Roost abandonment and behavioural shifts following human disturbance of vampire bats in complex landscapes

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Abstract

Background Geomorphologically complex landscapes constrain animal movement and, therefore, the spatial spread of host-associated pathogens. Monitoring animal movement in such landscapes is required to understand these processes but remains challenging because structural barriers to animal movement (forests, mountains) also disrupt the visibility and signal quality of satellites used by animal-borne Global Positioning System (GPS) tags. In Latin America, rabies transmitted by vampire bats (*Desmodus rotundus*) epitomises this challenge: viral spread is strongly constrained by mountains and may be exacerbated by bat dispersal responses to human disturbance.

Methods We used GPS tags to track the post-disturbance (i.e., capture, handling and tagging) movement of 93 vampire bats from five roosts in the highly complex

landscape of inter-Andean valleys in Peru, where signal degradation reduced usable data by 89%. To overcome this data sparsity, the information gap needed to be filled by modelling and data imputation. Therefore, we developed a probabilistic Bayesian state-space model to infer the movement dynamics of vampire bats and to identify correlates of departure time and distance from the roost, with a focus on disturbance effects.

Results Immediately following the disturbance of capture, 43% of bats, particularly males and stronger flyers, disappeared from their roosts for the remainder of the study period, suggesting an acute disturbance response. For the 55 remaining GPS-tagged vampire bats, we observed longer flight distances and high individual heterogeneity on the night of disturbance, with bats gradually remaining closer to the roost over the 9-day study period.

Conclusions Roost abandonment and expanded foraging areas are expected to exacerbate rabies spread, demonstrating how human disturbances that alter animal movement may have unintended consequences for disease transmission. More generally, our Bayesian model accounting for GPS uncertainty and missing data extends the utility of animal-borne tracking to species living in complex landscapes with poor satellite visibility.

Keywords Bayesian integrated model, disease control, elevation, Lyssavirus, perturbation effect, maximum distances, topography, wildlife management, satellite tracking, zoonoses

Background

The composition and geomorphological structure of landscapes are fundamental determinants of how animals move within their environment and therefore of how host-associated infectious diseases spread. For example, large urban areas shape the movement of bobcats (*Lynx rufus*) and their Feline Immunodeficiency Virus (Retroviridae: Lentivirus), while in less urban areas, the same virus in puma (*Puma concolor*) is structured by mountain ranges and other factors that determine host-relatedness and spatial proximity (1,2). Pathogen spread within or across complex landscapes may also influence management decisions. For example, the fungal pathogen *Batrachochytrium dendrobatidis* has spread through complex mountainous landscapes in Latin America, causing major amphibian declines; the capacity to forecast spatial and temporal spread would be valuable for invasion monitoring or prevention (3). The adoption of smaller, lighter and longer-lasting animal-borne Global Positioning System (GPS) tags has the potential to revolutionise our understanding of pathogen spread by providing a mechanistic understanding of the underlying animal movements (4). While declining size and capacity to remotely download data without recapture means such tags can now be applied to a larger number of wildlife species than ever before, satellite obstructions remain a limiting factor, particularly for animal species that live in complex habitats such as dense forests or mountains that block GPS signals. Currently, inferring animal movement in such habitats is frustrated by imprecise or entirely missing data points.

In Latin America, rabies transmitted by vampire bats (*Desmodus rotundus*) represents a key example of how uncertainty in animal movement through complex landscapes impedes control of an important disease. In this region, vampire bats are

95 the main reservoir of the rabies virus (Rhabdoviridae, Lyssavirus), which causes
96 sporadic lethal outbreaks in humans and a sustained agricultural burden through
97 livestock mortality (5). Outbreaks can spread as epizootic waves into historically
98 rabies-free areas. In mountainous regions, such as the Andes of Peru, spread is
99 highly constrained by terrain and varies considerably in speed, from about 9-20 km
100 per year (6,7). Moreover, invasions appear to be accelerated by efforts to control bat
101 population sizes through sanctioned use of anticoagulant poisons ('vampiricides') or
102 unsanctioned killing of captured bats and destruction, sealing or burning of roosts
103 (8–10). Consistent with this idea, evaluation of a culling campaign in Peru showed
104 that culling in response to livestock rabies cases increased viral spatial spread, an
105 effect that was hypothesised to arise from increased movement of rabies-incubating
106 bats (9). While these observations suggest that culling affects bat movement with
107 downstream repercussions for rabies virus transmission, the behavioural responses
108 of vampire bats to disturbance remain speculative.

109 In principle, GPS tracking of vampire bats could test how land use, landscape
110 geomorphology or human disturbance affect bat movement, connecting colonies and
111 allowing the rabies virus to spread to new areas. Indeed, analogous approaches
112 combining experimental perturbation and GPS tracking in topographically simpler
113 landscapes (i.e. flat farmland with forest patches) revealed increased ranging and
114 dispersal behaviours in badgers (*Meles meles*) that survived culls, likely explaining
115 increasing tuberculosis (*Mycobacterium bovis*) risk in cattle outside of culled areas in
116 the United Kingdom (UK) (11). Although recent technological advances, including
117 smaller size and remote data recovery, allow GPS monitoring of small animals such
118 as bats, reliance on satellite visibility introduces challenges in complex landscapes
119 where vampire bats occur and where the rabies problem can be most acute (6,12).

120 Indeed, to our knowledge, no GPS study on vampire bats has been reported.
121 Alternative techniques to directly measure fine-scale behaviour in vampire bats are
122 precluded by technical and ecological challenges. In mark-recapture studies, low
123 between-roost recapture rates limit inference on movement (13). Very high
124 frequency (VHF)-radio tracking has also been applied, but is labour-intensive, error-
125 prone and only records animal presence near antennas (14). Use of these methods
126 in vampire bats has thus been limited to coarse-scale studies at foraging sites and
127 identification of unknown roosts (15,16). Overcoming the limitations of GPS satellite
128 visibility and signal quality would therefore represent a major opportunity to study the
129 relationships between landscape composition, human activity and infectious disease
130 spread in geomorphologically complex areas.
131 We used lightweight GPS tags, enabling remote data recovery, to assess fine-
132 scale movement of vampire bats in response to human disturbance (i.e., from
133 capture, handling, and tagging). We focused on the Apurimac, Ayacucho and Cusco
134 (AAC) departments in the Peruvian Andes, where bats live within a network of
135 interconnected inter-Andean valleys. The AAC is a hotspot of vampire bat rabies
136 (VBR) in Peru, accounting for 60.2% of all reported livestock cases between 2003
137 and 2019. This region is subjected to regular bat culls and has experienced wave-
138 like invasions of rabies into historically rabies-free areas (9). To address the
139 challenges imposed by the obstructive local topography, we developed a new
140 Bayesian state-space method to reconstruct times and distances from sparse and
141 error-prone GPS data (17). This model characterised the trips of individual bats,
142 addressing data sparsity by 1) simultaneously reconstructing and identifying
143 ecological correlates for two key movement metrics, nightly departure time and
144 distance from the roost every 15 minutes of a night; and 2) fitting the model to all

145 bats at once, which allowed the full dataset to be used to inform and fill in missing
146 data. This approach leveraged all available information to statistically impute missing
147 data and propagate the uncertainty, resulting in more robust inference from sparse
148 datasets than conventional interpolation methods. We first investigated the causes of
149 immediate roost switching or abandonment after disturbance (hereafter, roost
150 abandonment, defined as the non-recapture of bats and non-recovery of GPS data
151 after disturbance during the study period). Then, for the bats that remained in the
152 roost, using the Bayesian model, we tested the hypothesis that disturbance would
153 induce longer flights.
154

155 ## Methods

156 **Study area and design**

157 The study was conducted during the Peruvian dry season, between April-
158 October 2022 and May-June 2023, in five vampire bat roosts (Table S1), each
159 located >50 km apart in southern Peru. The study area is characterised by rugged
160 topography, with altitudes ranging from 1200 to 6000 meters, with vampire bat
161 presence and rabies virus spread constrained to elevations below ca. 3600 meters
162 (6) (Fig. 1a).

