



Technical Report HCSU-041

A FIVE-YEAR STUDY OF HAWAIIAN HOARY BAT (*LASIURUS CINEREUS SEMOTUS*) OCCUPANCY ON THE ISLAND OF HAWAII

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July 2013



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This product was prepared under Cooperative Agreement CAG09AC00390 for the Pacific Island Ecosystems Research Center of the U.S. Geological Survey.



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ABSTRACT

Using acoustic recordings of the vocalizations of the endangered Hawaiian hoary bat (*Lasiurus cinereus semotus*) collected over a five-year period (2007–2011) from 25 survey areas across the island of Hawai`i, we modeled the relationship between habitat attributes and bat occurrence. Our data support the conclusion that hoary bats concentrate in the coastal lowlands of Hawai`i during the breeding season, May through October, and migrate to interior highlands during the winter non-breeding season. Highest occupancy peaked on the Julian date 15 September across the five-year average and during the season of fledging by the young of the year. Although the Hawaiian hoary bat is a habitat generalist species and occurs from sea level to the highest volcanic peaks on Hawai`i, there was a significant association between occupancy and the prevalence of mature forest cover. Trends in occupancy were stable to slightly increasing during the breeding season over the five years of our surveys.

INTRODUCTION

Although the Hawaiian hoary bat (*Lasiurus cinereus semotus*) was first collected in 1861 (Gray 1862) and occurs on all of the major volcanic islands in the state of Hawai`i (Tomich 1986), the ecology and even the systematics (Morales and Bickham 1995) of this bat remain poorly understood. Despite the listing of “endangered” for this Hawaiian endemic subspecies by the U.S. Fish and Wildlife Service (USFWS) since 1970 and publication of a recovery plan in 1998 (USFWS 1998), few studies provide insights about seasonal, annual, or multi-year cycles influencing this bat’s biology (Menard 2001, Fraser *et al.* 2005, Todd 2012, Bonaccorso *et al.* in press). The Recovery Plan (USFWS 1998) Executive Summary states, “there is a general lack of historic and current data on this subspecies, and its present status is not well-understood,” and this continues to be the status quo.

Perhaps the most important research goal in the 1998 recovery plan is to “determine actual population status and habitat requirements” for the Hawaiian hoary bat. The plan goes on to state, “determining actual population numbers for this subspecies is not practical, but indices of abundance are obtainable and can be used to identify quantifiable goals.” Indeed, practical tools for obtaining quantitatively robust information on this highly mobile, solitary, and cryptic foliage-roosting bat have only recently become available.

An important advance in the study of species distributions is the recent development of statistical methods that take into account the imperfect detection of subjects (i.e., where individuals are present but not observed). Models that estimate the probability of site occupancy given a detection probability conditional on occurrence, often termed “occupancy models” (MacKenzie *et al.* 2002, Royle and Dorazio 2006), are particularly well-suited to cryptic and wide-ranging animals such as foliage-roosting bats for which counts of individuals are not readily available (Gorresen *et al.* 2008, Rodhouse *et al.* 2012). Occupancy analysis provides an estimate of the proportion of area of interest where the species is present and can serve as an alternative approach for obtaining measures of distribution, habitat associations, and trends usually derived from abundance estimates, a metric typically unattainable for many bat species (O’Shea *et al.* 2003, Hayes *et al.* 2009). Furthermore, in the past decade technological advances in remote acoustic detection and data storage of ultrasonic bat vocalizations (Gorresen *et al.* 2008, Weller and Baldwin 2011) have resulted in hardware and software that quantitatively measure “bat calls” as a means to assess ecological attributes of bat populations. These

attributes include seasonal patterns of habitat use, timing of flight and foraging activity, and population trends.

Our objectives in this study were to: 1) model the relationship between habitat attributes and bat occurrence, 2) account for the effects of imperfect detection on model estimates, and 3) examine seasonal changes and annual trends in bat occurrence. Habitat availability and suitability for bats may be influenced by various factors operating at multiple spatial scales (e.g., Grindal and Brigham 1999, Gorresen *et al.* 2005). We have focused on “landscape” variables, that is, those measured at broad geographic extents because these attributes have been shown in various studies to correlate with bat, and more specifically, lasiurine bat occurrence. For example, Crampton and Barclay (1998) found silver-haired bats (*Lasionycteris noctivagans*) to be more prevalent in older, more structurally complex forest than in younger stands. Yates and Muzika (2006) demonstrated red bat (*Lasiurus borealis*) occurrence to be positively associated with forest cover and detection probability to be negatively related to precipitation. Rodhouse *et al.* (2012) showed net primary productivity and forest cover to be correlated with little brown bat (*Myotis lucifugus*) occurrence. Seasonal migratory movement, and consequently, local colonization and extinction rates (i.e., seasonal arrival and departure) may also be affected by temporally varying climatic attributes at large geographic extents. For example, Cryan (2003) proposed that the distribution of *L. cinereus* and *L. noctivagans* may be associated with seasonal continental-scale patterns of temperature and moisture. Moreover, drought is associated with lower prey availability (Hawkins and Holyoak 1998) and can cause physiological stress for many bat species, particularly in summer months when bats are reproductively active (Adams 2010). These and other environmental factors potentially influencing bat occurrence were used to guide model development for this five-year study of Hawaiian hoary bat ecology on the island of Hawai`i.

METHODS

Study Area and Sampling

Comprised of multiple volcanoes encompassing a 1,042,000 ha area and a peak elevation of just over 4,000 m, Hawai`i Island consists of five major climatic zones (coastal, dry, mesic, wet, and subalpine/alpine) and three tropical ecoregions (moist broadleaf forest, dry broadleaf forest, and grasslands, savannas, and shrublands; Gon and Olson 1999, Price 2004). Although the tropical temperature regime varies little throughout the year at any particular location, mean annual temperature ranges from about 25 °C near sea level to 5 °C at the highest elevations (Giambelluca and Schroeder 1998). Annual precipitation reaches from a mean of 250 mm in the arid lowlands to over 6,000 mm at mid-elevation montane sites. Detailed descriptions of vegetation types that occur on Hawai`i Island may be found in Cuddihy and Stone (1990) and Pratt and Gon (1998).

Twenty-five survey areas were established across Hawai`i Island and sampled for bat occurrence from 11 January 2007 to 16 May 2012 (Figure 1). Each survey area was comprised of several sampling units (referred herein as “sites”) at which bat occurrence was recorded (mean = 5.2 sites; range of survey area means = 2.8–7.5 sites). Sites were spaced at an average interval of about 800 m within each survey area. Bat occurrence was sampled during “visits” comprised of a series of consecutive nights at each site (mean = 6.9 nights; range of survey area means = 3.2–9.0 nights). Most survey areas were visited three to four times per year (mean = 3.8 visits; range of survey area means = 2.0–6.0 visits). The duration of sampling varied depending on logistics and access, with six survey areas receiving only one or

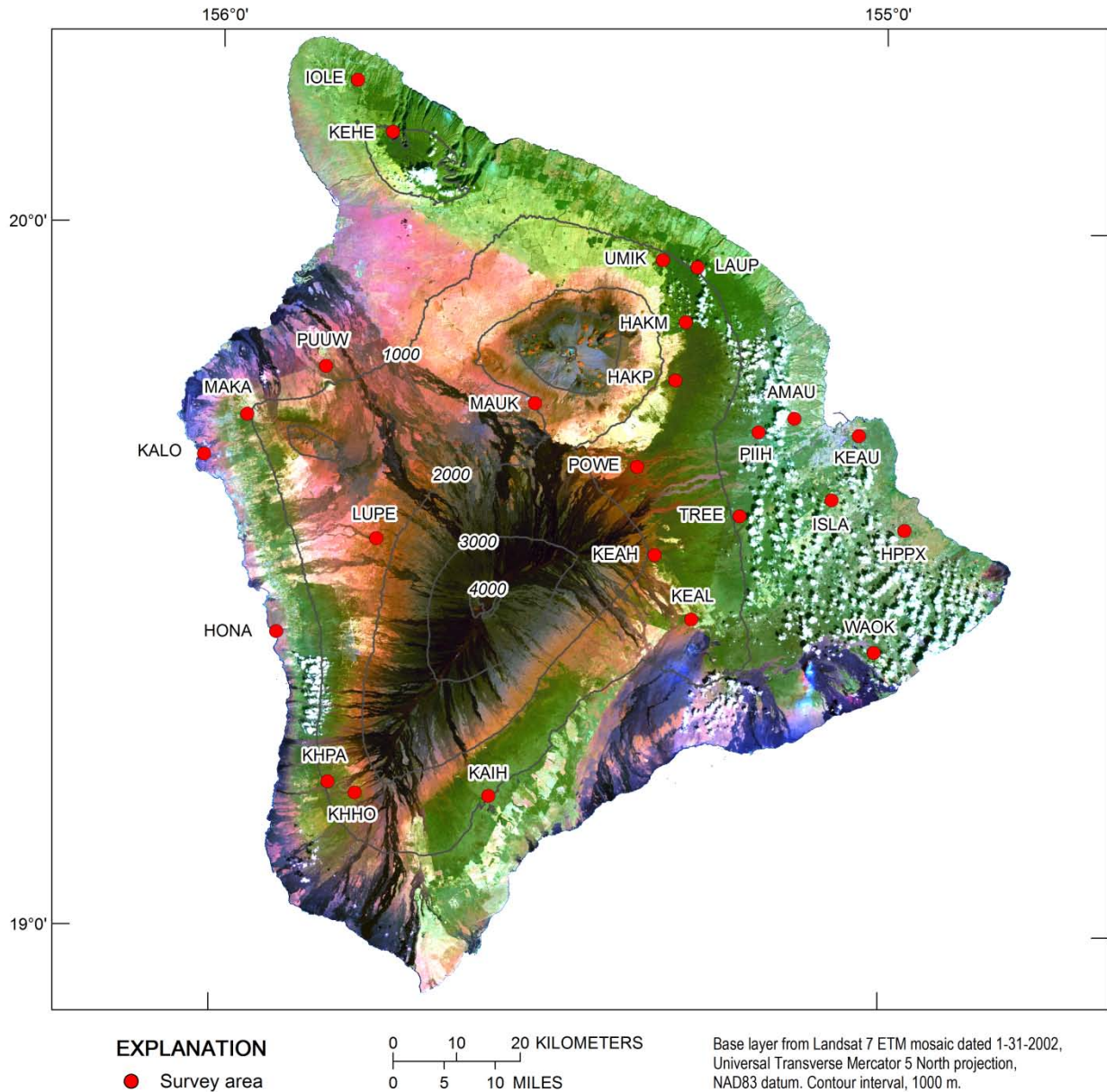


Figure 1. Survey areas sampled for Hawaiian hoary bat occurrence from 2007 to 2012 on Hawai`i Island. The complete name of each site shown by acronym here, as well as UTM coordinates, elevation, and habitat are provided in Appendix 1.

two years of sampling. The sampling data from survey areas spanning durations of less than five years were retained in development of habitat association models, but removed for assessments of trend in occupancy.

Bat echolocation calls were sampled using Anabat SD1 or Anabat II detectors (Titley Electronics, Ballina, New South Wales, Australia) and recorded with associated date and time data. Detector units were programmed to automatically switch on and off at pre-dusk and post-

dawn. Each detector was powered with a 12-V battery permitting operation for up to two weeks; however, to ensure that sampling was done when detectors were fully powered, nightly detection data were truncated to the first seven nights of each survey. Each detector microphone was placed within U-shaped polyvinyl chloride tubing to protect it from rain. An acrylic-glass plate was used to reflect calls upward into the downward-facing microphone. Each microphone assembly was attached to the top of a seven-meter pole and situated above understory vegetation, and if forested, within gaps ≥ 10 m wide in the forest canopy. Call files were processed with Analook software (version 4.9j, Titley Electronics) to filter ambient noise and identify bat echolocation calls. All call files were visually inspected to ensure that residual noises were not interpreted as echolocation pulses.

Occupancy modeling uses a matrix of detection histories obtained from repeated sampling at sites to estimate a species occurrence and detection probability. Each nightly site sample was treated as the unit of observation, and matrix elements were scored as 1 if bats were detected at a site during a survey and 0 if no detections were made. To improve comparability among samples from different survey areas, the number of observations incorporated into the detection history matrix was limited to seven nights (i.e., about the mean number of nightly samples across all survey areas).

