachment. Prior to suturing, hair was trimmed, and a small amount of cyanoacrylate-based glue was used to secure the tags. Sedation and tag suturing were carried out by a veterinarian, ensuring it didn't impair flight or walking. GPS tags were painted with UV fluorescent paint to aid in recovery for reuse (Starglow®, Glowtec, UK).

GPS tagging was limited to healthy adult bats, excluding pregnant and lactating females. The average weight of tagged bats was 43.4 g (± 3.4 g, N=93), so the tags represented a maximum of 7% of the bat's weight (mean = 6.5 ± 0.48%, N=93). Recommendations for bat tracking studies indicate that attached devices should not exceed 10% of body mass, with a best practice of limiting to 5%. However, heavier tags are acceptable for short-term use in some species (Aldridge & Brigham, 1988; O'Mara et al., 2014). From our prior fieldwork, adult vampire bats (N=3,429) weigh, on average 41.9 g (± 8.44, N=2,751) and 51.5 g (± 9.1, N=678) after feeding, indicating nightly weight gains of over 9 g. Additionally, during pregnancy and after birth, females can weigh over 85 g and continue foraging. These observations indicate that the tags would be tolerable for short-term use.

During the initial deployment in April 2022, GPS tags were programmed to record locations every 5 minutes (10 tags) or 10 minutes (5 tags) for 3 and 6 nights, respectively. To extend tracking duration, later deployments used a 15-minute interval for 9 nights. Our model (see below) considered this difference between deployments and reconstructed distances from the roost

every 15 minutes. Tags operated nightly from 6 PM to 6 AM, with data stored onboard and downloaded remotely via one or two solar-powered UHF base stations (PathTrack, UK) placed near the roost.

2.3| Data cleaning

Data cleaning was performed in R version 4.4.0 (R Core Team, 2024). The nanoFix GPS tags require at least 4 visible satellites to record a position ('fix'). The number of visible satellites, along with an accuracy indicator for high satellite counts, determines the positional accuracy. Due to the complex topography of the Peruvian Andes, most GPS points were missing since <4 satellites were in range at the attempted connection time, resulting in a sparse and irregular dataset that required the model framework outlined below to reconstruct movement.

GPS fixes recorded before tag application and 1 hour after capture were removed to account for the tag attachment process. Data from the first night were otherwise included because quantifying the disturbance immediately after capture was one of our objectives. Cleaning of the remained data excluded: one inaccurate fix (6 satellites connected, but accuracy indicator >30, considered unreliable), all fixes from one bat with a malfunctioning tag (distances up to 6 km recorded before attachment), all data from 3 bats with <3 fixes across the study period, and all data from an unrealistically sessile bat (suggesting tag loss or death). As detailed in the supplementary information, we also removed GPS fix jumps, and outliers of estimated flight speed (Gupte et al., 2022). The speed (km/hour) of each segment between subsequent fixes was calculated, along with the Euclidean distance from the roost for each fix, using base R and the sf package (v1.0-19) (Pebesma, 2018). Our state-space model was designed to be robust to GPS errors, so we could have

omitted data filtering based on speed entirely. However, we anticipated that simultaneously inferring and filtering speed within the model could hinder convergence.

2.3.1| Variable definition and processing

We investigated predictors of bats' nightly departure time and distance travelled from the roost. Vampire bats are thought to be lunar phobic, departing before moonrise or after moonset (Crespo et al., 1972). We therefore modelled departure time as a function of the number of hours until complete darkness, which depended on the interplay of moonrise, moonset, astronomical night start (occurs after sunset and dusk) and end (occurs before dawn). For each roost and night, we calculated the hours from sunset until darkness using the *suncalc* package (v0.5.1) (Thieurmel & Elmarhraoui, 2022). We predicted that longer periods until darkness delay departure times. We also hypothesised that sex influences departure time, as female vampire bats, which maintain cooperative relationships that include behaviours such as visiting other roosts, might leave earlier in the night (Ripperger & Carter, 2021; Wilkinson, 1985).

Distance from the roost was modelled with variables related to roost location, individual bat characteristics, and human disturbance (Table S1). Roost-related variables within 5 km radii of roosts included proportion of permanent water, predicted vampire bat roost density (Ribeiro et al., 2023) and cattle density (Greenhall et al., 1983), calculated using the packages *sf* (v1.0-19) and *terra* (v1.7-71) (Hijmans, 2024; Pebesma, 2018). We predicted that the availability of alternative roosts and preferred food sources (cattle)

near the roost would reduce the distance bats travel. Since cattle graze near water and vampire bats can use rivers as corridors, we hypothesized that permanent water sources near roosts could aid prey searching, decreasing distances from the roost (Mialhe, 2013). Individual characteristics included bat sex and forearm length. We hypothesised that males would fly further distances due to reduced offspring care (Delpietro et al., 2017). As flight speed is correlated with forearm length, we expected a positive effect of bat forearm length on distance from the roost (Hopkins et al., 2003).