163 At each roost, two capture and tagging sessions were carried out, with a
164 minimum interval of three months. Roost 2 (Fig. 1c) had a single tagging session due
165 to data recovery challenges. Each session aimed to tag 10 adult vampire bats (five
166 males, five females). All capture sessions began after dusk, except the first capture
167 in April 2022, when, due to logistical constraints, captures began in the morning.
168 Short-term follow-up recapture sessions (one to two nights) were conducted at the

169 end of the GPS-tracking study, whereas long-term sessions occurred during
170 subsequent tagging rounds or in later years to monitor colony dynamics (Table S1).
171

172 **Capture and handling of vampire bats**

173 Vampire bats were captured using mist and butterfly nets. Captured bats were
174 fitted with a 3.5 mm wing ring (Porzana, UK), and weight (g), sex, reproductive status
175 (non-reproductive, scrotal male, pregnant, or lactating female), age (adult, subadult,
176 or juvenile), and forearm length (mm) were recorded. We applied GPS tags (2.8 g, 8
177 cm length [including a 5 cm antenna]; nanoFix®, PathTrack, UK) to bats that met our
178 inclusion criteria (see below). After light sedation using intramuscular (pectoral)
179 injection (29-gauge needle, 1.0 mL syringe) of Ketamine (20–25 mg/kg) diluted in
180 saline (NaCl) at a 50/50 volume ratio or Midazolam (0.25 mg/kg, used in 2023 to
181 allow faster recovery times), GPS tags were attached to the skin of the dorsal side of
182 each bat using an absorbable suture (Monosyn®, B Braun), threaded through
183 custom tag loops (18). According to the manufacturer, the absorbable sutures lose
184 50% of their strength after 14 days, allowing natural tag detachment. Before suturing,
185 hair was trimmed, and a small amount of cyanoacrylate-based glue was used to
186 secure the tags. Sedation and tag suturing were performed by a veterinarian,
187 ensuring it did not impair flight or walking. GPS tags were painted with UV
188 fluorescent paint to aid recovery for reuse (Starglow®, Glowtec, UK).

189 GPS tagging was limited to healthy adult bats, excluding pregnant and
190 lactating females. The average weight of tagged bats was 43.4 g (± 3.4 g, N=93),
191 44.1 g (± 3.3 g, N=43) for females and 42.7 g (± 3.4 g, N=50) for males. For both
192 sexes, the tags represented a maximum of 7% of the bat's weight (mean = 6.4 ±
193 0.47% for females and mean = 6.6 ± 0.47% for males). 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 considered acceptable for short-term use in species with high physiological tolerance for weight change (19,20). Our previous records of wild adult vampire bat mass (N=3,429 individuals) showed that they can gain over 9 g of weight after feeding (pre-feeding: 41.9 g ± 8.44, N=2,751; post-feeding: 51.5 g ± 9.1, N=678), implying daily weight gains of >20% of body mass. Additionally, during pregnancy and after birth, females can weigh over 85 g and continue foraging with their pups attached. These weight fluctuations and their ability to carry significant additional mass strongly indicate that the tags we used should be tolerable for short-term use.

During initial deployment in April 2022, GPS tags were set to record locations every 5 minutes (10 tags) or 10 minutes (five tags) for three and six nights, respectively. To extend the duration of tracking for up to 9 nights in subsequent sessions, later deployments used a lower temporal resolution of 15 minutes (see later sections for how data with different time intervals were integrated). 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.

Ethical approval and permits for the capture, handling, and GPS tagging of vampire bats were granted by the Research Ethics Committee of the University of Glasgow (Reference EA28a/21) and by Peruvian national 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).

Data cleaning and management

According to the manufacturer, the nanoFix GPS accuracy depends on signal quality and the number of satellites tracked by the tag. Specifically, tags require at least four visible satellites to record a position ('fix') such that fixes with fewer than 4 satellites are automatically not available and not recoverable. Due to the complex topography of our study area, 89% of the GPS points were not recoverable, resulting in a sparse and irregular dataset. Prior to developing the modelling framework outlined below to reconstruct movement from such data, we carried out manual data cleaning in R version 4.4.0 (21). Specifically, 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 remaining data included one inaccurate fix flagged by the software, all fixes from one bat with a malfunctioning tag (distances up to 6 km recorded before attachment), all data from three bats with less than three fixes across the study period, and all data from an unrealistically sessile bat (suggesting tag loss or death). As detailed in the supporting information (S1), we also removed GPS fix jumps and outliers of estimated flight speed (22). 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) (23). 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.

To manage the three sampling rates (5, 10 and 15 minutes) and provide a uniform input for the Bayesian model, each GPS fix was assigned to a 15-minute block during the night. The model's input matrix was constructed from these blocks (i.e., 48 15-minute blocks between 6 PM and 6 AM of the following day), with each block recorded as either containing an observed distance from the roost or marked as missing (NA).

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 (24). 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) (25). We predicted that longer periods until darkness would delay departure times. We also tested whether sex influences departure time.

We modelled distance from the roost as a function of variables related to roost location, individual bat characteristics, and human disturbance. Roost-related variables within 5 km radii of roosts included proportion of permanent water, predicted vampire bat roost density (26) and cattle density (27) (Table S2), calculated using the packages *sf* (v1.0-19) and *terra* (v1.7-71) (23,28). We predicted that the availability of alternative roosts and preferred food sources (cattle) near the roost would reduce the distances travelled. Since cattle graze near water and vampire bats can use rivers as corridors, we hypothesised that permanent water

268 sources near roosts could aid prey searching, decreasing distances from the roost
269 (29). Individual characteristics included bat sex and forearm length. We
270 hypothesised that males would fly further distances and would be more likely to
271 abandon their roosts after capture due to reduced offspring care (30). We also
272 expected that individuals with longer forearms may travel farther from the roost or
273 would be more likely to switch roosts after capture, since forearm length scales with
274 wingspan and area, providing a proxy for wing loading and flight speed (31,32), and
275 is positively associated with migration distance in bats (33).
276 Human disturbance was defined as the effects of capture, handling, and
277 tagging. Key variables included the night of capture ('night 0') versus subsequent
278 nights, and the time post-disturbance, calculated as the difference in hours between
279 the start of the tracking session and each GPS fix date and time stamp. We
280 averaged the time post-disturbance for each bat and each night to obtain a single
281 value per bat per night. Averaging reduced the influence of irregular GPS fix intervals
282 and temporal autocorrelation, and provided a covariate structure consistent with our
283 model, which included effects of individual, roost and night. We anticipated that
284 disturbance would increase flight distance following capture, with distances
285 decreasing over time as behaviour normalised. Finally, because vampire bats in our
286 study area are deliberately or accidentally disturbed by humans (e.g., capture,
287 culling, roost destruction or shifts in agricultural practices), we included the number
288 of rural human settlements within 5 km of each roost as a proxy for historical
289 disturbance levels, allowing us to isolate the effects of the immediate disturbance
290 caused by our capture, handling and tagging from longer term behavioural effects
291 arising from historical persecution (Table S2).
292