Habitat and Temporal Model Covariates

We identified a suite of variables that potentially could affect bat presence and detectability from information in the literature and our knowledge of Hawaiian hoary bat ecology. These were used in models to estimate site occupancy in relation to climatic and land-cover characteristics (site covariates) and the probability of detection as a function of temporally varying attributes (sampling covariates). Eight site covariates were used in this analysis: forest cover, occurrence of koa (*Acacia koa*), occurrence of native or introduced vegetation, net primary productivity, elevation, precipitation, temperature, and wind velocity.

The covariates forest, koa, and native-introduced were determined from Landfire™, a GIS (geographic information system) layer of Hawaiian vegetation types (available from <http://www.landfire.gov/>; accessed 15 April 2012), and were treated as binary variables (i.e., present or absent). The forest attribute includes the moist broadleaf and dry broadleaf forest prevalent on Hawai`i Island and also identifies areas where koa occurs as a dominant or co-dominant tree species. Koa is an ecologically important component of some Hawaiian forest types and provides habitat for the koa moth (*Scotorythra paludicola*), an endemic moth that undergoes sporadic reproductive outbreaks in koa forests (Haines *et al.* 2009) and is a common prey item found in the diet of Hawaiian hoary bats (Bernard 2011, Todd 2012). The native-introduced covariate describes the pre-dominance of native and introduced vegetation for island land cover types.

Net primary productivity (NPP) was calculated by averaging the 2007 to 2011 annual values generated from the MOD17 algorithm for remotely sensed imagery collected at a one kilometer resolution by MODIS (Moderate Resolution Imaging Spectroradiometer; from the U.S. Geological Survey [USGS] Land Processes Distributed Active Archive Center available at <https://lpdaac.usgs.gov>; accessed 05 June 2012). Net primary productivity measures the amount of plant biomass (kg C/m^2) available to primary consumers such as insects which may be available as prey for insectivorous bats. An average for this period was used instead of annual values because NPP data were not available for 2012; as such, the covariate was treated as a site characteristic instead of an annually varying attribute.

Elevation was obtained from a USGS 10-m digital elevation model for the island (available from <http://nationalmap.gov/viewer.html>; accessed 01 June 2012). Precipitation as a site covariate describes qualities intrinsic to a particular locale (wet versus dry) and was based on mean annual rainfall (Giambelluca *et al.* 2011). Likewise, mean annual temperature was also used to define intrinsic site quality (acquired from <http://www.prism.oregonstate.edu/>; accessed on 20 July 2011). Finally, wind was included as a variable that may affect prey availability (Verboom and Spoelstra 1999). Mean annual wind velocity at 30 m above ground level was treated as a landscape attribute and measure of potential habitat suitability (available from http://www.state.hi.us/dbedt/gis/wind_data.htm; accessed 18 April 2012).

Two sampling covariates were used to model how bat occurrence varied by time of year: Julian date and reproductive period. (Julian date is an ordinal date starting on January 1 and ranging between 1 and 366.) In addition, two other temporal covariates (monthly precipitation and monthly temperature) were used to model how the colonization, extinction, and detection processes varied in relation to environmental conditions throughout the year. Julian date was converted to a sine function (Stolwijk *et al.* 1999) with its maxima (= 1) centered on September 15th, the period of peak bat detection. Sine values of 0 correspond to December 15th and June 16th, and a sine of -1 corresponds to March 16th. This conversion allowed the modal pattern observed in bat detection to be shifted such that the origin need not be fixed on Julian day 1. The sine function also effectively reduced the number of factor levels from 365 (days) to 1, thereby improving model performance. Hawaiian hoary bat reproductive periods were delimited based on a pre-pregnancy period (mid-December to March), a pregnancy period (April to mid-June), a lactation period (mid-June to August), and a post-lactation period (September to mid-December) adapted from Menard (2001). The pregnancy and lactation periods are generically referred to as the "breeding" season.

Although temperature is relatively constant in Hawai`i, precipitation varies considerably throughout a year (Giambelluca and Schroeder 1998). Inclusion of monthly mean precipitation and temperature permitted detection to be modeled based on temporally varying covariates, but independent of "fixed" site attributes determined by the annual means. Monthly temperature was obtained from Giambelluca *et al.* (2011; acquired from <http://rainfall.geography.hawaii.edu>; accessed 01 June 2012). Monthly precipitation was acquired from the PRISM Climate Group (<http://www.prism.oregonstate.edu/products/>; accessed on 20 July 2011). To improve model performance and the estimation of maximum likelihood values, all continuous variables were standardized to have a mean equal to 0 and standard deviation equal to 1. Predictor variables were examined to ensure that strong correlations ($r \geq 0.7$) were not present among covariates used in the same model.

Habitat Associations and Seasonal Patterns

A set of *a priori* hypotheses were formulated from the above variables that described the expected relationship of Hawaiian hoary bat site occupancy and detection probability (Table 1). We predicted that as a "tree bat," site occupancy by the Hawaiian hoary bat would be positively correlated to the presence of forest cover. This association was expected to vary by time of year, becoming more pronounced during pregnancy when energetic needs were assumed to be highest and during the lactation period when female adults and newly volant young bats might make the most use of shelter provided by forest cover. In addition, we anticipated forest cover to be a likely nuisance variable negatively influencing bat detection by the effects of "clutter" from the surrounding tree canopy. The presence of koa as a major vegetation component was expected to correlate positively to the occurrence of bats. We predicted that as a measure of

Table 1. Hypotheses and predictions describing Hawaiian hoary bat associations with habitat characteristics and temporal environmental conditions. Descriptions of associations are presented by reproductive period (pre-pregnancy = mid-December to March, pregnancy = April to mid-June, lactation = mid-June to August, and post-lactation = September to mid-December), but similarly apply to the time-of-year covariate Julian date where a Julian date of 1 = mid-September, 0 = mid-December and mid-June, and -1 = mid-March. The “breeding” season refers to the pregnancy and lactation periods combined.

Covariate	Hypothesis	Prediction
Forest cover	•Lasiurine bats preferentially use areas with high forest cover	•Forested sites positively associated with occupancy
	•Forested areas preferentially used during breeding season	•Forested sites positively associated with colonization during breeding season
	•Bats less detectable in areas with high forest cover	•Forested sites negatively associated with detection probability
Koa dominance	•Hawaiian hoary bats preferentially use koa-dominated forest cover	•Koa-dominated sites positively associated with occupancy
Native-introduced	•Hawaiian hoary bats preferentially use areas dominated by native land cover	•Native-dominated sites positively associated with occupancy
Net primary productivity	•Insectivorous bats preferentially use areas with high net primary productivity	•Net primary productivity positively associated with occupancy
Elevation	•Hawaiian hoary bats preferentially use low elevation areas during breeding season and high elevation areas during non-breeding season	•Elevation negatively associated with colonization and positively associated with extinction in breeding season; conversely, elevation positively associated with colonization and negatively associated with extinction in post-lactation and pre-pregnancy periods
Precipitation	•Bats avoid wet areas	•Precipitation (annual) negatively associated with occupancy
	•Bats avoid areas during rainy periods	•Precipitation (monthly) negatively associated with occupancy and colonization and positively associated with extinction
	•Bats less detectable during rainy periods	•Precipitation (monthly) negatively associated with detection probability
Temperature	•Bats preferentially use warmer areas	•Temperature (annual) positively associated with occupancy
	•Bats use warmer areas during breeding season and cooler areas during non-breeding season	•Temperature (monthly) positively associated with colonization and negatively associated with extinction in breeding season; temperature (monthly) negatively associated with colonization, positively associated with extinction in post-lactation and pre-pregnancy periods
Wind velocity	•Bats avoid areas with high winds	•Wind velocity negatively associated with occupancy

production of useful plant chemical energy, and indirectly as a potential correlate of insect biomass, NPP would be positively associated with bat occurrence. As an endemic species, we expected that Hawaiian hoary bats might preferentially use areas comprised of native-dominated vegetation.

We hypothesized that bats would preferentially use high elevations during the non-breeding season, a period during which Menard (2001) suggested that Hawaiian hoary bats migrate from lowland rainforests occupied during the summer and fall breeding season to the central highlands during post-lactation period in the winter. The seasonal variation in bat occurrence patterns was examined with terms describing the interaction between elevation and Julian date as well as elevation and reproductive period.

Annual mean precipitation was predicted to be negatively associated with bat occurrence (i.e., bats avoid very wet sites). This relationship was also extended to include the effect of within-year patterns in rainfall (i.e., monthly mean rainfall) as a sampling covariate. The effect of monthly rainfall on bat occurrence was examined separately for both the Julian date and reproductive period covariates. Our expectation was that, in addition to a negative association with wet sites, bat occurrence would be further adversely affected by periods of high precipitation. The seasonal variation in bat occurrence patterns was examined with interaction terms between monthly rainfall and Julian date and between rainfall and reproductive period. We also predicted that periods with high precipitation (during which bats stop flying) would negatively affect the probability of detecting bats.

Because of potential energetic and physiological requirements (Genoud 1990, Hickey and Fenton 1996), annual mean temperature was generally predicted to be positively associated with site occupancy by bats. However, because such requirements may depend on season, Julian date and reproductive period were included as sampling covariates. Finally, we included monthly mean temperature in models with site measures of annual mean temperature and time of year to examine whether within-year measures of temperature reversed the predicted positive relationship with warmer sites. That is, the expectation for these models was that bat occurrence during periods with high temperatures at warmer sites would be more negatively affected than at cooler sites, particularly during periods of otherwise higher detectability.

Bats may avoid sites when high wind speeds diminish availability or accessibility of insect prey. Therefore, we predicted that wind velocity would be negatively associated with bat occupancy. Although wind might also influence bat detection by creating ultrasonic noise that interferes with the recording of echolocation calls, we were not able to test this effect because this variable was not available as a sampling covariate (i.e., acquired at the same time as the samples for bat occurrence).

Analyses

We used the multi-season occupancy model described by MacKenzie *et al.* (2003) to quantify the underlying ecological process governing bat occupancy at sampled sites and the imperfect observation of such events. The occupancy state of sites may change over time, but there are periods during a study for which it is reasonable to assume that, for all sites, no changes occur (e.g., within a breeding season). Thus, a survey may consist of a series of primary sampling periods, between which changes in site occupancy and detection probability can occur. In this model ψ_t represents the probability that a site is occupied by the species of interest during sample period t , and p_{ij} is the probability of detecting the species, given its presence, in survey

j within period t . A primary sampling period was defined as a survey area sample (“visit”) totaling seven nights.

Multiple-season models can also explicitly incorporate colonization (γ) and extinction (ε) probabilities, two parameters that govern changes in the occupancy state between successive primary sampling periods (MacKenzie *et al.* 2003, 2006). Parameter ε_t denotes the probability that an occupied site in period t becomes unoccupied in period $t + 1$, and γ_t is the probability that an unoccupied site in period t becomes occupied by the species in period $t + 1$. For our purposes, “colonization” and “extinction,” as used in the literature on occupancy analysis, can more appropriately be thought of as events in an annual migration that describe seasonal Hawaiian hoary bat “arrival” and “departure” at a locality, and we will henceforth use those terms below except where referring to previous literature.

We fit the multi-season occupancy model with the program R (R Foundation for Statistical Computing) and the extension package named Unmarked (Fiske and Chandler 2011). The `colext` function in Unmarked was used to fit the colonization-extinction model of MacKenzie *et al.* (2003). The parameters ψ , γ , ε , and ρ were modeled with a logit link to ensure that estimates would be constrained to a 0 to 1 interval.

Model notation included two forms for each parameter; for example, $\psi(\bullet)$ represented occupancy as a constant over all sites, and $\psi(\text{cov})$ denoted occupancy as a function of some covariate. Likewise, notations of $\gamma(\bullet)$, $\varepsilon(\bullet)$, and $\rho(\bullet)$ indicated constant arrival, departure, and detection probability parameters equal to the overall mean effect. We used a null model, $\psi(\bullet)\gamma(\bullet)\varepsilon(\bullet)\rho(\bullet)$, that only included the intercept for each parameter as the basis for comparisons to models with site and sampling covariates. The null model also provided mean parameter estimates for all survey areas over the entire six-year sampling period. Four sets of models were used for assessing covariate effects:

occupancy-only model	$\psi(\text{cov})\gamma(\bullet)\varepsilon(\bullet)\rho(\bullet)$
detection probability-only model	$\psi(\bullet)\gamma(\bullet)\varepsilon(\bullet)\rho(\text{cov})$
arrival-departure-only model	$\psi(\bullet)\gamma(\text{cov})\varepsilon(\text{cov})\rho(\bullet)$
occupancy, arrival-departure, and detection probability model	$\psi(\text{cov})\gamma(\text{cov})\varepsilon(\text{cov})\rho(\text{cov})$

The first three sets were preliminary models used exclusively to assess the effect of a covariate on a particular parameter independent of its effects on other parameters; for example, $\psi(\text{forest})\gamma(\bullet)\varepsilon(\bullet)\rho(\bullet)$ measures the effect of forest on occupancy only. The fourth model set included covariates for all parameters (“full covariate models”) and was used for developing habitat models.