Human disturbance was defined as the effects of capture, handling, and tagging, with key variables being the night of capture ('night 0') versus subsequent nights, and the time (in hours) post-disturbance, calculated as the difference between the start of the tracking session and each GPS fix. We averaged time post-disturbance per bat and night to summarise nightly patterns, while reducing the effect of the irregular GPS fix intervals and potential autocorrelation. This also aligns with our model structure, which accounts for individual, roost and night effects. We anticipated that disturbance would increase flight distance following capture, with distances decreasing over time as behaviour normalised. Finally, because vampire bats in our study area are deliberately or accidentally disturbed by humans (e.g., capture, culling, roost destruction or shifts in agricultural practices), we also included a variable describing the number of rural human settlements within 5 km of each roost as a proxy for historical disturbance levels.

2.3.2| Modelling framework

We developed a Bayesian state-space model with two latent variables: the bats' departure time (t, in minutes since the daily activation of the GPS at 6 PM) and

its distance from the roost (ψ, in km). The model reconstructed distances from the roost every 15 minutes and estimated the duration of activity and return time to the roost, accounting for both process error (i.e., the natural stochasticity in the biological processes) and observation error (i.e., GPS measurement error). The model assumed nightly returns to the roost. Although our data indicated that returns occurred on at least 56.6% of bats and nights, this is likely a conservative estimate due to data limitations – including missed fixes during 15-minute intervals when bats departed or returned quickly, and signal loss at the roost – potentially leading to underestimation of return rates. We also assumed that most bats would depart before 1 AM, as our experiments were conducted on nights when the moon set before 1 AM in 95% of cases.

For each individual bat i and night j, $t_{i,j}$ is the departure time in minutes after 6 PM, with a maximum value of 420 minutes (1 AM). The expected and realised departure instances, $\bar{\tau}_{i,j}$ and $\tau_{i,j}$, are expressed as a proportion of the interval between 6 PM and 1 AM,

(1) $\tau_{i,j} = \frac{t_{i,j}}{420}$,

(2) $t_{i,j} = 420\tau_{i,j}$.

The expected departure instance $\bar{\tau}_{i,j}$ was modelled as a logit function of the number of hours until darkness and bat sex,

(3) $logit(\bar{\tau}_{i,j}) = \theta_0 + \theta_1 hours_dark_j + \theta_2 sex_i$.

$\tau_{i,j}$ was modelled by a Beta distribution, with mean $\bar{\tau}_{i,j}$ and a process error, quantified by the standard deviation of departure instance, σ (Table S2), capturing pooled inter-trip and inter-individual variation,

(4) $\tau_{i,j} \sim Beta(a_{i,j}, b_{i,j})$,

(5) $a_{i,j} = \bar{\tau}_{i,j}(\frac{\bar{\tau}_{i,j}(1-\bar{\tau}_{i,j})}{\sigma^2} - 1)$,

(6) $b_{i,j} = (1 - \bar{\tau}_{i,j})(\frac{\bar{\tau}_{i,j}(1-\bar{\tau}_{i,j})}{\sigma^2} - 1)$.

The duration of nightly activity after departure was modelled with a uniform distribution, assuming that once a bat departed, it remained away for at least 20 minutes. The maximum duration of a trip was the time left after departing and the end of GPS activation (720 minutes),

(7) $\Delta t_{i,j} \sim U(20, 720 - t_{i,j})$.

To estimate distances travelled from the roost, we defined a parametric model of distance against time, for each individual bat i, night j, and each block k of 15 minutes after 6 PM,

(8) $\bar{\psi}_{i,j,k} = \exp(\beta_0 - \frac{((k15 - t_{i,j}) - \Delta t_{i,j}\tau_{mid,i,j})^2}{(\Delta t_{i,j}\sigma_{mid,i,j})^2} + \beta_i night_j + \sum_{n=1}^{N} B_n X_{i,j,n} + \zeta_i)$.

This equation assumes that only one trip is made per night and is flexible regarding the point of start, end, and maximum distance. It also assumes that the net velocity is away from the roost until the maximum distance is reached, and then toward the roost thereafter, for 15-minute intervals. The exponential of the intercept β_0, corresponds to the maximum distance from the roost. β_i corresponds to the terms for the effect of night of disturbance ($night_j$) for each bat, and B_n is the parameter for the nth covariate effect (forearm length, sex, roost density, number of human rural settlements, cattle density, permanent water and time post-disturbance). We added an individual-level random effect ζ_i with mean 0 and standard deviation σ_1 ($\zeta_i = \mathcal{N}(0, \sigma_1)$), to capture the influence of individual variation (Table S2). In both departure time and distance models, we considered random effects of individual,

roost, calendar night, and session of capture. Only the random effect of individual on the distance model was relevant, hence it was kept.