293 **Drivers of roost abandonment**

294 By placing UHF base stations at roost sites, we were able to monitor whether
295 GPS-tagged bats returned to the roosts where they were first tagged during the 9
296 nights of GPS tracking. An absence of recorded GPS data from base stations across
297 the study period, therefore, indicated roost switching or, at a minimum, short-term
298 roost abandonment. We fitted binomial generalised linear models (GLM) to examine
299 whether roost abandonment was associated with individual bat traits (i.e., sex and
300 forearm length). Vampire bat weight was not included because it fluctuates
301 considerably within a night, depending on feeding and time since feeding.
302 Nevertheless, with this caveat, for each bat, the percentage of body mass
303 represented by the tag was treated as a fixed covariate to evaluate the potential
304 influence of tag burden on roost abandonment behaviour. We assessed
305 multicollinearity between variables by calculating variance inflation factors, adopting
306 a threshold of 2.5 as an indicator of high multicollinearity (34). Model performance
307 was compared across 14 models (single effect models and their interaction terms)
308 using the Akaike information criterion (AIC) and pseudo-R^2. Nested ANOVAs were
309 used to test the statistical significance of interaction terms and added variables.
310

311 **Modelling framework to infer bat movement metrics**

312 We developed a Bayesian state-space model with two latent variables: the
313 bats' departure time (t, in minutes since the daily activation of the GPS at 6 PM) and
314 its distance from the roost (ψ, in km). The model reconstructed distances from the
315 roost every 15 minutes and estimated the duration of activity and return time to the
316 roost, accounting for both process error (i.e., the natural stochasticity in the biological
317 processes) and observation error (i.e., GPS measurement error). To reconstruct

nightly trips for each bat and distances from the roost, the model needs to have a known starting and ending point. Hence, we assumed that each trip begins and ends at the main roost. Although this assumption could be challenged by the potential use of multiple roosts, a preliminary analysis showed that at least 56.6% of bats-nights returned to the roost, as indicated by GPS fixes near the roost the following morning. This estimate is likely conservative due to data limitations, such as missed fixes during rapid returns and signal loss at the roost, which may underestimate actual return rates. We also assumed that most bats would depart before 1 AM, as 95% of our experiments were conducted on nights when the moon set before 1 AM.

For each 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 using a Beta distribution with mean $\bar{\tau}_{i,j}$ and a process error quantified as the standard deviation of departure instances σ. This error represents variability in trip start times and was assigned a wide prior (estimated by the model, table S3), to capture 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) $b_{i,j} = \left(1 - \bar{\tau}_{i,j}\right)\left(\frac{\bar{\tau}_{i,j}\left(1-\bar{\tau}_{i,j}\right)}{\sigma^2} - 1\right)$.

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

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

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

This equation assumes that only one trip is made by each bat every night (i.e., the bat leaves the roost, travels to a destination and then comes back), but is flexible regarding specific details of the trip, such as when it starts, ends, and maximum distance from the roost. 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 ($\zeta_i = N(0, \sigma_1)$), to capture the influence of individual variation (Table S3). 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 the 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) $\sigma_{mid,i,j} = \left(\tau_{mid,i,j}, 1 - \tau_{mid,i,j}\right)/2$.

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) $\psi_{i,j,k} \sim N(\bar{\psi}_{i,j,k},\ O_{i,j,k})$, 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., in equation 11, 0.6 km is the GPS error for four satellites, the minimum number of visible satellites required),

(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 zero (Table S3) to prioritise the identification of biological effects. The nanoFix manufacturer indicated using the number of visible satellites to estimate GPS error. 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 four 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 on a variable being retained in the model (35). 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.

We assessed goodness of fit by calculating the R^2, comparing observed distances from the roost to the posterior predicted distance for every single GPS fix, both for the entire model and for each bat separately. The models were fitted in JAGS 4.3.2 using rjags (v4-15) and runjags (v2.2.2-4) (36,37). The model ran with four independent chains, for 10,000 samples per chain after discarding the first 500,000 iterations 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) (38)). Table S3 lists the final model parameter priors and posteriors.

Results

Between April 2022 and June 2023, 93 adult vampire bats were GPS tagged across five roosts in southern Peru (Table S1). Twenty-four percent of tags (20 out of 83 tags used) were recovered after use, most of them found inside roosts, allowing partial redeployment. Among the 60 bats with recovered GPS data, 89% of possible observations (14,142 out of 15,842) were not recorded due to having less than four visible satellites, leaving a total of 1700 GPS fixes. GPS fix availability was highest on the night of capture (‘night 0’, 24.7%), followed by ‘night 1’ after capture (18.2%), and generally declined each subsequent night to a minimum of 0.6% on ‘night 8’ after capture (Fig. S1). Data cleaning excluded a further 22.3% of the fixes, leaving 1321 fixes from 55 bats (Fig. S2). Visualisation of the GPS data showed that vampire bats occasionally flew to distances higher than 5 km from the roost but spent most time near roosts (Fig. 1b-f; Fig. S3). Individual bats from the same roost foraged in different areas, did not visit the same locations every night, and used a variety of flight paths, highlighting behavioural heterogeneity among and within individuals (Fig. 1b, d, e, f; Fig. S4d, e).

Filtering out three bats which were confirmed dead, we recovered no GPS data from 30 bats, and nine additional bats were not detected after ‘night 0’, indicating the possibility that 43% (39/90) of bats left our study areas following our capture and tagging effort. While we cannot rule out tag loss or death of these missing animals in unobservable locations within our study area, recapture data point to short-or medium-term roost abandonment rather than death or tag loss.

439 Specifically, of the 39 bats which disappeared, we recaptured only one (short-term
440 recapture rate = 2.6%) during capture sessions immediately following each tracking
441 period. In contrast, of the 51 bats that we were able to GPS track, eight were
442 recaptured in the sessions immediately after the GPS tracking period (short-term
443 recapture rate = 15.7%). As missing bats would be expected to have similar short-
444 term recapture rates if their apparent disappearance from the study area was an
445 artefact of GPS tag loss or failure, we would have expected at least six recaptures.
446 Moreover, during surveys conducted 4-32 months after GPS tagging, six of the
447 missing bats were recaptured (long-term recapture rate=15.4%), while six of the bats
448 that had remained were also recaptured (long-term recapture rate=11.8%). These
449 results suggest that disappearance immediately after tagging was due to roost
450 abandonment or switching rather than bat mortality.

451 A binomial GLM testing for the effects of bat forearm length and sex, and tag
452 burden, revealed that bats with longer forearms (-0.96 [SE = 0.35], P<0.01) and male
453 bats (-1.11 [SE = 0.66], P=0.09) were less likely to return to the roost during the 9-
454 day study period, although there was only weak evidence for the latter effect (Fig. 2;
455 Table S4; Fig. S5). Non-random disappearance of bats following patterns that might
456 be expected from bat behaviour and physiology provides further support for the idea
457 that disappearances reflected short- to medium-term roost abandonment by vampire
458 bats following disturbance. Across all models tested, including those with interaction
459 terms, we found no evidence that the tag burden influenced the probability of roost
460 abandonment.