Assessing habitat associations

Consideration of a model suite containing all possible combinations of covariates for all four parameters was problematic because of the potential to over-fit models and yield Type I errors (Burnham and Anderson 2002). To limit the number of covariates tested, we specified a suite of hypotheses and ensuing predictions (described in Table 1).

Within each set of the four types of models described above, a comparison of Akaike’s information criterion (AIC) values was used to select the covariate that provided the best fit to the data. Models were ranked by differences between each candidate model and the model

with the lowest value (ΔAIC), and a difference of less than two AIC units indicated that both fit a data set similarly on the grounds of parsimony (Burnham and Anderson 2002). Several site (forest and elevation) and sampling covariates (Julian date and reproductive period) were examined for potential interaction effects on γ , ϵ , and ρ . We present AIC values for all four model types, and for full covariate models we also interpret and report parameter estimates and odds ratios. We considered covariates to have a significant association with bat detection patterns when the 95% confidence intervals (CI) for odds ratios did not overlap 1. The sign of slope parameter estimates provided information about the nature of the relationship. Parameter estimates for the final habitat association model were produced from linear combinations of covariate values (e.g., forest present [1] or not present [0]) using the “predict” function in the Unmarked package.

Assessing population trends

In addition to the habitat association models described above, models were also fit to estimate the dynamic parameters that drive population equilibrium and trends in site occupancy (MacKenzie *et al.* 2006:208). Occupancy estimates are generally produced with the recursive equation from colonization and extinction estimates that are conditional on the previous sampling period:

$$\hat{\psi}_t = \hat{\psi}_{t-1} (1 - \hat{\epsilon}_{t-1}) + (1 - \hat{\psi}_{t-1})\hat{\gamma}_{t-1}$$

An alternative parameterization is available in which a smoothed estimate of occupancy is derived from the latent, imperfectly detected occurrence data for sampled sites rather than the entire hypothetical super-population of sites from which the samples were drawn (Weir *et al.* 2009). The smoothing method is a conservative approach applicable to situations where generalizing from the sample of sites to a theoretically larger population of sites is questionable. This approach was used in this study and is preferable when a survey does not follow a strictly probabilistic sampling design (i.e., sites cannot be randomly or systematically selected), and sampled sites are not known with certainty to be a representative sample of the entire population of sites. A non-parametric bootstrap method was used to obtain standard errors of the smoothed estimates of occupancy for each year (Kéry and Chandler 2012). To improve model precision and minimize bias, models were run on the subset of observations centered on the peak period of bat detectability (June to October) and restricted to one primary sampling period per year. Note that the duration of the resultant time series totaled five years (2007 to 2011) since arrival and departure parameters were not estimated for 2012 (i.e., surveys ended in mid-May 2012). Trends were assessed for 19 survey areas for which sufficient data were available to calculate annual measures of occupancy. Annual occupancy estimates for each survey area were obtained from a model incorporating covariates from the top-ranked single-parameter models; in other words, ψ (survey area) γ (cov) ϵ (cov) ρ (cov). Averages of the annual estimates for each survey area were used to graphically depict occupancy across Hawai`i Island.

Change in the occupancy probability over time was assessed with a Bayesian approach to log-linear regression. Bayesian results are generally more easily interpreted than frequentist tests of the null hypothesis and enable the distinction of negligible trends from statistically non-significant outcomes attributable to high variance (Wade 2000, Camp *et al.* 2008). Bayesian log-linear regression produced a posterior probability (P) distribution for the parameter describing the rate of change (i.e., slope), and the proportion of the distribution that fell within or outside threshold bounds was used to determine the significance of the trend. We conservatively set

the bounds to detect a 25% change in occupancy over a 25-year period. This rate corresponded to a lower bound (ϕ_l) of -0.0119 and an upper bound (ϕ_u) of 0.0093 units of change (i.e., occupancy per year). We categorized trends as increasing, decreasing, or negligible. The evidence for a particular trend was based on how the distribution of posterior probabilities was apportioned by category, and was interpreted as weak ($P < 0.5$), moderate ($0.5 \leq P < 0.7$), strong ($0.7 \leq P < 0.9$), or very strong ($P \geq 0.9$; adapted from Wade 2000). An inconclusive result (referred to as “no consensus” by Crome *et al.* 1996) occurred when variance was high and the posterior distribution yielded only weak evidence across the increasing, decreasing, and negligible trend categories. A negligible trend was interpreted as a stable population.

Log-linear regression was performed with WinBUGS (Lunn *et al.* 2000; www.mrc-bsu.cam.ac.uk/bugs; retrieved 01 December 2006) in program R (R version 2.15.1; The R Foundation for Statistical Computing). The parameter α described occupancy at time $t = 0$ (i.e., intercept), β was the rate of change, and τ equaled the variance-1 (i.e., precision). The parameters α and β were given uninformative normal priors, and an uninformative gamma prior was given for τ . An uninformative prior distribution was chosen to restrict the posterior distribution to the likelihood. Year values were centered on a year corresponding to the mid-point of the time series. The model parameters were estimated from 100,000 iterations for each of three chains (i.e., model runs) after discarding the first 2,000 iterations (a “burn-in” period). The three chains were pooled (300,000 total samples) to calculate the posterior distribution of parameters α and β .

RESULTS

General Bat Occurrence Patterns

The Hawaiian hoary bat was detected during 3,886 of the 9,882 detector-nights (number of detectors \times number of sampling nights) of sampling from 2007 to 2012. Mean occupancy of all survey areas for all times of year was 0.63 (95% CI = 0.55 to 0.71; null model; Table 2, panel a), where a $\hat{\psi}$ value of 1 indicates full occupancy at all sample sites. However, there were considerable differences among survey areas in the measures of occupancy. Averages of annual $\hat{\psi}$ for survey areas ranged from 0 to 1 during the period of relatively high detection probability (June to October; Table 2, panel b). Likewise, seasonal drivers of bat occurrence were evident from the cyclic patterns in detection probability. Survey area-specific estimates of \hat{p} ranged from near 0 for some sites in the January–March period to 1 at other sites in the August–September period, where a \hat{p} value of 1 indicates bat detection on all nights within a seven-night sampling period (Figure 2). Mean year-round detection probability for all survey areas was 0.56 (95% CI = 0.54 to 0.57; null model; Table 2, panel a).

Habitat Associations and Seasonal Patterns

Preliminary habitat association models

Covariates describing habitat attributes in ψ -only models (i.e., those not incorporating covariates for γ , ϵ , and ρ) had AIC values greater or within two AIC units of the null model, indicating that they provided little explanatory power (Appendix 2; panel a). This was not surprising given the expectation that there are strong seasonal patterns to bat occurrence, and heterogeneity not modeled in the ψ -only models likely obscured associations with specific site covariates.

Table 2. Parameter estimates for the following models: null, survey area, detection probability, arrival-departure probability, and trend in occupancy. The null model provides mean parameter (μ) estimates for all survey areas and primary sampling periods over the duration of the study (panel a). Values for the survey area model are area-specific averages of annual occupancy estimates during the period of peak detection probability (June to October; panel b). The detection probability model provides estimates of ρ as a function of forested and non-forested conditions and Julian date (corresponding to sine values of 1 [mid-September], 0 [mid-June and mid-December], and -1 [mid-March]; panel c). The arrival-departure probability model provides separate γ and ε estimates based on reproductive period (pre-pregnancy, pregnancy, lactation, post-lactation) and elevation (minimum: 2 m; mean: 947 m; maximum: 2,058 m; panel d). Annual estimates of island-wide occupancy and associated standard errors (SE) are summarized for the trend model (panel e).

(a) Null model

Par	Covariate	Covariate state	Estimate	SE	Lower 95% CI	Upper 95% CI
ψ	•	•	0.632	0.043	0.545	0.712
γ	•	•	0.555	0.028	0.500	0.608
ε	•	•	0.215	0.014	0.189	0.243
ρ	•	•	0.555	0.006	0.543	0.566

(b) Survey area model

Par	Covariate	Covariate state	Estimate	SD ¹	Lower 95% CI	Upper 95% CI
ψ	study area	AMAU	0.742	0.056	0.631	0.853
ψ		HAKM	1.000	0.000	1.000	1.000
ψ		HAKP	0.913	0.053	0.809	1.016
ψ		HPPX	0.000	0.000	0.000	0.000
ψ		IOLE	0.915	0.053	0.811	1.020
ψ		ISLA	1.000	0.000	1.000	1.000
ψ		KAIH	1.000	0.121	0.763	1.236
ψ		KEAH	0.900	0.080	0.743	1.057
ψ		KEAL	0.800	0.098	0.608	0.993
ψ		KEAU	0.880	0.067	0.749	1.011
ψ		KEHE	0.960	0.028	0.904	1.015
ψ		KHHO	0.840	0.063	0.717	0.963
ψ		KHPA	0.943	0.020	0.905	0.982
ψ		LAUP	0.971	0.032	0.908	1.035
ψ		LUPE	1.000	0.000	1.000	1.000
ψ		MAKA	1.000	0.000	1.000	1.000
ψ		MAUK	0.862	0.090	0.685	1.039
ψ		PIIH	0.753	0.102	0.552	0.954
ψ		POWE	0.846	0.114	0.623	1.069

¹ Values obtained by averaging annual estimates of occupancy; confidence intervals were derived for the standard deviation (SD) associated with the mean estimate.

Table 2. continued

(c) Detection probability model

Par	Covariate	Covariate state	Estimate	SE	Lower 95% CI	Upper 95% CI
ρ	forest, Julian	forested, March	0.378	0.015	0.348	0.408
ρ		forested, June, December	0.569	0.008	0.553	0.586
ρ		forested, September	0.742	0.011	0.720	0.762
ρ		non-forested, March	0.393	0.018	0.358	0.428
ρ		non-forested, June, December	0.490	0.010	0.471	0.509
ρ		non-forested, September	0.587	0.015	0.558	0.616

(d) Arrival-departure probability model

Par	Covariate	Covariate state	Estimate	SE	Lower 95% CI	Upper 95% CI
	reproductive period, elevation					
γ		Pre-pregnancy, min elevation (2 m)	0.475	0.078	0.328	0.626
γ		Pregnancy, min elevation (2 m)	0.474	0.087	0.313	0.641
γ		Lactation, min elevation (2 m)	0.412	0.113	0.219	0.637
γ		Post-lactation, min elevation (2 m)	0.244	0.086	0.115	0.446
γ		Pre-pregnancy, mean elevation (947 m)	0.557	0.044	0.469	0.641
γ		Pregnancy, mean elevation (947 m)	0.627	0.061	0.502	0.738
γ		Lactation, mean elevation (947 m)	0.604	0.076	0.449	0.740
γ		Post-lactation, mean elevation (947 m)	0.428	0.074	0.292	0.575
γ		Pre-pregnancy, max elevation (2,058 m)	0.650	0.085	0.471	0.794
γ		Pregnancy, max elevation (2,058 m)	0.779	0.098	0.536	0.914
γ		Lactation, max elevation (2,058 m)	0.792	0.107	0.516	0.932
γ		Post-lactation, max elevation (2,058 m)	0.667	0.128	0.393	0.861
ε		Pre-pregnancy, min elevation (2 m)	0.350	0.071	0.225	0.499
ε		Pregnancy, min elevation (2 m)	0.209	0.059	0.116	0.347
ε		Lactation, min elevation (2 m)	0.197	0.050	0.117	0.314
ε		Post-lactation, min elevation (2 m)	0.313	0.054	0.218	0.427
ε		Pre-pregnancy, mean elevation (947 m)	0.298	0.036	0.233	0.372
ε		Pregnancy, mean elevation (947 m)	0.147	0.028	0.100	0.210
ε		Lactation, mean elevation (947 m)	0.130	0.020	0.095	0.175
ε		Post-lactation, mean elevation (947 m)	0.315	0.029	0.262	0.374
ε		Pre-pregnancy, max elevation (2,058 m)	0.243	0.058	0.148	0.372
ε		Pregnancy, max elevation (2,058 m)	0.094	0.037	0.042	0.197

Table 2. continued

Par	Covariate	Covariate state	Estimate	SE	Lower 95% CI	Upper 95% CI
ϵ		Lactation, max elevation (2,058 m)	0.076	0.025	0.040	0.142
ϵ		Post-lactation, max elevation (2,058 m)	0.318	0.050	0.229	0.424

(e) Trend model

Par	Covariate	Covariate state	Estimate	SE	Lower 95% CI	Upper 95% CI
ψ	year	2007	0.752	0.044	na ¹	na
ψ		2008	0.886	0.035	na	na
ψ		2009	0.917	0.020	na	na
ψ		2010	0.833	0.035	na	na
ψ		2011	0.778	0.028	na	na

¹Confidence intervals are not available for occupancy estimates produced with the derived parameter approach.