The mid-point of the trip, $\tau_{mid,i,j}$, was defined as the proportion of time between departure and return until reaching maximum distance, with a parameter $\sigma_{mid,i,j}$, which made sure that the distance from the roost climbed smoothly from the start of the trip to the midpoint and then declined to the trip's endpoint, preventing unrealistic jumps in movement. $\tau_{mid,i,j}$ was given a beta prior distribution and was set to be close to the middle of the trip duration (mean 0.5 and variance 0.001). $\sigma_{mid,i,j}$ was fixed to a sufficiently large value to ensure that the bats did not immediately reach their maximum distance after departure or instantaneously returned to the roost,

(9) $\sigma_{mid,i,j} = \max\left(\tau_{mid,i,j}, 1 - \tau_{mid,i,j}\right)/2.$

The realisation of distance giving rise to observations, $\psi_{i,j,k}$, was modelled using a normal distribution, with mean $\bar{\psi}_{i,j,k}$ and variance $O_{i,j,k}$,

(10) $\psi_{i,j,k} \sim \mathcal{N}(\bar{\psi}_{i,j,k},\ O_{i,j,k})$, with $\psi_{i,j,k} \geq 0$ km.

$O_{i,j,k}$ is a combined error, that incorporates observation error $\xi_{i,j,k}$, the standard deviation of GPS error, and process error, in the form of an overdispersion parameter φ, to account for further uncertainty that cannot be explained by the observation model (i.e., 0.6 km is the GPS error for 4 satellites),

(11) $O_{i,j,k} = \xi_{i,j,k}^2 + 0.6\varphi^2.$

The overdispersion parameter φ was estimated by the model, but we encouraged it to be close to 0 (Table S2) to prioritize the identification of biological effects. Using data from a GPS tag placed at a single location in our study area, we fitted a regression of the standard deviation of distances against the number of satellites and

estimated the standard deviation of GPS error for each satellite count (standard deviation of 0.3 km when 4 satellites were visible; deviance explained = 0.986). This regression produced the two parameters γ_0 and γ_1 which, in combination with the number of visible satellites that generated each positional fix, $N_{i,j,k}$, informed $\xi_{i,j,k}$,

(12) $\xi_{i,j,k} = \exp\,(\gamma_1 + \gamma_2 N_{i,j,k})$.

We used Bayesian Stochastic Search Variable Selection (SSVS) with spike and slab priors to estimate model coefficients conditional to a variable being retained in the model (O'Hara & Sillanpää, 2009). If a variable was participating in the model, the coefficient value was given a normal distribution, with mean 0 and standard deviation τ_1, with τ_1 being estimated by the model, except for the coefficient for hours until darkness, which was given a gamma prior distribution to preserve its positivity (mean 0.01 and variance 0.0001). The posterior for the probability of retention ρ was modelled with a Bernoulli distribution (variable included or excluded), with the parameter ρ being estimated by the model with a constrained Beta prior (i.e., a variable has a 25% probability of being included), meaning that variables need strong evidence to be included.

To assess goodness of fit, we calculated the R^2 by comparing the observed and predicted distances from the roost. The models were fitted in JAGS 4.3.2 using rjags (v4-15) and runjags (v2.2.2-4) (Denwood & Plummer, 2024; Plummer, 2023). The model ran with four independent chains, for 10,000 samples per chain after discarding the first 500,000 interactions as burn-in, with thinning of 200 (retaining every 200th iteration). Convergence across chains was assessed through visual inspections of the posterior and the Gelman-Rubin diagnostic test (using coda (v0.19-4.1) (Plummer et al., 2006)). Table S2 lists the final model parameter priors and posteriors.

421

422 2.3.2.1| Drivers of roost abandonment

423 We fitted binomial generalised linear models (GLM) to examine whether
424 roost abandonment was associated with bat individual traits (sex, forearm
425 length, and weight), hypothesising that stronger bats (i.e., males, heavier, and
426 bats with longer forearms) would be less likely to return. Model performance
427 was compared across six models using the Akaike information criterion (AIC)
428 and pseudo-R^2.

429

430 3| RESULTS

431 Between April 2022 and June 2023, 93 adult vampire bats were GPS
432 tagged across 5 roosts in southern Peru (Table S3). Twenty-four percent of
433 tags (20/83) were recovered after use, most of them found inside roosts,
434 allowing partial redeployment. Among the 60 bats with recovered GPS data,
435 89% of possible observations (14,142 out of 15,842) were not recorded due to
436 having <4 visible satellites, leaving a total of 1700 GPS fixes. The night of
437 capture (‘night 0’) had the most fixes (24.7%), followed by ‘night 1’ after
438 capture (18.2%), ‘night 2’ (17.9%), ‘night 3’ (14.1%), ‘night 4’ (11.1%), ‘night 5’
439 (7.7%), ‘night 6’ (4.5%), ‘night 7’ (1.2%) and ‘night 8’ (0.6%). Data cleaning
440 excluded a further 22.3% of the fixes, leaving 1321 fixes from 55 bats (Fig.
441 S1). Visualization of the GPS data showed that vampire bats occasionally flew
442 to distances >5km from the roost but spent most time near roosts (Fig. 1b-f;
443 Fig.S2). Individual bats from the same roost foraged in different areas, did not
444 visit the same locations every night, and used a variety of flight paths,

445 highlighting great behavioural variation among and within individuals (Fig. 1b, d, e, f;
446 Fig. S3d, e).