461 We next explored correlates of departure time and maximum nightly distance
462 from the roost among the bats that remained sufficiently close to the roost to
463 contribute GPS data. A Bayesian state-space model demonstrated a strong overall

464 fit to the GPS data (R^2 = 0.80). Because the number of observed GPS fixes varied
465 across bats, we also calculated individual-level R^2 values to assess model fit
466 consistency. The model fitted well for most bats, with a median individual R^2 of 0.71.
467 Only 10.9% of bats were poorly fit (R^2 <0.20) (Fig. S6). Predicted maximum
468 distances were larger than observed maximum distances per bat and night,
469 reflecting the property of our model to fill gaps due to missing observations (Fig. 3c-
470 d). Our model estimated patterns and correlates of the time that bats departed from
471 the roost. On average, bats departed ~2 hours after the GPS started at 6 PM
472 (posterior mean of 124 minutes, 95% credible interval (CI) [58.3; 220.5]) and were
473 out of the roost for >5 hours (posterior mean of 345 minutes, 95% CI [190.0; 497.4])
474 (Fig. S7). Although the number of hours until darkness had a low posterior inclusion
475 probability, its posterior distribution indicated that bats left the roost as soon as there
476 was no sunlight or moonlight (Fig. 3a; Table S5).
477 Among drivers of the nightly distances that bats moved from the roost, time
478 post-disturbance was the only variable with strong posterior support for inclusion
479 (probability = 0.95, Fig. 3a, d; Table S5; Figs. S8-S9). This negative effect implied
480 that bats initially flew farther from the roost following disturbance, then shifted to
481 flying shorter distances, presumably returning to a more typical flight distance.
482 Specifically, the maximum nightly distance decreased by 0.17 km per night (Fig. S8)
483 and stabilised approximately four nights after tagging (Fig. 3d). Deeper examination
484 of model outputs also showed an interaction between individual bat identity and night
485 (night of disturbance versus all the other nights), whereby on the night of the
486 disturbance, some bats stayed unusually close to the roost, and others undertook
487 the longest movements recorded in the study period (Figs. 3b, 4; Table S6; Figs.

488 S10-S11). This putative individual heterogeneity in the response to disturbance
489 occurred across all roosts except roost 2, which had data from only one bat (Fig.
490 S12). Taken together, these results suggest that while on average bats flew further
491 from the roost on the night of disturbance, this result was dampened by marked
492 individual heterogeneity, where some bats had the opposite response of reducing
493 movement.
494

495 ## Discussion

496 Fine-scale studies of wildlife movement are currently restricted to relatively
497 geomorphologically simple habitats, limiting our ability to understand how natural or
498 human-induced behavioural variation affects infectious disease transmission in
499 complex habitats. By developing a Bayesian state-space model to reconstruct
500 movement metrics from sparse and error-prone GPS data from 93 vampire bats in a
501 rabies hotspot in the Peruvian Andes, we identified three behavioural responses to
502 human disturbance which could exacerbate rabies transmission and dilute the
503 effectiveness of bat population control efforts.

504 First, 43% of the GPS-tagged bats were not detected in the study area for the
505 duration of the tracking sessions that followed capture and tagging. Because any
506 return to the roost area would have triggered GPS data upload to our receivers,
507 these findings suggest that a surprisingly large fraction of bats abandoned the focal
508 roosts for at least nine nights (length of the study) because of the disturbance arising
509 from capture and tagging. While we cannot completely rule out the possibility that
510 tags detached in areas with poor satellite coverage, the scarcity of stationary tags
511 and lack of GPS fixes before presumed detachment make this explanation unlikely.

512 Moreover, missing bats had lower short-term recapture rates, but higher long-term
513 recapture rates compared to bats that remained in the study area during the GPS
514 tracking study, arguing against mortality as a main cause. Previous research has
515 shown that vampire bats switch roosts frequently (39,40), so some disappearances
516 in our data could reflect normal switching rather than disturbance-induced
517 abandonment. Unfortunately, since our measure of roost abandonment (GPS data
518 upload to a receiver at the roost site) required GPS tagging, a non-disturbance
519 control was not feasible to rule out this explanation. However, given that vampire bat
520 dispersal is generally male-biased and that forearm length is linked to flight ability,
521 the results of our GLM that males and stronger flyers more frequently disappeared
522 after tagging further support transient roost abandonment (7,30). Future studies
523 might use less invasive monitoring of roost fidelity, for example, automated
524 monitoring systems with radio frequency identification (RFID) tags, to estimate
525 baseline roost switching rates.

526 We observed two other behavioural responses among bats that remained
527 detectable: a general tendency for longer distance movements after disturbance and
528 elevated individual heterogeneity on the night of capture. As with the roost
529 abandonment analysis, the necessity of GPS tagging meant baseline flight distances
530 in the absence of tagging could not be inferred. While we interpret the negative effect
531 of time post-disturbance on flight distances as an initial increase with gradual return
532 to shorter distances, we cannot entirely rule out that data from the initial nights after
533 capture and tagging represented normal behaviour and the shorter distances
534 observed at the end of the observation period reflected shorter than typical flight
535 distances, perhaps because of fatigue from tags. However, we argue this
536 interpretation is unlikely since high individual heterogeneity on the night of capture

537 (Fig. 3b) and the putative roost abandonment effect (Fig. 2), are more consistent with
538 an immediate disturbance effect (41).
539 Collectively, these three perturbations could have unintended consequences
540 for both the transmission and management of VBR. Roost abandonment following
541 the application of vampiricide poison would dilute local population reduction and may
542 disperse bats to lower-density roosts or roosts where bats have fewer social
543 connections, reducing the efficiency of poison transfer. Disturbance-induced roost
544 abandonment could also have complex effects on rabies transmission. On the one
545 hand, roost abandonment could decelerate rabies spread if rabies-infected bats
546 immigrate into areas where bats have been dispersed into many small roosts, as this
547 would reduce the likelihood of the virus successfully establishing in new areas. On
548 the other hand, if disturbance occurs in areas where rabies already circulates, roost
549 abandonment or greater travel distances by rabies-infected bats are predicted to
550 raise rabies incidence in bats, through overlap of foraging areas and colony mixing,
551 and promote spread to nearby roosts. As such, our results potentially explain
552 findings that reactive culls accelerated viral spatial spread while preventive culls
553 slowed spread (8,9). Since viral spatial spread is believed to be strongly influenced
554 by male bat movement, the tendency for male bats to abandon roosts after capture
555 would be particularly problematic (7). In contrast, disturbance-induced movement
556 could benefit the recently proposed application of vaccines with the capacity for self-
557 dissemination since roost switching would 'seed' vaccine transmission to a larger
558 number of roosts than previously appreciated (42).
559 A caveat when drawing conclusions about culling is that our study measured
560 the effects of a relatively mild disturbance. While our disturbance shares similarities
561 with culling (capture, handling, the application of a foreign object, and release), there

562 are key differences. Vampire bats have strong cooperative networks, characterised
563 by blood meal sharing and intense allogrooming, which could be disrupted by the
564 sickness behaviours and mortality associated with poisoning (43,44). As such, culls
565 may lead to stronger effects on movement than the relatively mild disturbance we
566 induced. Capture locations may also vary between our study and real-world
567 management. While we carried out captures in roosts for greater tractability,
568 captures can also occur at properties where bats attack livestock (9,45). Additional
569 field experiments that separate the effects of human presence at roost sites, capture,
570 handling and poisoning, could clarify vampire bat population management.