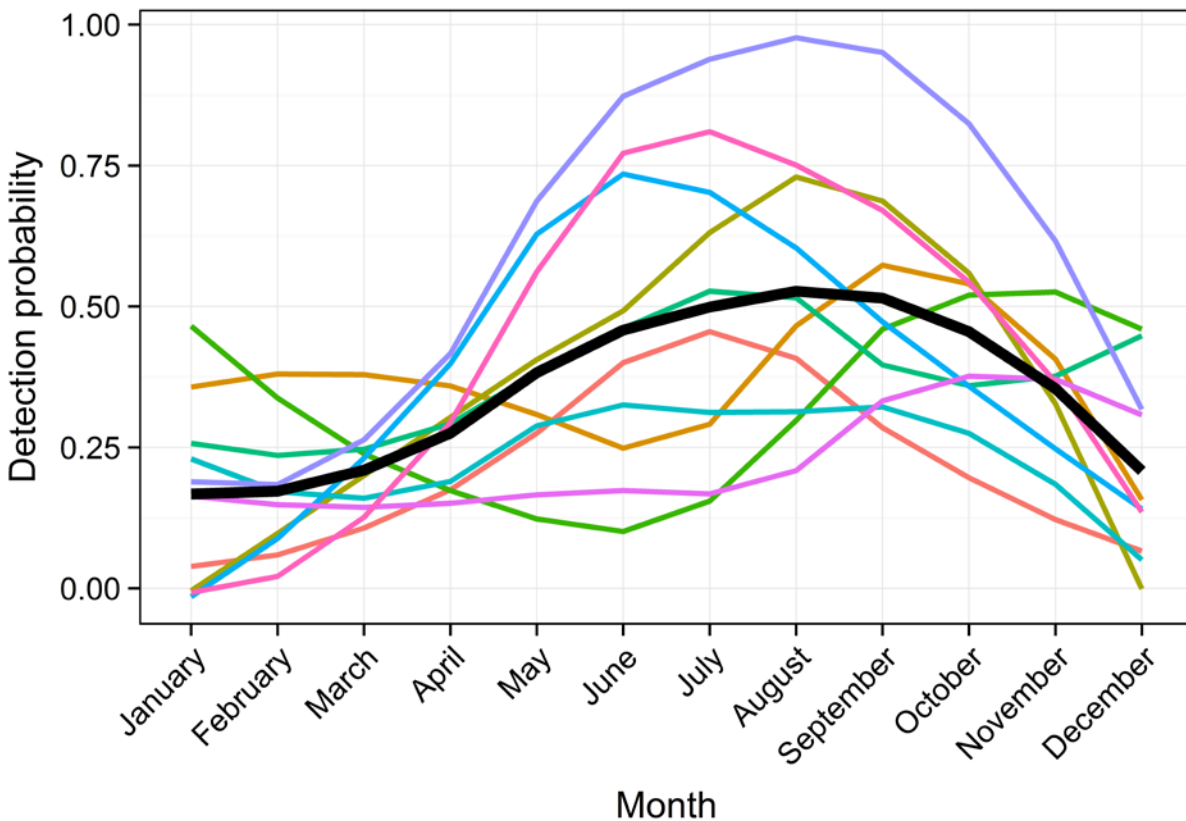


Figure 2. Seasonal variability in bat detection probability among selected survey areas. Survey areas depicted with color lines include only those for which detection probability values were available for all months. Detection probability averaged for all survey areas is shown in black.

The set of preliminary ρ -only models showed that all sampling covariates provided a much-improved fit to the data with respect to AIC values compared to the reference null model (Appendix 2; panel b). That is, all sampling covariates appeared to significantly affect the likelihood of detecting bats. In general, the covariate Julian date was included in the preponderance of models with the lowest AIC values, indicating that it provided a better fit to the data than did the covariate reproductive period. This result was expected given that the sine function describing Julian date was centered on a period of peak bat detection (September 15), but it also confirms that there are strong time-of-year effects on bat detection that need to be incorporated into models describing species-habitat associations and distribution. The best-fitting model in the ρ -only set was $\psi(\bullet)\gamma(\bullet)\varepsilon(\bullet)\rho(\text{Julian*forest})$, indicating that not only does bat detection vary by time of year, but it also does so as a function of whether a site is or is not forested (Figure 3; Table 2, panel c). Mean ρ values for forested sites peaked at 0.74 in September from a low of 0.38 in March. In contrast, mean ρ values for non-forested sites for the same months rose from a low of 0.39 to 0.59.

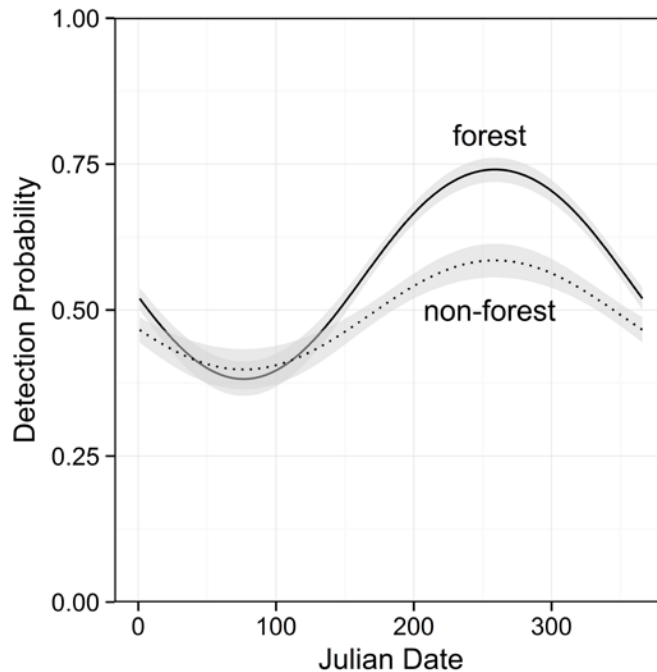


Figure 3. Probability of detecting Hawaiian hoary bats as a function of time of year and occurrence of forest.

Whereas Julian date was an important variable affecting ρ , reproductive period was the most prevalent covariate in the top-ranked models describing arrival-departure processes (Appendix 2; panel c). Again, this result is expected given that Hawaiian hoary bats demonstrate a marked seasonal pattern in occurrence that is broadly associated with reproductive periods (Menard 2001; USGS unpublished data). That these patterns of bat occurrence are also related to elevation is supported by the top-ranked arrival-departure-only model $\psi(\bullet)\gamma(\text{reproduction*elevation})\varepsilon(\text{reproduction*elevation})\rho(\bullet)$. Patterns of arrival and departure are inversely related, in that sites are likelier to have arrivals when departure rates

are low and vice versa (Figure 4; Table 2, panel d). Although the confidence intervals of the γ estimates overlap within seasons, the results tentatively indicate that high elevation sites demonstrate higher hoary bat arrival rates than low elevation sites. The effect of the interaction of elevation and reproductive period on departure rates was not conclusive.

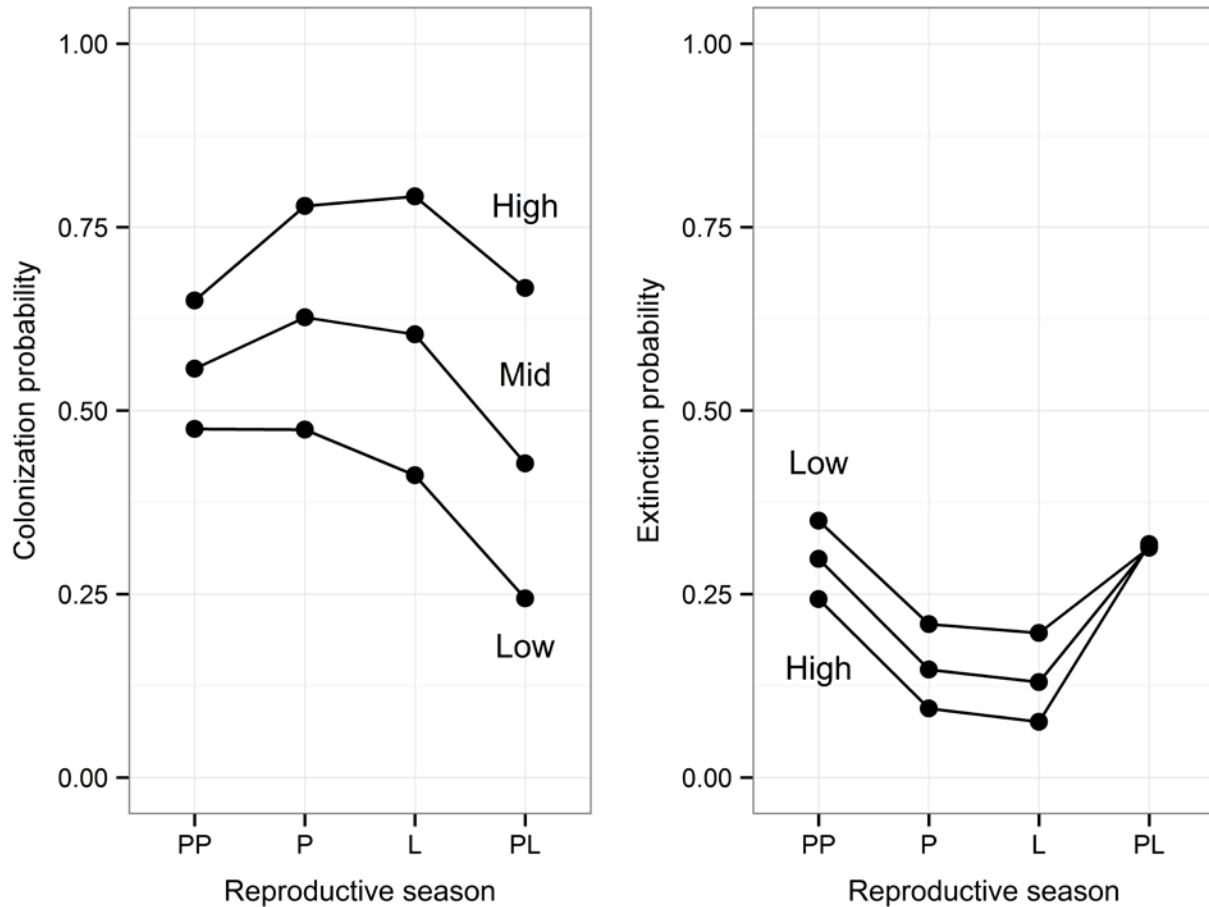


Figure 4. Arrival (colonization) and departure (extinction) probabilities as a function of reproductive season and elevation. Reproductive seasons (periods) are listed in the following order: pre-pregnancy (PP), pregnancy (P), lactation (L), and post-lactation (PL). Labels “high,” “mid,” and “low” correspond to the maximum, mean, and minimum elevations sampled (2,058 m, 947 m, and 2 m, respectively).

Final habitat association models

The relationship of bat occurrence with habitat attributes and how such patterns vary by season and time of year was examined with 36 fully parameterized models (including the null model). Model rankings are listed in Appendix 3 and coefficients from which assessments are drawn are presented in Appendix 4.