447 Filtering out 3 bats which were confirmed dead, we recovered no GPS data
448 from 30 bats and 9 additional bats were not detected after night 0, indicating the
449 possibility that 43% (39/90) of bats abandoned our study areas following our capture
450 and tagging effort. While we cannot rule out tag loss or death of these missing
451 animals in unobservable locations within our study area, recapture data point to long-
452 or medium-term roost abandonment. Of the 51 bats which returned to the roost
453 according to GPS records, 15.7% were recaptured during capture sessions
454 immediately following the tracking period. In contrast, of the 39 missing bats, we
455 recaptured only 1 bat (2.6%) from roost 2 (where we faced challenges in recovering
456 data), while none from other roosts were recaptured. As missing bats would be
457 expected to have similar recapture rates if their apparent disappearance from the
458 study area was an artefact of GPS tag loss or failure, we would have expected at
459 least 6 recaptures. Moreover, during surveys conducted between 4-32 months after
460 GPS tagging, 5 of the missing bats (12.8%) were recaptured. Comparable long-term
461 recapture rates between bats that disappeared from the study area and those that
462 remained argue against disappearance being due to mortality.

463 A binomial GLM revealed that roost abandonment was non-random and
464 consistent with expectations of vampire bat dispersal biology. Bats with longer
465 forearms (-0.96 [SE = 0.35], P<0.01) and male bats (-1.11 [SE = 0.66], P=0.09) were
466 less likely to return to the roost, although there was only weak evidence for the latter
467 effect (Fig. 2; Table S4; Fig. S4). These findings strongly support considerable short-
468 term roost abandonment by vampire bats following disturbance. Complementing this,

469 the GPS data also revealed high variation in movement on the night of
470 disturbance across all roosts except roost 2, which had data from only one bat
471 (Fig. S5).
472 By fitting a Bayesian state-space model to the GPS data, we explored
473 correlates of departure time and maximum nightly distance from the roost. The
474 model gave a good fit to the data with an R^2 of 0.80 (Fig. S6), estimating that
475 bats typically departed ~2 hours after the GPS started at 6 PM (posterior
476 mean of 124 minutes, 95% credible interval (CI) [58.3; 220.5]) and were out of
477 the roost for <6 hours (345 minutes, 95% CI [190.0; 497.4]) (Fig. S7). The
478 number of hours until darkness had a small but significant effect on departure
479 time, with bats leaving the roost as soon as there was no sunlight or moonlight
480 (Fig. 3a; Table S5). Our model, which reconstructs the movement curve for
481 each bat, filling gaps due to missing observations, predicted larger distances
482 from the roost compared to observed data (Fig 3c-d). Within the distance
483 component of the model, time post-disturbance had a negative effect on
484 maximum nightly distance travelled from the roost (retention probability
485 [P]=0.95) (Fig. 3a, d; Table S5; Figs. S8-S9). This result indicates that bats
486 tended to fly further away after disturbance but then returned to their baseline
487 distances, with a decrease in maximum nightly distance of 0.17 km per night
488 (Fig. S8). The interaction between bat and night highlighted high heterogeneity
489 among individuals, particularly on the night of the disturbance, when some
490 bats stayed unusually close to the roost and others undertook the longest
491 movements recorded in the study period (Figs. 3b, 4; Table S6; Figs. S10-
492 S11).
493

494 4| DISCUSSION

495 Behavioural responses of wildlife to human disturbances can undermine
496 efforts to prevent disease spillover but fine-scale studies are currently restricted to
497 relatively large-bodied species and in simple habitats. By developing a Bayesian
498 state-space model to reconstruct movement histories from sparse and error-prone
499 GPS data from 93 vampire bats in the Peruvian Andes, we identified three
500 behavioural responses to human disturbance which could exacerbate rabies
501 transmission and dilute the effectiveness of bat population control efforts seeking to
502 prevent bat bites and rabies spillover.