571 High-resolution GPS tracking also revealed that geomorphological constraints
572 on bat movement and VBR spread may be less restrictive than implied by previous
573 observational or radiotelemetry data. For example, rather than consistently foraging
574 downstream of their roosts, following valleys or rivers, we observed vampire bats
575 travelling over mountains and foraging in both directions along rivers (46,47).
576 Furthermore, similar to other colonial species such as seabirds, vampire bats
577 exhibited high movement behavioural heterogeneity within the colony (48). Our data
578 also challenge the notion that vampire bats return to the same foraging location and
579 even individual animals for blood feeding every night (49). Overall, heterogeneity
580 across individual bats and within bats over short periods helps explain the
581 sometimes-sporadic evidence of vampire bat bites on livestock and humans (50) and
582 implies that pathogen-infected bats are likely to expose multiple animals at different
583 locations. Incorporating these behavioural ecological insights on vampire bats into
584 models of rabies spread could enhance our understanding of its dynamics.

585 The Bayesian framework we developed incorporated all available data on
586 departure times and distances from the roost, jointly estimating movement

587 parameters across individuals. By partially pooling information across bats, the
588 model leveraged well-sampled individuals to inform estimates for those with sparse
589 data, statistically imputing missing values and propagating their uncertainty.
590 Importantly, our objective was not to infer exact animal locations throughout the
591 night, but rather to estimate how individual, landscape, disturbance and temporal
592 factors affected key characteristics of bat movement while accounting for
593 uncertainty. Furthermore, this approach enabled us to estimate the true distances
594 bats can travel (Fig. 3c-d), which are critical for disease management, but are often
595 missed in sparse datasets, which tend to underrepresent maximum distances (51). A
596 potential limitation of our modelling approach is the assumption that vampire bats do
597 a single trip and return to the roost every night. This assumption was broadly
598 supported by overall model fit and parameter convergence. However, a subset of
599 bat-nights (13%) had bimodal posterior distributions that were more consistent with
600 multiple trips within a night (Fig. S10). If some long-distance movements instead
601 reflect roost switching, our results may overestimate true foraging distances;
602 however, we note that eventual return to the roost was required for data recovery, so
603 either behaviour reflects short-term movements after disturbance and will not affect
604 our estimates of maximum distances travelled.
605

606 ## Conclusions

607 Our study demonstrates how advances in GPS technology, despite persistent
608 data challenges in complex habitats, can be utilised through analytical frameworks to
609 extend wildlife tracking to species and environments where conventional analyses
610 may fail, or be strongly biased by satellite visibility constraints. Moreover, our
611 findings demonstrate that human disturbance can have significant repercussions for

VBR management, revealing movement dynamics that would otherwise remain unknown in complex landscapes and highlighting how altered bat dispersal and colony mixing may facilitate livestock rabies emergence into new areas in Latin America.

List of abbreviations

AAC – Ayacucho, Apurímac, Cusco

AIC - Akaike Information Criterion

ANOVA – Analysis of Variance

CI – Credible interval

GLM – Generalised linear model

GPS – Global Positioning System

NA – Not available

RFID - radio frequency identification

SE – Standard Error

SSVS - Bayesian Stochastic Search Variable Selection

VBR – vampire bat rabies

VHF – Very high frequency

Declarations

Ethics approval

Ethical approval and permits for the capture, handling, and GPS tagging of vampire bats were granted by the Research Ethics Committee of the University of Glasgow (Reference EA28a/21) and by Peruvian national 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).

Consent for publication

Not applicable.

Availability of data and materials

Data and code for this study are deposited in the Dryad Digital Repository, and will be available after publication of the manuscript.

Competing interests

The authors declare that they have no competing interests.

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Authors' contributions

Conceptualisation: R.R., J.M., D.G.S. Methodology: R.R., J.C., J.M., D.G.S. Analysis and visualisation: R.R., J.M. Investigation: R.R., C.M.Z., W.C., K.P.R., J.C.M.,

M.A.R.H., R.Z.V., W.C.Q., N.M-U., H.F., D.G.S. Resources and management: C.M.Z., C.S., N.F., W.V. Data Curation: R.R. Project administration: D.G.S., Funding acquisition: D.P.W., T.E.R., J.M., D.G.S. Supervision: R.R., J.M., D.G.S. Writing (original draft): R.R., J.M., D.G.S. All authors contributed critically to the drafts and gave final approval for publication.

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References

1. Fountain-Jones NM, Craft ME, Funk WC, Kozakiewicz C, Trumbo DR, Boydston EE, et al. Urban landscapes can change virus gene flow and evolution in a fragmentation-sensitive carnivore. Mol Ecol. 2017 Nov;26(22):6487–98.
2. Fountain-jones NM, Kraberger S, Gagne RB, Trumbo DR, Salerno PE, Funk WC, et al. Host relatedness and landscape connectivity shape pathogen spread in the puma, a large secretive carnivore. Commun Biol. 2021;1–9. Available from: http://dx.doi.org/10.1038/s42003-020-01548-2

686 3. Cheng TL, Rovito SM, Wake DB, Vredenburg VT. Coincident mass extirpation
687 of neotropical amphibians with the emergence of the infectious fungal
688 pathogen *Batrachochytrium dendrobatidis*. PNAS. 2011;108(23):9502–7.
689 4. Nathan R, Monk CT, Arlinghaus R, Adam T, Alós J, Assaf M, et al. Big-data
690 approaches lead to an increased understanding of the ecology of animal
691 movement. Science (1979). 2022;375(6582).
692 5. Schneider MC, Romijn PC, Uieda W, Tamayo H, da Silva DF, Belotto A, et al.
693 Rabies transmitted by vampire bats to humans: An emerging zoonotic disease
694 in Latin America? Rev Panam Salud Publica. 2009 Mar;25(3):260–9.
695 6. Benavides JA, Valderrama W, Streicker DG. Spatial expansions and travelling
696 waves of rabies in vampire bats. Proceedings of the Royal Society B:
697 Biological Sciences. 2016;283(1832):1–9.
698 7. Streicker DG, Winternitz JC, Satterfield DA, Condori-Condori RE, Broos A,
699 Tello C, et al. Host-pathogen evolutionary signatures reveal dynamics and
700 future invasions of vampire bat rabies. Proc Natl Acad Sci U S A.
701 2016;113(39):10926–31.
702 8. Blackwood JC, Streicker DG, Altizer S, Rohani P. Resolving the roles of
703 immunity, pathogenesis, and immigration for rabies persistence in vampire
704 bats. Proc Natl Acad Sci U S A. 2013 Dec;110(51):20837–42.
705 9. Viana M, Benavides JA, Broos A, Loayza DI, Niño R, Bone J, et al. Effects of
706 culling vampire bats on the spatial spread and spillover of rabies virus. Sci
707 Adv. 2023;9(10).
708 10. O'Shea TJ, Cryan PM, Hayman DTS, Plowright RK, Streicker DG. Multiple
709 mortality events in bats: A global review. Mamm Rev. 2016;46(3):175–90.