Forested sites were positively associated with bat occupancy, arrival, and detection probabilities (model 1). Moreover, Julian date was also positively related to detection probability (model 2), particularly where it was included as either an additive or an interaction term with the site covariate forest (models 3 and 4). A more nuanced picture is apparent in models that included reproductive period as the sampling covariate. Generally, arrival was negatively associated with forested sites during post-lactation and pre-pregnancy periods (September through March), and in a complimentary process, departure was positively affected during these same periods (models 5 to 7). This process appeared somewhat tempered by the inclusion of forest as an interaction term (model 7); that is, the negative coefficients for arrival are partly modified by positive coefficients for the interaction of forest and post-lactation and pre-pregnancy periods. The above models demonstrate support for the predictions that bats are positively associated with forested habitats and that the relationship varies seasonally. The results also supported our *a priori* expectation that negative arrival and positive departure dynamics would begin during the post-lactation period and extend through the pre-pregnancy period (i.e., non-breeding season). Taken together, the Julian and reproductive period models indicate that after a period of widespread occurrence at forest sites that peaks in late summer, bats begin to vacate sites during the period beginning in September, perhaps to use a greater range of less forested land cover types. Contrary to our expectation, detection probability appeared to be positively associated with forested sites (model 1). In fact it is now known that hoary bats increase the pulse rate of echolocation calls when in vegetative clutter near a forest canopy in comparison to open landscapes and this actually enhances bat detection with acoustic detectors (Jantzen 2012).

The model results for several vegetation-related site covariates did not support our predictions. Although bat occurrence was associated with forested sites, this relationship was not evident at sites where koa was a dominant or co-dominant component of landcover (models 8 and 9). Likewise, native-dominated vegetation (models 10 and 11) and net primary productivity (models 12 and 13) did not appear to be significant factors affecting bat occupancy.

Elevation was not significantly associated with bat occupancy for either set of temporal models; in other words, those inclusive of the sampling covariate Julian date (models 14–16), or alternatively, reproductive period (models 17–19). However, elevation was related to γ (positively) and ε (negatively), demonstrating that sites at higher elevations tend to undergo higher arrival and lower departure rates compared to lower elevations (models 15–16, 18–19). The influence of season was also apparent (as noted previously for the γ - and ε -only models), but the interaction of elevation and reproductive period was only significant for the post-lactation period (model 19) indicating that the covariate effects are primarily additive. In general, the results were mixed and only partly supported our predictions; specifically, the prediction that departure rates during the non-breeding season would be greater at low elevations. This partial result is supported by our field observations of Hawaiian hoary bats being less prevalent at low elevation during the non-breeding season.

Contrary to our expectation, we did not find evidence that bats were less likely to occur in areas with above-average rainfall. That is, cumulative annual rainfall was not significantly associated with site occupancy for models inclusive of the sampling covariates Julian date or reproductive period (models 20–26). Moreover, models that included monthly rainfall yielded mixed results for the two types of sampling covariates. Although Julian date was not significant, models that included this covariate indicated that bat arrival and departure rates were related to monthly rainfall (models 21–23). Conversely, the effect of monthly rainfall on parameters γ and ε was

not evident in models inclusive of reproductive period (models 24–26), perhaps in part because the sampling covariate describing time-of-year already captured the seasonal pattern of precipitation (i.e., monthly measures of rainfall are confounded with seasonal patterns of bat occurrence). That is, the correlation between monthly rainfall and season (or date) yields models in which only one or the other of the variables retains a significant effect on parameters γ and ε . In general, γ declines and ε increases with increasing monthly rain, and lends support to the prediction that bats avoid areas during wetter times of year. The absence of significant interactions between covariates (models 23 and 26) demonstrated that main effects for monthly rainfall adequately describe the seasonal nature of this effect. Finally, the prediction that detection probability was adversely affected by periods with above-average monthly rainfall was supported by both sets of temporal models; in other words, those inclusive of the sampling covariate Julian date (models 21–23), or alternatively, reproductive period (models 25–26).

Cumulative annual temperature was not found to be significantly associated with the dynamics of bat occurrence in any of the models (models 27–33), and this result did not support the prediction that bats would preferentially use warmer sites year-round. This result is not surprising given that Hawaiian hoary bats demonstrate seasonal patterns in occurrence that vary by elevation (Menard 2001), a variable that is generally correlated with temperature. That is, seasonal movement along elevation gradients may be expected to weaken any association to particular annual temperature attributes.

In contrast to the results for annual temperature, bat occurrence did exhibit a relationship to monthly temperature. In general, the probability of arrival between surveys varies cyclically through the year, peaking in mid-September and declining in mid-April, and does so inversely relative to departure. For models without a time-of-year covariate (i.e., Julian date or season), monthly temperature was negatively related to γ (model 27), indicating that arrival is favored during cooler months. For models with Julian date as the time-of-year covariate (models 28–30), monthly temperature was only significant when incorporated as an interaction term with ε (model 30). This indicates that although departure rates decrease in the fall, the effect is countered by above-average monthly temperatures.

For monthly temperature models with reproductive period as the time-of-year covariate, the effect of above-average monthly temperatures was to lower arrival rates (model 32). However, the interaction of monthly temperature with the parameter γ indicates that the negative effect of warmer periods on arrival was moderated during the pre-pregnancy period (model 33). Likewise, the interaction of parameter ε with monthly temperature indicates that departure rates are diminished by warm months during the post-lactation period. Taken together these results suggest that arrival is negatively affected, whereas departure is positively affected by abnormally warm periods (with the reverse holding for unusually cool periods). Bat detection also increases with increasing monthly mean temperature, and is higher in the lactation period than the other three periods (model 32). Moreover, the interaction of reproductive period and monthly temperature appear to counter their respective effects. That is, the general increase in detectability in the post-lactation and pre-pregnancy periods is in part negated and (possibly) reversed with increasing monthly temperature (model 33).

We did not find evidence that Hawaiian hoary bats were less likely to occur in areas with above-average wind speeds. Neither time-of-year covariates (Julian date in model 34) or reproductive period (model 35) were significant contributors to the models. The result is not remarkable given the observed occurrence of bats at windy locations on Hawai`i Island.

Trends in bat occupancy

Surveys demonstrated evidence of an increasing trend in Hawaiian hoary bat occupancy from 2007 to 2011 for samples acquired during a broad period of relatively high detection probability (June to October; Figure 5, Table 3). The weight-of-evidence from the posterior probability for the increasing trend category ($P = 0.567$), coupled to that of the negligible trend category ($P = 0.296$), indicates that the occurrence of the species on Hawai`i Island exhibits a stable to increasing trend over the five-year period of the study.

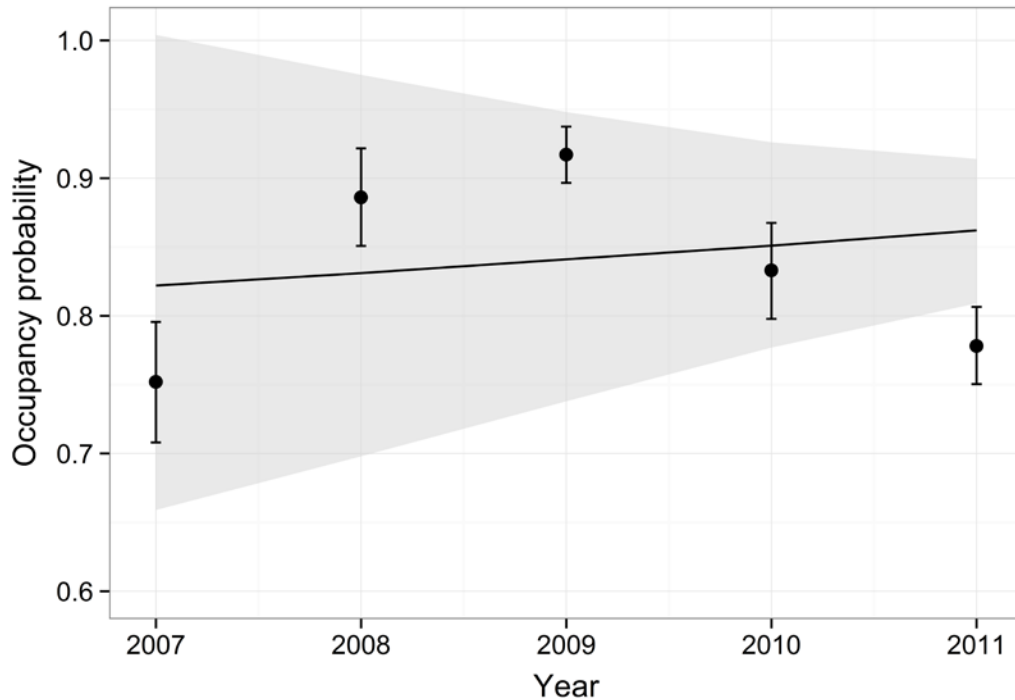


Figure 5. Trend in Hawaiian hoary bat occupancy on Hawai`i Island from 2007 to 2011 during the period of relatively high detection probability (June to October). Points depict mean annual survey area occupancy (\pm SE) for all survey areas. Mean trend (black line) and 95% CI (shaded band) were obtained from Bayesian log-linear regression of the annual estimates of occupancy for each survey area. The weights-of-evidence (Bayesian posterior probabilities) by trend category are presented in Table 3.

DISCUSSION

The Hawaiian hoary bat has a ubiquitous distribution with fairly high occupancy throughout almost all regions of the island of Hawai`i. During the breeding season (June to October) bats were absent from only a single geographic site (HPPK in Table 2, panel b) during our study; whereas the remaining 18 sites observed during the breeding season had occupancy values greater than the annual mean for all sites.

Table 3. Assessment of change in Hawaiian hoary bat occupancy by trend category. The thresholds for determining the ecological significance of a trend were defined as a 25% change in occupancy over 25 years. The metric corresponds to an annual rate of change with significance defined by a threshold lower bound of $\phi_l = -0.0119$ and an upper bound of $\phi_u = 0.0093$. Bayesian log-linear regression statistics include the slope coefficient ($\hat{\beta}$), standard deviation (SD) and 95% credible interval (CI). The posterior probabilities (P) of the regression slope are assessed for declining, negligible, and increasing trends, where $P > 0.9$ indicates very strong evidence, $0.7 < P < 0.9$ strong evidence, $0.5 < P < 0.7$ moderate evidence, and $P < 0.5$ weak evidence of a trend. An inconclusive result is obtained when the posterior distribution yields only weak evidence across the increasing, decreasing, and negligible trend categories.

$\hat{\beta}$	SD	95% CI	Posterior probability		
			Declining $\hat{\beta} < \phi_l$	Negligible $\phi_l < \hat{\beta} < \phi_u$	Increasing $\hat{\beta} > \phi_u$
0.013	0.023	-0.032 to 0.059	0.138	0.296	0.567

We observed a marked and consistent seasonal pattern in occupancy and detection probability throughout the five years of our study. Highest occupancy peaked on the Julian date 15 September across the five years average and was expected because August and September compose the fledging season for the young of the year. During fledging the absolute population should be at its annual maximum and a population decline generally follows until the next year's fledging. Conversely, the lowest period of occupancy occurred between December and March each year as bats disperse to high elevations in the annual migration. Unfortunately, the elevation range in our present study did not cover the full winter range of Hawaiian hoary bats. Current and ongoing research now indicates that Hawaiian hoary bats occupy and forage at elevations between 2,200 and 3,600 m during November through March (F. Bonaccorso personal observation). Thus, our data support the previous conclusion of Menard (2001) that hoary bats on the island of Hawai`i concentrate in the coastal lowlands during the breeding season, May through October, and migrate to interior highlands during the winter. These strong annual effects on bat detection should be incorporated into future sampling designs and models describing species-habitat associations and distribution.

Although the Hawaiian hoary bat is a habitat generalist species (Tomich 1986), we found a significant association between occupancy and the prevalence of mature forest cover. Native vegetation, however, is not related to occupancy because non-native vegetation is capable of providing abundant prey (e.g., macadamia nut orchards; authors' personal observations) or shelter for roosting (e.g., mature eucalyptus plantations; authors' personal observations). One of the native forest dominant species, the koa tree, although abundant in habitats used by bats, is not significantly associated with bat occupancy in our models most likely because it does not offer sufficient shade cover for day-roosts (Bonaccorso *et al.* in press). Also koa may not be sufficiently important in affecting overall prey availability other than for brief periods of the annual cycle, and hoary bats opportunistically consume a wide variety of prey species (Whitaker and Tomich 1983, Jacob 1999, Valdez and Cryan 2009, Bernard 2011, Todd 2012).