503 First, we found that 43% of the GPS-tagged bats appeared to abandon the
504 roost, an effect that was unlikely to be explained by bat mortality or GPS failure.
505 Since return to the vicinity of the roost at any point in the study would have triggered
506 data upload to our receivers, we believe this indicates that bats left the study area, at
507 least for the 9-day duration of the study, though their destination is unknown. Given
508 that vampire bat dispersal is generally male-biased and that forearm length is linked
509 to flight ability, the finding of putatively stronger flyers more frequently disappearing
510 after tagging further supports transient roost abandonment (Delpietro et al., 2017;
511 Streicker et al., 2016). Although we cannot rule out the possibility that tags detached
512 in areas with poor satellite coverage, the small number of stationary tags detected,
513 and the absence of GPS fixes prior to this putative detachment makes this
514 explanation unlikely. We observed two other behavioural responses among bats that
515 remained detectable: a general tendency for longer distance movements after
516 disturbance and elevated individual heterogeneity on the night of capture.

517 Collectively, these three perturbations could have unintended consequences
518 for both the transmission and management of VBR. Roost switching following the

application of vampiricide poison would dilute local population reduction and may potentially disperse bats to lower density roosts or roosts where bats have fewer social connections, reducing the efficiency of poison transfer. Similarly, increased dispersal of rabies-positive vampire bats following disturbance is predicted to raise rabies incidence in bats from nearby roosts, potentially explaining findings why reactive culls increased livestock rabies risk in adjacent areas (Blackwood et al., 2013; Viana et al., 2023). Since viral spatial spread is believed to be strongly influenced by male bat movement, the tendency for male bats to abandon roosts after capture would be particularly problematic (Streicker et al., 2016). For future research, the effects of disturbance that we report are consistent with those from other mammals, indicating that studies seeking to understand the natural, post-disturbance behaviour of vampire bats using GPS tags should delay data recording for 4 nights (Stiegler et al., 2024).

A caveat when drawing conclusions about culling is that our study measured the effects of a relatively mild disturbance. While our disturbance shares similarities with culling - capture, handling, the application of a foreign object, and release - there are key differences. Vampire bats have strong cooperative networks, characterised by blood meal sharing and intense allogrooming, which could be disrupted by the sickness behaviours and mortality associated with poisoning (Carter & Leffer, 2015; Ripperger & Carter, 2021). As such, culls may lead to stronger effects on movement than the relatively mild disturbance we induced. Capture locations may also vary between our study and real-world management. While we carried out captures in roosts for greater tractability, this form of capture accounts for only 26% of

544 culling events, with captures at properties where bats attack livestock being more
545 common (Viana et al., 2023). Additional field experiments that separate effects of
546 human presence at roost sites, capture, handling and poisoning, could clarify
547 vampire bat population management.

548 High resolution GPS tracking also revealed that constraints on bat movement
549 and VBR spread may be less restrictive than implied by previous observational or
550 radiotelemetry data. For example, rather than consistently foraging downstream of
551 their roosts, following valleys or rivers we observed vampire bats travelling over
552 mountains and foraging in both directions along rivers (Ávila-Flores et al., 2019;
553 Trajano, 1996). Furthermore, similar to other colonial species such as seabirds,
554 vampire bats exhibited high movement behavioural heterogeneity within the colony
555 (Cleasby et al., 2023). Our data also challenge the notion that vampire bats return to
556 the same foraging location and even individual animals for blood feeding every night
557 (Greenhall, 1988). Overall, heterogeneity across individual bats and within bats over
558 short time periods helps explain the sometimes-sporadic evidence of vampire bat
559 bites on livestock and humans (Streicker & Allgeier, 2016) and implies that
560 pathogen-infected bats are likely to expose multiple animals at different locations.
561 Incorporating these behavioural ecological insights on vampire bats into models of
562 rabies spread could enhance our understanding of its dynamics.

563 Our study fills an analytical gap that has arisen between the declining size and
564 increasing battery life of GPS tags - which have expanded their applicability in
565 wildlife research - and the problematic data generated when such studies are
566 conducted in challenging habitats (D'Eon et al., 2002). The Bayesian framework,
567 which jointly estimated departure times and distances from a fixed starting point (the
568 roost), enabled inferences from sparse and irregular GPS data. While our objective

569 was not intended to infer exact animal locations throughout the night, it did
570 allow us to estimate how individual, landscape, disturbance and temporal
571 factors affected key characteristics of bat movement while accounting for
572 uncertainty. Furthermore, this approach enabled us to estimate the true
573 distances bats can travel - that are critical for disease management – but that
574 are often missed in sparse datasets, which tend to underrepresent maximum
575 distances (Hooten et al., 2017). By enabling inference from such a challenging
576 dataset, our approach extends the use of GPS tracking to other species and
577 environmental conditions where conventional analyses may fail or be strongly
578 biased by satellite visibility constraints.