710 11. Ham C, Donnelly CA, Astley KL, Jackson SYB, Woodroffe R. Effect of culling
711 on individual badger *Meles meles* behaviour: Potential implications for bovine
712 tuberculosis transmission. Journal of Applied Ecology. 2019;56(11):2390–9.
713 12. Kays R, Crofoot MC, Jetz W, Wikelski M. Terrestrial animal tracking as an eye
714 on life and planet. Science (1979). 2015;348(6240):aaa2478.
715 13. Britzke ER, Gumbert MW, Hohmann MG. Behavioral response of bats to
716 passive integrated transponder tag reader arrays placed at cave entrances. J
717 Fish Wildl Manag. 2014;5(1):146–50.
718 14. Thomas B, Holland JD, Minot EO. Wildlife tracking technology options and
719 cost considerations. Wildlife Research. 2011;38(8):653–63.
720 15. Streicker DG, Recuenco S, Valderrama W, Benavides JG, Vargas I, Pacheco
721 V, et al. Ecological and anthropogenic drivers of rabies exposure in vampire
722 bats: Implications for transmission and control. Proceedings of the Royal
723 Society B: Biological Sciences. 2012;279(1742):3384–92.
724 16. Rocha F, Ulloa-Stanojlovic FM, Rabaquim VCV, Fadil P, Pompei JC, Brandão
725 PE, et al. Relations between topography, feeding sites, and foraging behavior
726 of the vampire bat, *Desmodus rotundus*. J Mammal. 2020;101(1):164–71.
727 17. Patterson TA, Thomas L, Wilcox C, Ovaskainen O, Matthiopoulos J. State –
728 space models of individual animal movement. Trends in Ecology and
729 Evolution. 2008;(2)23:87-94.
730 18. Castle KT, Weller TJ, Cryan PM, Hein CD, Schirmacher MR. Using sutures to
731 attach miniature tracking tags to small bats for multimonth movement and
732 behavioral studies. Ecol Evol. 2015;5(14):2980–9.

19. Aldridge HDJN, Brigham RM. Load Carrying and Maneuverability in an Insectivorous Bat: a Test of the 5% “Rule” of Radio-Telemetry. J Mammal 1988 May 20;69(2):379–82. Available from: https://doi.org/10.2307/1381393
20. O’Mara MT, Amorim F, Scacco M, McCracken GF, Safi K, Mata V, et al. Bats use topography and nocturnal updrafts to fly high and fast. Current Biology. 2021;31(6):1311-1316.e4.
21. R Core Team. R: A Language and Environment for Statistical Computing. Vienna, Austria: R Foundation for Statistical Computing, Vienna, Austria; 2024. Available from: https://www.r-project.org/
22. Gupte PR, Beardsworth CE, Spiegel O, Lourie E, Toledo S, Nathan R, et al. A guide to pre-processing high-throughput animal tracking data. Journal of Animal Ecology. 2022;91(2):287–307.
23. Pebesma E. Simple Features for R: Standardized Support for Spatial Vector Data. R J. 2018;10(1):439–46.
24. Crespo RF, Linhart SB, Burns RJ, Mitchell GC. Foraging Behavior of the Common Vampire Bat Related to Moonlight. J Mammal. 1972;53(2):366–8.
25. Thieurmel B, Elmarhraoui A. Package “suncalc”: Compute Sun Position, Sunlight Phases, Moon Position and Lunar Phase. 2022. Report No.: R package version 0.5.1. Available from: https://cran.r-project.org/package=suncalc
26. Ribeiro R, Matthiopoulos J, Lindgren F, Tello C, Zariquiey CM, Valderrama W, et al. Incorporating environmental heterogeneity and observation effort to predict host distribution and viral spillover from a bat reservoir. Proceedings of the Royal Society B: Biological Sciences. 2023 Jan 1;290(20231739):11.

27. Greenhall AM, Joermann G, Schmidt U. *Desmodus rotundus*. Mammalian Species. 1983;202:1–6.

28. Hijmans R. terra: Spatial Data Analysis. 2024. Available from: https://cran.r-project.org/package=terra

29. Mialhe P. Characterization of *Desmodus rotundus* (E. Geoffroy, 1810) (Chiroptera, Phyllostomidae) shelters in the Municipality of São Pedro - SP. Brazilian Journal of Biology. 2013;73(3):521–6.

30. Delpietro HA, Russo RG, Carter GG, Lord RD, Delpietro GL. Reproductive seasonality, sex ratio and philopatry in Argentina's common vampire bats. R Soc Open Sci. 2017;4(4):1–14.

31. Norberg UM, Rayner JM V. Ecological Morphology and Flight in Bats (Mammalia; Chiroptera): Wing Adaptations, Flight Performance, Foraging Strategy and Echolocation. Philos Trans R Soc Lond B Biol Sci. 1987 Nov 20;316(1179):335–427. Available from: http://www.jstor.org/stable/2396486

32. Findley JS, Studier EH, Wilson DE. Morphologic Properties of Bat Wings. J Mammal. 1972 Sep 27;53(3):429–44. Available from: https://doi.org/10.2307/1379035

33. Lehnert LS, Kramer-schadt S, Teige T, Hoffmeister U, Popa-lisseanu A, Bontadina F, et al. Variability and repeatability of noctule bat migration in Central Europe: evidence for partial and differential migration. Proceedings of the Royal Society B: Biological Sciences. 2018;(285).

34. Johnston R, Jones K, Manley D. Confounding and collinearity in regression analysis: A cautionary tale and an alternative procedure, illustrated by studies of British voting behaviour. Qual Quant. 2018;52(4):1957–76.

35. O'Hara RB, Sillanpää MJ. A review of bayesian variable selection methods: What, how and which. Bayesian Anal. 2009;4(1):85–118.

36. Plummer M. rjags: Bayesian graphical models using MCMC. 2023. Available from: https://cran.r-project.org/package=rjags

37. Denwood M, Plummer M. runjags: Interface Utilities, Model Templates, Parallel Computing Methods and Additional Distributions for MCMC Models in JAGS. R package version 2.2.2-4; 2024. p. 61. Available from: https://github.com/ku-awdc/runjags

38. Plummer M, Best N, Cowles K, Vines K. CODA: Convergence Diagnosis and Output Analysis for MCMC. R News. 2006;6:7–11.

39. Wilkinson GS. The social organization of the common vampire bat. Behav Ecol Sociobiol. 1985;17(2):111–21.

40. Hartman CAR, Wilkinson GS, Razik I, Hamilton IM, Hobson EA, Carter GG. Hierarchically embedded scales of movement shape the social networks of vampire bats. Proceedings of the Royal Society B: Biological Sciences. 2024;291(2021):1–12.

41. Streicker DG, Franka R, Jackson FR, Rupprecht CE. Anthropogenic roost switching and rabies virus dynamics in house-roosting big brown bats. Vector-Borne and Zoonotic Diseases. 2013;13(7):498–504.

42. Griffiths ME, Broos A, Bergner LM, Meza DK, Suarez NM, Da Silva Filipe A, et al. Longitudinal deep sequencing informs vector selection and future deployment strategies for transmissible vaccines. PLoS Biol. 2022;20(4):1–19. Available from: http://dx.doi.org/10.1371/journal.pbio.3001580

43. Carter G, Leffer L. Social grooming in bats: Are vampire bats exceptional? PLoS One. 2015;10(10):1–11.

44. Ripperger SP, Carter GG. Social foraging in vampire bats is predicted by long-term cooperative relationships. PLoS Biol. 2021;19(9):1–17.