Net primary productivity was not related to bat occupancy because higher NPP values generally are associated with lowland forests in Hawai`i which are almost exclusively non-native. The

majority of the native forest remaining in Hawai`i occurs at montane elevations. These facts probably account for the lack of association of native vegetation and elevation with occupancy.

Annual events of site arrival and departure generally were associated with elevation, but elevation and reproductive period did not demonstrate much interaction and this relationship was mostly additive, not multiplicative. Our results tentatively indicate that high elevation sites demonstrate higher hoary bat arrival rates than do low elevation sites where some bat activity persists throughout the year. The effect of the interaction of elevation and reproductive period on departure rates was not conclusive. Although occupancy was not associated with measures of annual mean temperature and rain as site attributes, arrival and departure generally were associated with monthly temperature and rain as predicted. The influence of elevation, weather-related variables, and seasonal interactions in our models probably was under-represented because the winter range of Hawaiian hoary bats on the island now is understood to importantly include sites at elevations greater than 2,000 m (authors' personal observations), and these elevations were not sampled for this present study. Additionally, the influence of elevation may have been obscured, because although bats remain active and commonly occupy higher elevations in winter months, they apparently can traverse a broad range in elevation and between habitats even within a single night to forage where weather and prey availability offer optimal local foraging opportunities (e.g., avoiding local rains, fogs, and high winds). Bonaccorso *et al.* (in press) documented radio-tagged individuals moving 15 km within a night from near sea level to 1,500 m. This is possible because of the steep altitudinal gradients of Hawai`i; for example, Mauna Kea (4,000 m) is only 30 km from the coast, a distance that Hawaiian hoary bats can traverse in about 45 minutes.

Trends in occupancy were stable to slightly increasing at our sites during a period of relatively high detection probability from June through October over our five-year study. Because the survey areas were not selected within a probabilistic sampling design, the inferences of habitat association and trend should be treated with some caution; that is they are strongly suggestive but not conclusive. The assessments of occupancy in our study were based on detection criteria that are not sensitive to absolute differences in the number of echolocation pulses or call sequences or the relative abundance of bats. In the future, it would be informative to consider analysis of these types of data based on step-wise thresholds of activity.

Bat occurrence and abundance are probably primarily associated with proximity to locally available day-roost habitat, prey abundance, and suitable microclimate fostering success in rearing pups. However, other variables including localized population irruptions of prey species and weather conditions such as prolonged, higher-than-normal trade winds or stationary fronts contribute to very complex patterns in bat occupancy, arrivals, and departures over time. Day-roost habitat requirements for Hawaiian hoary bats are tall (greater than five meters crown height), shady trees frequently including mature native `ōhi`a lehua (*Metrosideros polymorpha*) but also including a wide variety of introduced species such as lychee (*Litchi chinensis*), various species of eucalyptus (*Eucalyptus* spp.), mango (*Mangifera indica*), and numerous other tree species (Bonaccorso *et al.* in press). Nevertheless, the mobility offered by flight renders virtually all the island from coastal embayments (Tomich 1986 and authors' personal observations) to the upper slopes of the highest mountains of Hawai`i accessible to foraging opportunities for Hawaiian hoary bats.

ACKNOWLEDGEMENTS

Our study was funded jointly by grants from the Hawai`i Division of Forestry and Wildlife, the U.S. Department of Federal Highways, the U.S. Fish and Wildlife Service through the Science Support Partnership, and with additional support provided by the USGS Pacific Island Ecosystems Research Center. This report was improved by manuscript reviews from R. Adams, R. Camp, and S. Nash. We thank R. Bernard, N. Cortez Delgado, A. Hubancheva, C. Leopold, R. Mosely, B. Yuen, V. Zrcinc, and T. Zinn for assistance with field work. We thank the following organizations and individuals for assistance with site access, logistical support, and issuance of permits; Hakalau National Wildlife Refuge (J. Jeffrey, J. Glynn, and S. Kendal), Hawai`i Division of Forestry and Wildlife (H. Sin, J. Mello, J. Leialoha, J. Omick, and S. Fretz), Island Harvest (J. Trump), Island Princess Estates (D. Shell), Kamehameha Schools, Keaukaha Military Reservation (C. Blaisdell), National Park Service, New Moon Foundation, Kohala Watershed Partnership (M. Purell), OK Farms LLC, Parker Ranch (K. Wood), Three Mountain Alliance (C. Cole, A. Christie, and N. Okuda), The Nature Conservancy of Hawai`i (E. Naboia and S. Crysdale), and the USDA Forest Service and Hawaii DLNR (for access to the Laupahoehoe Unit of the Hawaii Experimental Tropical Forest).

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APPENDIX 1. SURVEY AREAS SAMPLED FOR HAWAIIAN HOARY BAT OCCURRENCE FROM 2007 TO 2012 ON HAWAI`I ISLAND

Universal Transverse Mercator (UTM) coordinates in zone 5. Coordinates, elevation, and habitat type are averaged or summary attributes are given for multiple sample sites within each survey area.

Acronym	Survey area	Easting	Northing	Elevation (meters)	Habitat type
AMAU	OK Farms, Amau`ulu Road, Hilo	278290	2182574	175	mostly herbaceous-grass, some forest
HAKM	Hakalau National Wildlife Refuge Maulua Tract	258247	2198425	1642	forest
HAKP	Hakalau National Wildlife Refuge Pua Akala Tract	256671	2189772	1846	forest
HONA	Pu`uhonua o Hōnaunau National Historical Park	194627	2149506	10	mostly shrub, some forest
HPPX	Hawaiian Paradise Park, Kea`au	293378	2167371	44	mostly forest
IOLE	I`ole Road, New Moon Foundation	208256	2238204	1156	mostly forest
ISLA	Island Princess Farms, Kea`au	281270	2170355	231	mixed herbaceous-grass and forest (plantation)
KAIH	TNC Kaiholena Preserve	228852	2122659	399	mostly forest
KALO	Kaloko-Honokōhau National Historical Park	182667	2179173	906	mostly shrub, some forest
KEAH	Keahou Ranch (high elevation)	254310	2160859	1627	mixed herbaceous-grass and forest
KEAL	Keahou Ranch (low elevation)	259326	2152659	813	mixed herbaceous-grass and forest
KEAU	Keaukaha Military Reservation	286781	2180031	859	mostly herbaceous-grass, some forest
KEHE	Kehena, Kohala Mountains	211935	2229498	692	mostly forest
KHHO	TNC ¹ Kona Hema Preserve, Honomolino Unit	207584	2125657	22	mixed herbaceous-grass and forest
KHPA	TNC ¹ Kona Hema Preserve, Papa Unit	202860	2127311	869	forest
LAUP	Laupahoehoe Natural Area Reserve	260680	2206531	1341	forest
LUPE	Lupea	209428	2164665	1069	mostly shrub, some forest

Acronym	Survey area	Easting	Northing	Elevation (meters)	Habitat type
MAKA	Maka`ula-`O`oma Mauka Tract Forest Reserve	190392	2183777	992	forest
MAUK	Mauna Kea Forest Reserve	236697	2185104	1385	shrubland
PIIH	Pi`ihonua Tract; Hilo Forest Reserve	271535	2180526	1788	mixed herbaceous-grass and forest
POWE	Powerline Road; Upper Waiakea Forest Reserve	251809	2174719	2026	mostly forest, some shrub and barren areas
PUUW	Pu`u Wa`awa`a Forest Reserve	202799	2191232	779	forest
TREE	Tree Planting Road; Upper Waiakea Forest Reserve	268626	2167088	567	forest
UMIK	Umikoa Ranch	255682	2208499	823	forest
WAOK	Wao Kele O Puna Forest Reserve	289922	2148536	808	forest

¹ TNC = The Nature Conservancy

APPENDIX 2. RANKING OF PRELIMINARY MODELS DESCRIBING THE RELATION OF HOARY BAT OCCURRENCE TO SITE AND SAMPLING COVARIATES

Table separately lists results for three types of parameter models: (panel a) occupancy-only, $\psi(\text{cov})\gamma(\bullet)\varepsilon(\bullet)\rho(\bullet)$; (panel b) detection probability-only, $\psi(\bullet)\gamma(\bullet)\varepsilon(\bullet)\rho(\text{cov})$; and (panel c) arrival-departure-only, $\psi(\bullet)\gamma(\text{cov})\varepsilon(\text{cov})\rho(\bullet)$. The notation (\bullet) indicates a constant parameter (i.e., modeled as an intercept only), and the null model is shown as $\psi(\bullet)\gamma(\bullet)\varepsilon(\bullet)\rho(\bullet)$. Models with interaction terms are indicated with the asterisk symbol between covariate names. Column AIC lists values used to rank models based on best fit to the data. Column ΔAIC is the relative difference in AIC values from the model with the smallest value, and w is the AIC model weight. Column k is the number of model parameters. See Methods section for an explanation of covariate names and abbreviations.

(a) Occupancy-only models

Model parameters				AIC	ΔAIC	w	k
ψ	γ	ε	ρ				
forest	•	•	•	11335.4	0.0	0.21	5
•	•	•	•	11335.7	0.3	0.18	4
elev	•	•	•	11336.3	0.9	0.13	5
temp (ann)	•	•	•	11336.9	1.4	0.10	5
native	•	•	•	11337.0	1.6	0.09	5
wind	•	•	•	11337.3	1.9	0.08	5
rain (ann)	•	•	•	11337.5	2.0	0.08	5
NPP	•	•	•	11337.7	2.2	0.07	5
koa	•	•	•	11337.7	2.3	0.07	5

(b) Detection probability-only models

Model parameters				AIC	ΔAIC	w	k
ψ	γ	ε	ρ				
•	•	•	Julian*forest	10965.6	0.0	1.00	7
•	•	•	Julian+forest	10990.2	24.6	0.00	6
•	•	•	Julian+rain (mo)	10996.6	31.0	0.00	6
•	•	•	repro period*forest	11022.8	57.1	0.00	11
•	•	•	repro period+forest	11034.0	68.3	0.00	8
•	•	•	Julian+temp (mo)	11035.7	70.1	0.00	6
•	•	•	Julian	11040.7	75.0	0.00	5
•	•	•	Julian+elev	11041.3	75.7	0.00	6

Model parameters				AIC	Δ AIC	w	k
ψ	γ	ϵ	ρ				
•	•	•	Julian*elev	11043.1	77.5	0.00	7
•	•	•	repro period+rain (mo)	11050.6	84.9	0.00	8
•	•	•	repro period+temp	11084.1	118.4	0.00	8
•	•	•	repro period*elev	11089.4	123.8	0.00	11
•	•	•	repro period	11090.3	124.7	0.00	7
•	•	•	repro period+elev	11091.8	126.2	0.00	8
•	•	•	rain (mo)	11279.2	313.6	0.00	5
•	•	•	forest	11285.6	320.0	0.00	5
•	•	•	temp (mo)	11286.9	321.3	0.00	5
•	•	•	•	11335.7	370.1	0.00	4

(c) Arrival-departure-only models

Model parameters				AIC	Δ AIC	w	k
ψ	γ	ϵ	ρ				
•	repro period+elev	repro period+elev	•	11281.8	0.0	0.97	12
•	repro period*elev	repro period*elev	•	11288.8	7.0	0.03	18
•	repro period+temp (mo)	repro period+temp (mo)	•	11293.0	11.2	0.00	12
•	repro period+rain (mo)	repro period+rain (mo)	•	11297.0	15.2	0.00	12
•	repro period	repro period	•	11297.3	15.5	0.00	10
•	repro period+forest	repro period+forest	•	11297.9	16.1	0.00	12
•	repro period*forest	repro period*forest	•	11304.8	23.0	0.00	18
•	Julian+elev	Julian+elev	•	11321.3	39.5	0.00	8
•	temp (mo)	temp (mo)	•	11321.5	39.7	0.00	6
•	Julian*elev	Julian*elev	•	11323.5	41.7	0.00	10
•	Julian+temp (mo)	Julian+temp (mo)	•	11324.5	42.7	0.00	8
•	rain (mo)	rain (mo)	•	11327.2	45.3	0.00	6
•	Julian+rain (mo)	Julian+rain (mo)	•	11327.7	45.9	0.00	8
•	•	•	•	11335.7	53.9	0.00	4
•	forest	forest	•	11336.5	54.7	0.00	6
•	Julian	Julian	•	11337.1	55.3	0.00	6
•	Julian+forest	Julian+forest	•	11337.8	56.0	0.00	8
•	Julian*forest	Julian*forest	•	11340.0	58.1	0.00	10

APPENDIX 3. RANKING OF FULLY PARAMETERIZED HABITAT ASSOCIATION MODELS

The ψ covariate is listed separately from covariates used for γ , ε , and ρ . The null model $\psi(\bullet)\gamma(\bullet)\varepsilon(\bullet)\rho(\bullet)$ is indicated with the term “intercept”. Models with interaction terms are indicated with the asterisk symbol between covariate names. Column AIC lists values that rank models based on best fit to the data. Column Δ AIC is the relative difference in AIC values from the model with the smallest value, and w is the AIC model weight. Column k is the number of model parameters. See Methods section for an explanation of covariate names and abbreviations.