579 A potential limitation of our approach are the assumptions that vampire
580 bats do a single trip and return to the roost every night. If some long-distance
581 movements instead reflect roost switching, our results may overestimate true
582 foraging distances; however, we note that eventual return to the roost was
583 required for data recovery so either behaviour reflects short term movements
584 after disturbance. The assumption of a single trip per night was broadly
585 supported by overall model fit and parameter convergence. However, a subset
586 of bat-nights (13%) showed non-convergence, resulting in a bimodal
587 distribution more consistent with multiple trips within a night (Fig. S10).
588 However, our model can identify such misspecifications and highlight that
589 vampire bats may undertake multiple trips per night. The significance of
590 multiple trips from a rabies perspective will depend on whether trips represent
591 scouting activities that inform foraging activities (e.g. evaluating lunar
592 brightness) or multiple bouts of foraging which would increase rabies
593 exposures in prey. Empirical data on vampire bat activity, roost-switching and

abandonment rates through automated radio frequency identification (RFID) systems would be useful to validate our interpretation.

Understanding animal movement in response to disturbance is important to design effective strategies for disease management but conventionally has been frustrated in some species and environments due to sparse data and error in movement data. This study provides evidence to support a change in the management of VBR. By enabling simultaneous inference and predictors of nightly movement curves for individual vampire bats, we show three responses to disturbance (increase in maximum distance travelled, individual heterogeneity in movement, and roost abandonment) which are compatible with the hypothesis that disturbing vampire bats by culling may trigger them to abandon the roost or to fly further, potentially promoting viral spread. Increased movement and roost abandonment immediately following disturbance from culling would also be expected to dilute the distribution of poison across roosts, potentially reducing efficacy. In contrast, disturbance induced movement could benefit the recently proposed application of vaccines with the capacity for self-dissemination since roost switching would 'seed' vaccine transmission to a larger number of roosts than previously appreciated (Griffiths et al., 2022). Most generally, our study highlights the value and analytical challenges of incorporating new data streams provided by increasingly accessible field-deployable technologies into wildlife ecology and management.

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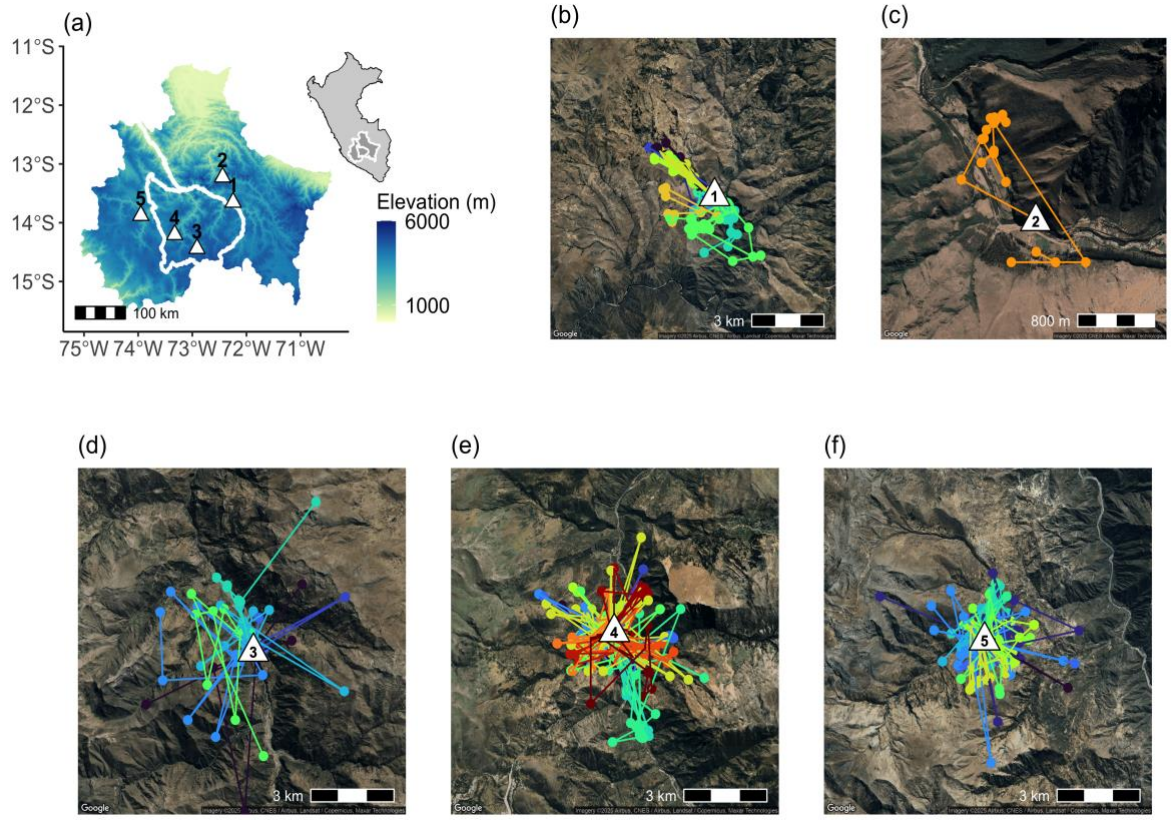

Figure 1: Study area and GPS data from 55 bats (1 colour, 1 bat) captured from 5 roosts (numbered triangles) and tracked for up to 9 nights. (a) Elevation map with the 5 study roosts in AAC, with an inset map of Peru highlighting the study region. (b) roost 1, (c) roost 2, (d) roost 3, (e) roost 4 and (f) roost 5. Due to the varying scales of movement across the roosts, this figure does not use a standardised scale, and only 95% of the fixes closest to the roost were plotted to avoid outliers. Maps used ggmap (Kahle & Wickham, 2013).