45. Vargas LÁ. Anticoagulants for the Control of the Common Vampire Bat (*Desmodus rotundus*). Zoonoses and Public Health. 2025;101–16.

46. Ávila-Flores R, Bolaina-Badal AL, Gallegos-Ruiz A, Sánchez-Gómez WS. Use of linear features by the common vampire bat (*Desmodus rotundus*) in a tropical cattle-ranching landscape. Therya. 2019;10(3):229–34.

47. Trajano E. Movements of cave bats in southeastern Brazil, with emphasis on the population ecology of the common vampire bat, *Desmodus rotundus* (Chiroptera). Biotropica. 1996;28(1):121–9.

48. Cleasby IR, Owen E, Butler A, Baer J, Blackburn J, Bogdanova MI, et al. Assessing the importance of individual- and colony-level variation when using seabird foraging ranges as impact assessment and conservation tools. Ibis. 2023;166(3):871–95.

49. Greenhall AM. Feeding behavior. In: Schmidt AM, Greenhall RK, editors. Natural History of Vampire Bats. 1st Editio. Florida: CRC Press Inc, Boca Raton; 1988. p. 7–17.

50. Streicker DG, Allgeier JE. Foraging choices of vampire bats in diverse landscapes: potential implications for land-use change and disease transmission. Journal of Applied Ecology. 2016;53(4):1280–8.

51. Hooten MB, Johnson DS, McClintock BT, Morales JM. Animal Movement: Statistical Models For Telemetry Data. 1st Editio. Florida: CRS Press, Boca Raton; 2017. 320 p.

52. Kahle D, Wickham H. ggmap: Spatial visualization with ggplot2. R Journal. 2013;5(1):144–61. Available from: http://journal.r-project.org/archive/2013-1/kahle-wickham.pdf

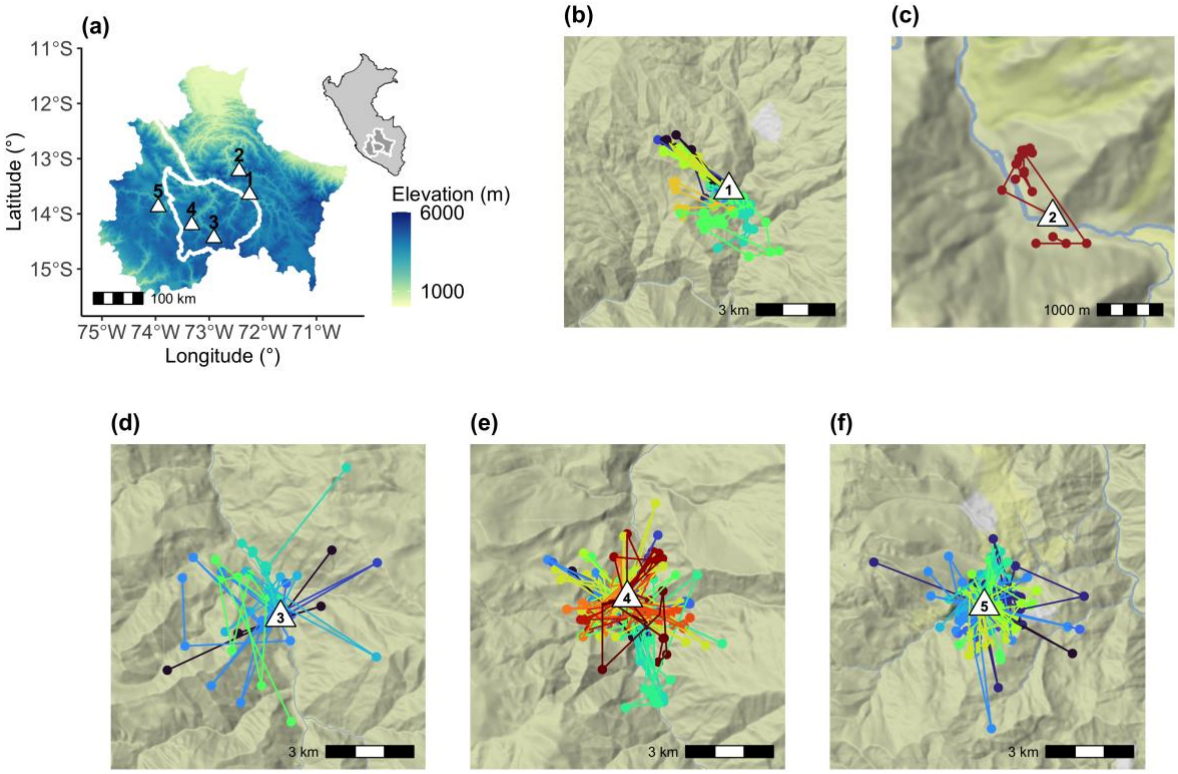

Figure 1. Study area and GPS data from 55 vampire bats (*Desmodus rotundus*) from five roosts. (a) Elevation map with the five study roosts (numbered triangles) in AAC, with an inset map of Peru highlighting the study region. (b) roost 1, (c) roost 2, (d) roost 3, (e) roost 4 and (f) roost 5. In panels b-f, each colour represents a bat tracked for up to nine nights. 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 (52). Base map tiles show terrain; in panel (c) the map is zoomed in. Data © OpenStreetMap

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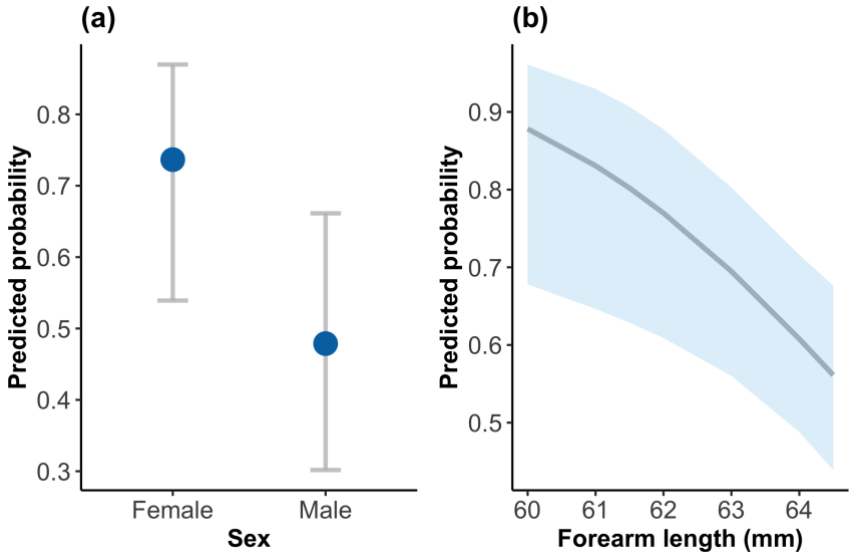

Figure 2. Predicted probabilities of vampire bats (*Desmodus rotundus*) returning to the roost following disturbance. Results from a binomial GLM: (a) Shows sex-specific estimates with 95% confidence intervals; (b) shows the relationship of probability of return with forearm length (mm), with the 95%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