ψ covariate	γ , ε , and ρ covariates	AIC	Δ AIC	w	k
forest	Julian*forest	10970.6	0.0	1.00	14
rain (ann)	Julian*rain (mo)	10990.0	19.4	0.00	14
rain (ann)	Julian+rain (mo)	10993.7	23.0	0.00	11
forest	Julian+forest	10994.2	23.6	0.00	11
temp (ann)	repro period*temp (mo)	10997.0	26.4	0.00	26
forest	repro period*forest	11000.6	30.0	0.00	26
forest	repro period+forest	11007.0	36.4	0.00	17
temp (ann)	Julian*temp (mo)	11019.4	48.8	0.00	14
rain (ann)	repro period+rain (mo)	11024.5	53.9	0.00	17
temp (ann)	Julian+temp (mo)	11026.2	55.5	0.00	11
elevation	Julian+elevation	11028.7	58.1	0.00	11
rain (ann)	repro period*rain (mo)	11029.9	59.3	0.00	26
elevation	Julian*elevation	11032.6	61.9	0.00	14
forest	Julian	11042.4	71.7	0.00	8
elevation	Julian	11043.1	72.5	0.00	8
temp (ann)	Julian	11043.5	72.9	0.00	8
native	Julian	11043.7	73.1	0.00	8
wind	Julian	11044.0	73.4	0.00	8
rain (ann)	Julian	11044.1	73.5	0.00	8
NPP	Julian	11044.4	73.8	0.00	8
koa	Julian	11044.4	73.8	0.00	8
elevation	repro period+elevation	11048.1	77.5	0.00	17
temp (ann)	repro period+temp (mo)	11050.1	79.5	0.00	17
elevation	repro period*elevation	11054.5	83.9	0.00	26
forest	repro period	11060.8	90.2	0.00	14
elevation	repro period	11061.3	90.7	0.00	14
temp (ann)	repro period	11061.7	91.1	0.00	14
native	repro period	11062.1	91.4	0.00	14
wind	repro period	11062.3	91.7	0.00	14
rain (ann)	repro period	11062.5	91.9	0.00	14
koa	repro period	11062.7	92.1	0.00	14
NPP	repro period	11062.7	92.1	0.00	14
rain (ann)	rain (mo)	11273.7	303.0	0.00	8
temp (ann)	temp (mo)	11273.7	303.0	0.00	8
forest	forest	11286.8	316.2	0.00	8
null (intercept only)	null (intercept only)	11335.7	365.1	0.00	4

APPENDIX 4. PARAMETER ESTIMATES FOR HABITAT ASSOCIATION MODELS

Results presented for each model parameter (occupancy [ψ], arrival [γ], departure [ε], detection probability [ρ]) include covariate names and covariate state (e.g., forest, non-forested), coefficient values (logit scale), standard error (SE), and mean and lower and upper 95% confidence intervals of the odds ratio. $P(>|z|)$ is the probability of getting a test statistic as extreme as, or more so, than the observed statistic under the null hypothesis. Values in bold represent significant P values or odds ratios for which the 95% CI does not bracket an odds ratio equal to 1.

Model	Parameter	Covariate	Covariate state	Coefficient (logit scale)	SE	$P(> z)$	Odds ratio	Lower 95% CI	Upper 95% CI
null	ψ	-	-	0.542	0.185	0.003	1.719	1.480	1.958
	γ	-	-	0.220	0.112	0.049	1.246	1.093	1.399
	ε	-	-	-1.300	0.082	0.000	0.273	0.192	0.353
	ρ	-	-	0.219	0.024	0.000	1.245	1.211	1.278
1	ψ	intercept	non-forested	0.191	0.312	0.541	1.210	0.782	1.639
	ψ	forest	forested	0.548	0.391	0.161	1.730	1.225	2.234
	γ	intercept	non-forested	0.061	0.158	0.699	1.063	0.844	1.282
	γ	forest	forested	0.331	0.225	0.140	1.393	1.089	1.696
	ε	intercept	non-forested	-1.254	0.124	0.000	0.285	0.161	0.410
	ε	forest	forested	-0.080	0.166	0.630	0.923	0.694	1.153
	ρ	intercept	non-forested	0.015	0.038	0.687	1.015	0.963	1.067
	ρ	forest	forested	0.355	0.050	0.000	1.426	1.359	1.493
2	ψ	intercept	non-forested	0.216	0.317	0.496	1.241	0.807	1.675
	ψ	forest	forested	0.572	0.399	0.151	1.772	1.260	2.283
	γ	intercept	June, December	0.155	0.125	0.216	1.168	0.995	1.340
	γ	Julian	September	-0.213	0.175	0.222	0.808	0.568	1.048
	ε	intercept	June, December	-1.375	0.089	0.000	0.253	0.168	0.338
	ε	Julian	September	0.091	0.126	0.467	1.095	0.922	1.269
	ρ	intercept	June, December	0.139	0.026	0.000	1.149	1.113	1.185
	ρ	Julian	September	0.612	0.037	0.000	1.844	1.798	1.891
3	ψ	intercept	non-forested	0.281	0.324	0.387	1.324	0.884	1.765
	ψ	forest	forested	0.482	0.403	0.232	1.619	1.091	2.147

Model	Parameter	Covariate	Covariate state	Coefficient (logit scale)	SE	P(> z)	Odds ratio	Lower 95% CI	Upper 95% CI
	γ	intercept	non-forested; June, December	-0.007	0.173	0.970	0.994	0.754	1.233
	γ	Julian	September	-0.222	0.176	0.208	0.801	0.560	1.042
	γ	forest	forested	0.325	0.236	0.168	1.384	1.066	1.703
	ε	intercept	non-forested; June, December	-1.365	0.135	0.000	0.255	0.126	0.385
	ε	Julian	September	0.093	0.126	0.462	1.097	0.923	1.271
	ε	forest	forested	-0.031	0.176	0.858	0.969	0.725	1.213
	ρ	intercept	non-forested; June, December	-0.074	0.040	0.062	0.928	0.873	0.984
	ρ	Julian	September	0.614	0.037	0.000	1.848	1.801	1.894
	ρ	forest	forested	0.369	0.052	0.000	1.447	1.378	1.516
4	ψ	intercept	non-forested	0.231	0.318	0.468	1.260	0.825	1.695
	ψ	forest	forested	0.555	0.400	0.166	1.742	1.227	2.257
	γ	intercept	non-forested; June, December	0.055	0.177	0.755	1.057	0.812	1.302
	γ	Julian	September	-0.014	0.242	0.953	0.986	0.651	1.321
	γ	forest	forested	0.202	0.252	0.424	1.223	0.878	1.569
	γ	forest*Julian	forested*September	-0.460	0.354	0.194	0.631	0.165	1.098
	ε	intercept	non-forested; June, December	-1.303	0.131	0.000	0.272	0.142	0.401
	ε	Julian	September	0.040	0.191	0.834	1.041	0.776	1.305
	ε	forest	forested	-0.127	0.179	0.478	0.881	0.634	1.128
	ε	forest*Julian	forested*September	0.085	0.254	0.737	1.089	0.737	1.440
	ρ	intercept	non-forested; June, December	-0.038	0.039	0.339	0.963	0.909	1.018
	ρ	Julian	September	0.390	0.056	0.000	1.477	1.403	1.551
	ρ	forest	forested	0.313	0.053	0.000	1.368	1.297	1.439
	ρ	forest*Julian	forested*September	0.389	0.074	0.000	1.476	1.377	1.575
5	ψ	intercept	non-forested	0.218	0.319	0.493	1.244	0.807	1.681

Model	Parameter	Covariate	Covariate state	Coefficient (logit scale)	SE	P(> z)	Odds ratio	Lower 95% CI	Upper 95% CI
	ψ	forest	forested	0.549	0.399	0.169	1.732	1.217	2.246
	γ	intercept	lactation	0.422	0.297	0.156	1.524	1.130	1.918
	γ	repro period	post-lactation	-0.732	0.414	0.077	0.481	-0.026	0.988
	γ	repro period	pre-pregnancy	-0.214	0.354	0.546	0.807	0.322	1.293
	γ	repro period	pregnancy	-0.051	0.388	0.895	0.950	0.413	1.487
	ε	intercept	lactation	-1.972	0.183	0.000	0.139	0.007	0.272
	ε	repro period	post-lactation	1.120	0.228	0.000	3.065	2.822	3.308
	ε	repro period	pre-pregnancy	1.013	0.256	0.000	2.754	2.470	3.038
	ε	repro period	pregnancy	0.241	0.281	0.392	1.273	0.889	1.656
	ρ	intercept	lactation	0.637	0.052	0.000	1.891	1.826	1.956
	ρ	repro period	post-lactation	-0.228	0.067	0.001	0.796	0.705	0.887
	ρ	repro period	pre-pregnancy	-1.109	0.079	0.000	0.330	0.245	0.414
	ρ	repro period	pregnancy	-0.561	0.074	0.000	0.571	0.476	0.666
6	ψ	intercept	non-forested	0.285	0.326	0.382	1.330	0.887	1.773
	ψ	forest	forested	0.457	0.404	0.258	1.579	1.047	2.112
	γ	intercept	non-forested; lactation	0.208	0.328	0.527	1.231	0.781	1.681
	γ	repro period	post-lactation	-0.714	0.416	0.086	0.490	-0.023	1.002
	γ	repro period	pre-pregnancy	-0.179	0.355	0.615	0.836	0.348	1.324
	γ	repro period	pregnancy	0.027	0.396	0.946	1.027	0.479	1.576
	γ	forest	forested	0.353	0.243	0.147	1.423	1.096	1.750
	ε	intercept	non-forested; lactation	-1.964	0.211	0.000	0.140	-0.013	0.294
	ε	repro period	post-lactation	1.133	0.230	0.000	3.105	2.861	3.348
	ε	repro period	pre-pregnancy	1.010	0.260	0.000	2.744	2.455	3.033
	ε	repro period	pregnancy	0.258	0.283	0.362	1.294	0.908	1.680
	ε	forest	forested	-0.045	0.175	0.798	0.956	0.714	1.199
	ρ	intercept	non-forested; lactation	0.421	0.059	0.000	1.523	1.445	1.602
	ρ	repro period	post-lactation	-0.232	0.067	0.001	0.793	0.701	0.885
	ρ	repro period	pre-pregnancy	-1.127	0.079	0.000	0.324	0.240	0.408
	ρ	repro period	pregnancy	-0.562	0.074	0.000	0.570	0.475	0.665