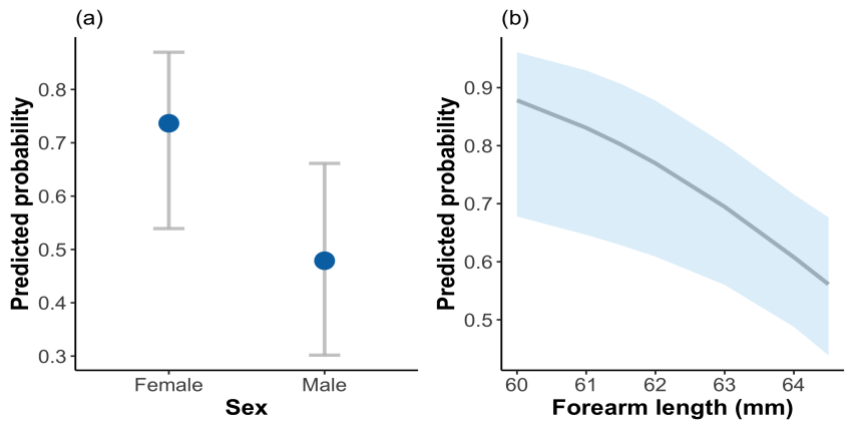

Figure 2: Predicted probabilities of vampire bats returning to the roost following disturbance, from a binomial GLM. (a) Shows sex-specific estimates with 95% confidence intervals; (b) shows the relationship of probability of return with forearm length (mm), with the 95% confidence interval shaded.