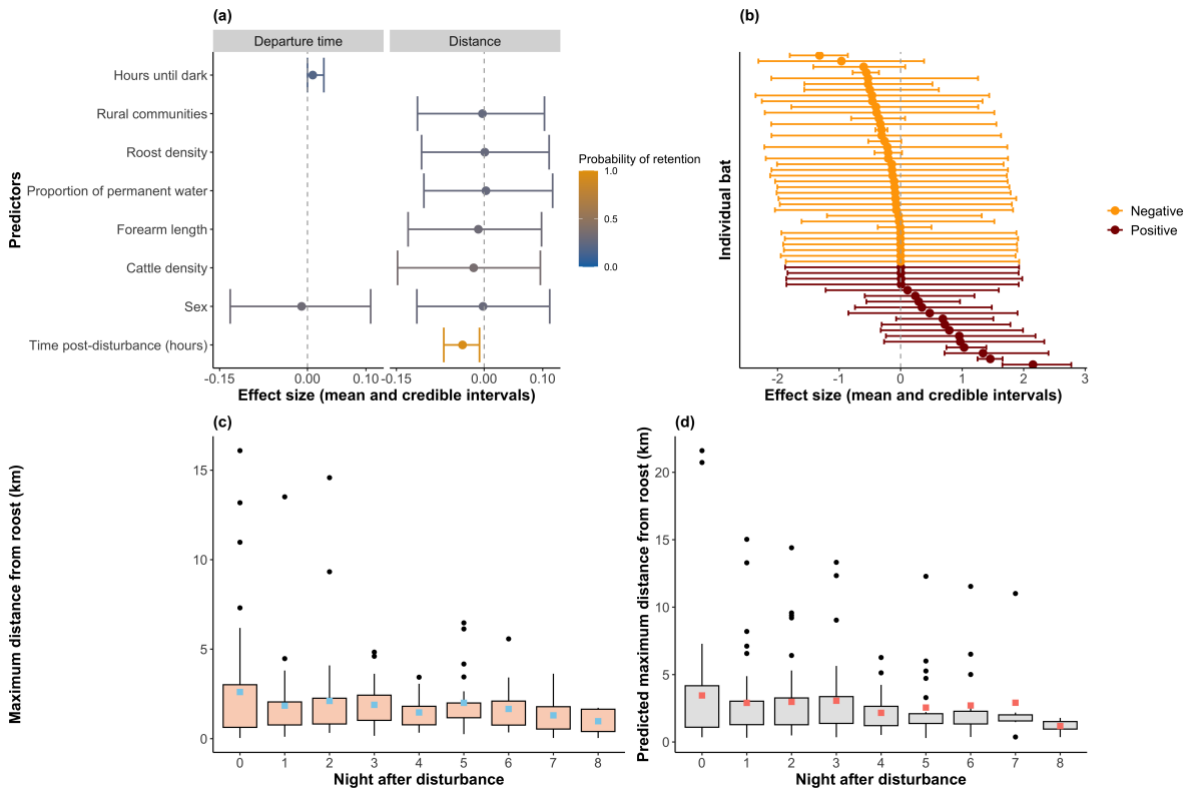

Figure 3. Predictors of vampire bat (*Desmodus rotundus*) departure time and distance from the roost. (a) Standardised effect sizes on the log-odds scale (departure time, logit model) or log scale (distance, exponential model), coloured by SSVS retention probability. (b) Individual variation in the distance 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.

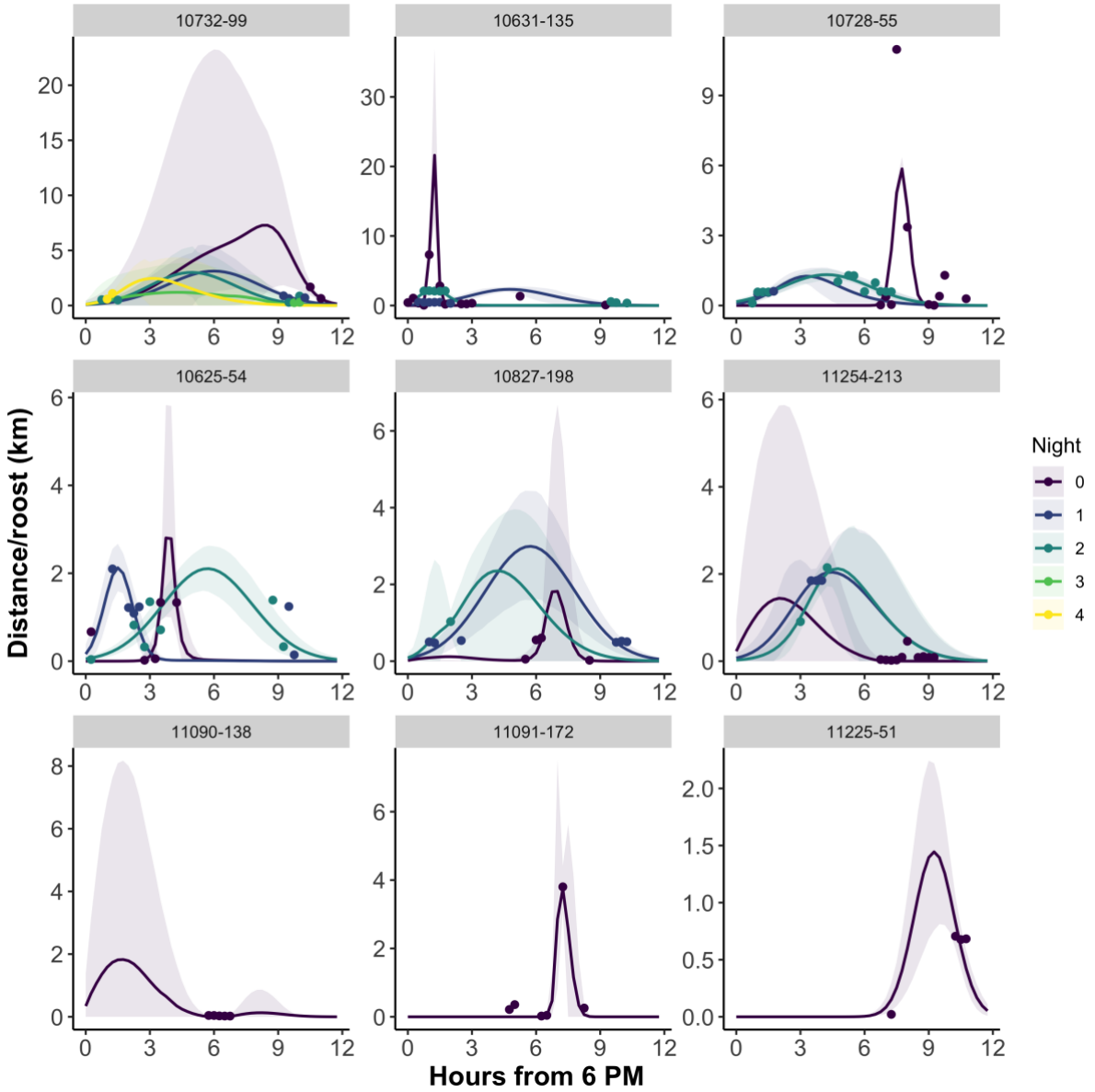

Figure 4. Reconstructed movement curves for nine vampire bats (*Desmodus rotundus*) across nine nights. First row: bats that travelled longer distances on night 0; middle row: bats that travelled similar distances across different nights; bottom row: bats that left the roost after night 0 and did not return. The shaded area indicates the credible intervals, and the dots the observed values. 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.