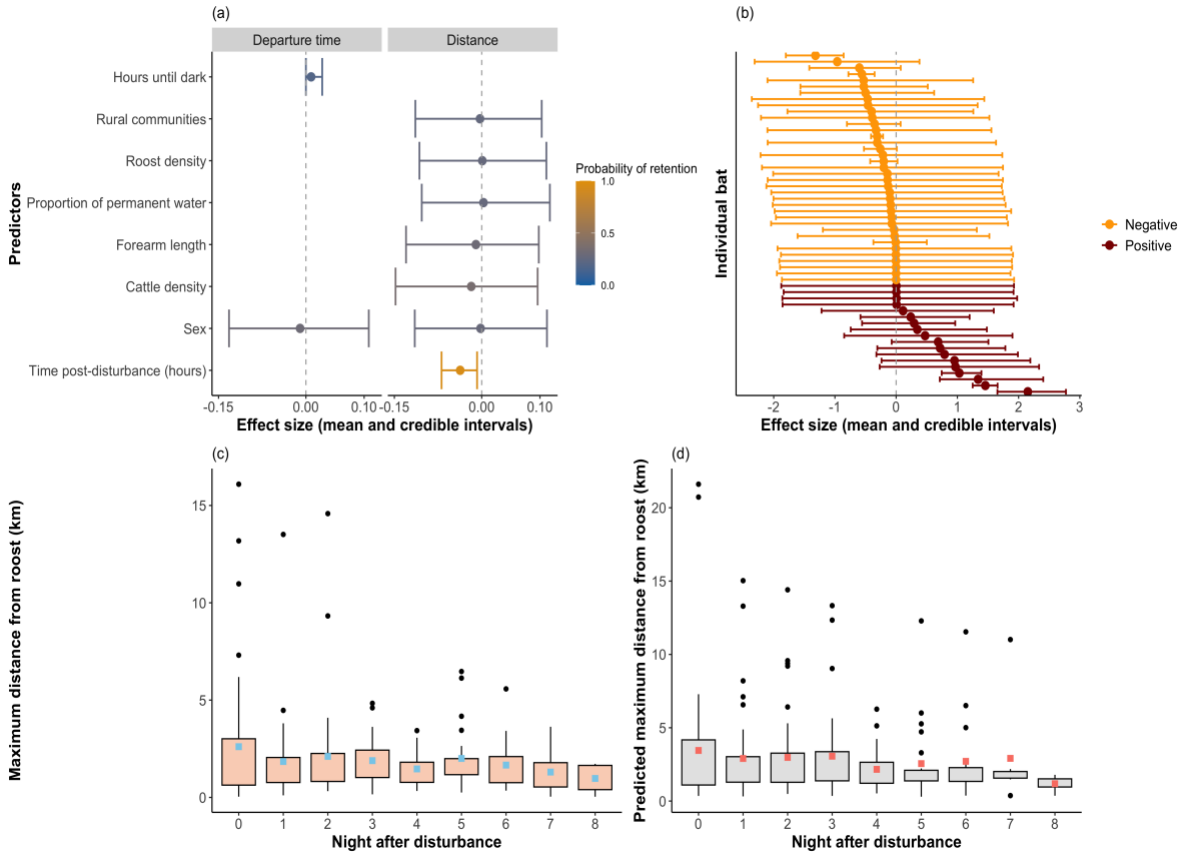

Figure 3: Predictors of vampire bat departure time and distance from the roost. (a) Standardised effect sizes on the log-odds scale (departure time, logit model) or log scale (distance, exponential model), coloured by SSVS retention probability. (b) Individual variation in the distance from the roost on the disturbance night (bat-night interaction). (c) Observed maximum distances (km) from the roost per bat and night. (d) Predicted maximum distances (km) per bat and night. In (c) and (d), night 0 is the disturbance night; squares indicate means, and black dots are outliers.

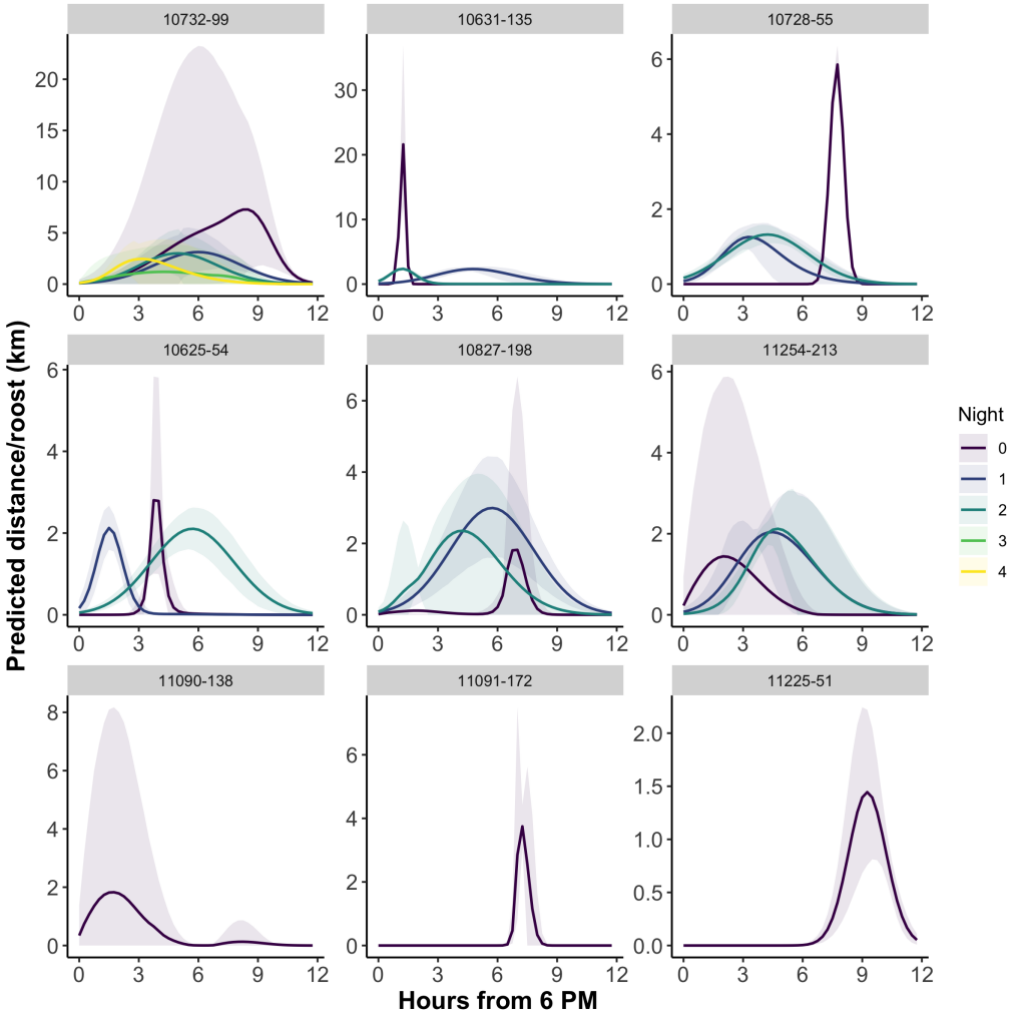

Figure 4: Reconstructed movement curves for 9 bats across 9 nights. First row: bats that travelled longer distances on night 0; middle row: bats that travelled similar

distances across different nights; bottom row: bats that left the roost after night 0 and did not return. The shaded area indicates the credible intervals. Purple lines indicate night zero, with progressively lighter colours indicating later nights. Due to the varying scales of movement, the y-axis is not standardised.