Model	Parameter	Covariate	Covariate state	Coefficient (logit scale)	SE	P(> z)	Odds ratio	Lower 95% CI	Upper 95% CI
7	ρ	forest	forested	0.384	0.051	0.000	1.468	1.400	1.537
	ψ	intercept	non-forested	0.233	0.320	0.466	1.262	0.825	1.700
	ψ	forest	forested	0.520	0.400	0.194	1.682	1.162	2.202
	γ	intercept	non-forested; lactation	0.671	0.505	0.184	1.956	1.326	2.586
	γ	repro period	post-lactation	-1.168	0.653	0.074	0.311	-0.371	0.993
	γ	repro period	pre-pregnancy	-0.866	0.566	0.126	0.421	-0.243	1.084
	γ	repro period	pregnancy	-0.332	0.604	0.583	0.717	-0.097	1.532
	γ	forest	forested	-0.438	0.625	0.483	0.645	-0.182	1.472
	γ	forest*repro period	forested*post-lactation	0.770	0.850	0.365	2.160	1.131	3.188
	γ	forest*repro period	forested*pre-pregnancy	1.314	0.738	0.075	3.721	2.997	4.445
	γ	forest*repro period	forested*pregnancy	0.473	0.813	0.561	1.605	0.537	2.672
	ε	intercept	non-forested; lactation	-1.845	0.268	0.000	0.158	-0.048	0.364
	ε	repro period	post-lactation	0.941	0.339	0.006	2.563	2.177	2.950
	ε	repro period	pre-pregnancy	1.068	0.376	0.005	2.909	2.500	3.318
	ε	repro period	pregnancy	0.251	0.402	0.533	1.285	0.736	1.833
	ε	forest	forested	-0.263	0.368	0.476	0.769	0.268	1.270
	ε	forest*repro period	forested*post-lactation	0.363	0.460	0.431	1.437	0.820	2.055
	ε	forest*repro period	forested*pre-pregnancy	-0.060	0.515	0.907	0.942	0.229	1.655
	ε	forest*repro period	forested*pregnancy	-0.010	0.567	0.987	0.990	0.205	1.776
	8	ρ	intercept	non-forested; lactation	0.335	0.077	0.000	1.397	1.294
ρ		repro period	post-lactation	-0.227	0.100	0.023	0.797	0.660	0.934
ρ		repro period	pre-pregnancy	-0.773	0.120	0.000	0.462	0.317	0.607
ρ		repro period	pregnancy	-0.443	0.111	0.000	0.642	0.495	0.789
ρ		forest	forested	0.544	0.105	0.000	1.724	1.588	1.859
ρ		forest*repro period	forested*post-lactation	-0.013	0.135	0.921	0.987	0.800	1.174
ρ		forest*repro period	forested*pre-pregnancy	-0.603	0.160	0.000	0.547	0.344	0.751
ρ		forest*repro period	forested*pregnancy	-0.216	0.149	0.148	0.805	0.601	1.010
ψ		intercept	not present	0.600	0.213	0.005	1.822	1.550	2.093
ψ		koa	present	-0.052	0.477	0.913	0.949	0.289	1.610

Model	Parameter	Covariate	Covariate state	Coefficient (logit scale)	SE	P(> z)	Odds ratio	Lower 95% CI	Upper 95% CI
	γ	intercept	June, December	0.150	0.125	0.230	1.162	0.990	1.334
	γ	Julian	September	-0.215	0.175	0.218	0.807	0.567	1.046
	ε	intercept	June, December	-1.379	0.089	0.000	0.252	0.167	0.337
	ε	Julian	September	0.093	0.126	0.460	1.097	0.923	1.271
	ρ	intercept	June, December	0.138	0.026	0.000	1.148	1.112	1.184
	ρ	Julian	September	0.612	0.037	0.000	1.844	1.798	1.891
9	ψ	intercept	not present	0.585	0.212	0.006	1.794	1.523	2.065
	ψ	koa	present	-0.030	0.477	0.949	0.970	0.309	1.631
	γ	intercept	lactation	0.421	0.295	0.153	1.523	1.132	1.915
	γ	repro period	post-lactation	-0.734	0.413	0.076	0.480	-0.026	0.986
	γ	repro period	pre-pregnancy	-0.212	0.353	0.547	0.809	0.325	1.293
	γ	repro period	pregnancy	-0.064	0.386	0.868	0.938	0.404	1.472
	ε	intercept	lactation	-1.974	0.182	0.000	0.139	0.007	0.271
	ε	repro period	post-lactation	1.122	0.228	0.000	3.071	2.829	3.313
	ε	repro period	pre-pregnancy	1.017	0.256	0.000	2.765	2.481	3.049
	ε	repro period	pregnancy	0.231	0.281	0.411	1.260	0.876	1.644
	ρ	intercept	lactation	0.637	0.052	0.000	1.891	1.826	1.956
	ρ	repro period	post-lactation	-0.228	0.067	0.001	0.796	0.705	0.887
	ρ	repro period	pre-pregnancy	-1.110	0.079	0.000	0.330	0.245	0.414
	ρ	repro period	pregnancy	-0.561	0.074	0.000	0.571	0.476	0.666
10	ψ	intercept	not present	0.409	0.284	0.150	1.505	1.127	1.883
	ψ	native	present	0.320	0.383	0.403	1.377	0.860	1.895
	γ	intercept	June, December	0.148	0.125	0.237	1.160	0.987	1.332
	γ	Julian	September	-0.213	0.175	0.223	0.808	0.568	1.048
	ε	intercept	June, December	-1.380	0.089	0.000	0.252	0.166	0.337
	ε	Julian	September	0.095	0.126	0.450	1.100	0.926	1.274
	ρ	intercept	June, December	0.138	0.026	0.000	1.148	1.112	1.184
	ρ	Julian	September	0.612	0.037	0.000	1.844	1.798	1.891
11	ψ	intercept	not present	0.407	0.284	0.152	1.502	1.124	1.880

Model	Parameter	Covariate	Covariate state	Coefficient (logit scale)	SE	P(> z)	Odds ratio	Lower 95% CI	Upper 95% CI
	ψ	native	present	0.303	0.382	0.427	1.354	0.836	1.872
	γ	intercept	lactation	0.424	0.296	0.153	1.528	1.135	1.921
	γ	repro period	post-lactation	-0.737	0.414	0.075	0.479	-0.028	0.985
	γ	repro period	pre-pregnancy	-0.218	0.354	0.538	0.804	0.319	1.289
	γ	repro period	pregnancy	-0.074	0.387	0.849	0.929	0.393	1.465
	ε	intercept	lactation	-1.971	0.182	0.000	0.139	0.007	0.271
	ε	repro period	post-lactation	1.119	0.228	0.000	3.062	2.819	3.305
	ε	repro period	pre-pregnancy	1.011	0.256	0.000	2.748	2.464	3.033
	ε	repro period	pregnancy	0.225	0.282	0.425	1.252	0.866	1.638
	ρ	intercept	lactation	0.637	0.052	0.000	1.891	1.826	1.956
	ρ	repro period	post-lactation	-0.228	0.067	0.001	0.796	0.705	0.887
	ρ	repro period	pre-pregnancy	-1.110	0.079	0.000	0.330	0.245	0.414
	ρ	repro period	pregnancy	-0.561	0.074	0.000	0.571	0.476	0.666
12	ψ	intercept	mean NPP	0.592	0.191	0.002	1.807	1.564	2.051
	ψ	NPP	1 SD of NPP	0.031	0.186	0.869	1.031	0.774	1.289
	γ	intercept	June, December	0.150	0.125	0.229	1.162	0.990	1.334
	γ	Julian	September	-0.213	0.175	0.224	0.808	0.568	1.048
	ε	intercept	June, December	-1.379	0.089	0.000	0.252	0.167	0.337
	ε	Julian	September	0.094	0.126	0.455	1.098	0.924	1.272
	ρ	intercept	June, December	0.138	0.026	0.000	1.148	1.112	1.184
	ρ	Julian	September	0.612	0.037	0.000	1.844	1.798	1.891
13	ψ	intercept	mean NPP	0.578	0.190	0.002	1.783	1.540	2.026
	ψ	NPP	1 SD of NPP	-0.006	0.188	0.975	0.994	0.734	1.255
	γ	intercept	lactation	0.421	0.295	0.153	1.523	1.132	1.915
	γ	repro period	post-lactation	-0.734	0.413	0.076	0.480	-0.026	0.986
	γ	repro period	pre-pregnancy	-0.212	0.353	0.547	0.809	0.325	1.293
	γ	repro period	pregnancy	-0.065	0.386	0.866	0.937	0.402	1.471
	ε	intercept	lactation	-1.974	0.182	0.000	0.139	0.007	0.271
	ε	repro period	post-lactation	1.122	0.228	0.000	3.071	2.829	3.313

Model	Parameter	Covariate	Covariate state	Coefficient (logit scale)	SE	P(> z)	Odds ratio	Lower 95% CI	Upper 95% CI
	ε	repro period	pre-pregnancy	1.017	0.256	0.000	2.765	2.481	3.049
	ε	repro period	pregnancy	0.231	0.281	0.412	1.260	0.876	1.644
	ρ	intercept	lactation	0.637	0.052	0.000	1.891	1.826	1.956
	ρ	repro period	post-lactation	-0.228	0.067	0.001	0.796	0.705	0.887
	ρ	repro period	pre-pregnancy	-1.110	0.079	0.000	0.330	0.245	0.414
	ρ	repro period	pregnancy	-0.561	0.074	0.000	0.571	0.476	0.666
	ψ	intercept	mean elevation	0.764	0.279	0.006	2.147	1.809	2.485
	ψ	elevation	1 SD of elevation	0.237	0.198	0.231	1.267	0.997	1.538
	ψ	elevation^2	1 SD of elevation^2	-0.149	0.205	0.466	0.862	0.579	1.144
	γ	intercept	June, December	0.149	0.125	0.231	1.161	0.988	1.333
	γ	Julian	September	-0.194	0.175	0.267	0.824	0.583	1.064
	ε	intercept	June, December	-1.385	0.090	0.000	0.250	0.165	0.336
	ε	Julian	September	0.104	0.126	0.409	1.110	0.935	1.284
	ρ	intercept	June, December	0.138	0.026	0.000	1.148	1.112	1.184
	ρ	Julian	September	0.612	0.037	0.000	1.844	1.798	1.891
	ψ	intercept	mean elevation	0.759	0.281	0.007	2.136	1.795	2.477
	ψ	elevation	1 SD of elevation	0.244	0.197	0.216	1.276	1.007	1.545
	ψ	elevation^2	1 SD of elevation^2	-0.153	0.205	0.456	0.858	0.576	1.141
	γ	intercept	lactation	0.414	0.295	0.161	1.512	1.120	1.904
	γ	repro period	post-lactation	-0.697	0.412	0.091	0.498	-0.012	1.008
	γ	repro period	pre-pregnancy	-0.214	0.352	0.544	0.808	0.325	1.290
	γ	repro period	pregnancy	-0.075	0.386	0.845	0.927	0.393	1.462
	ε	intercept	lactation	-1.978	0.183	0.000	0.138	0.006	0.270
	ε	repro period	post-lactation	1.130	0.228	0.000	3.096	2.854	3.337
	ε	repro period	pre-pregnancy	1.012	0.257	0.000	2.751	2.466	3.037
	ε	repro period	pregnancy	0.223	0.282	0.428	1.250	0.864	1.636
	ρ	intercept	lactation	0.637	0.052	0.000	1.891	1.826	1.956
	ρ	repro period	post-lactation	-0.228	0.067	0.001	0.796	0.705	0.887
	ρ	repro period	pre-pregnancy	-1.110	0.079	0.000	0.330	0.245	0.414

Model	Parameter	Covariate	Covariate state	Coefficient (logit scale)	SE	P(> z)	Odds ratio	Lower 95% CI	Upper 95% CI
	ρ	repro period	pregnancy	-0.561	0.074	0.000	0.571	0.476	0.666
14	ψ	intercept	mean elevation	0.621	0.194	0.001	1.861	1.615	2.106
	ψ	elevation	1 SD of elevation	0.228	0.202	0.259	1.256	0.980	1.532
	γ	intercept	June, December	0.146	0.125	0.242	1.157	0.985	1.330
	γ	Julian	September	-0.200	0.175	0.253	0.819	0.579	1.059
	ε	intercept	June, December	-1.385	0.090	0.000	0.250	0.165	0.336
	ε	Julian	September	0.103	0.126	0.417	1.108	0.934	1.283
	ρ	intercept	June, December	0.138	0.026	0.000	1.148	1.112	1.184
	ρ	Julian	September	0.612	0.037	0.000	1.844	1.798	1.891
15	ψ	intercept	mean elevation	0.613	0.194	0.002	1.846	1.600	2.092
	ψ	elevation	1 SD of elevation	0.176	0.202	0.382	1.192	0.915	1.470
	γ	intercept	mean elev; June, December	0.212	0.133	0.111	1.236	1.054	1.418
	γ	Julian	September	-0.201	0.181	0.267	0.818	0.570	1.066
	γ	elevation	1 SD of elevation	0.400	0.115	0.001	1.492	1.339	1.645
	ε	intercept	mean elev; June, December	-1.349	0.090	0.000	0.260	0.173	0.346
	ε	Julian	September	0.095	0.126	0.451	1.099	0.925	1.273
	ε	elevation	1 SD of elevation	-0.140	0.081	0.083	0.870	0.759	0.981
	ρ	intercept	mean elev; June, December	0.134	0.027	0.000	1.143	1.106	1.179
	ρ	Julian	September	0.613	0.037	0.000	1.846	1.799	1.892
	ρ	elevation	1 SD of elevation	0.023	0.024	0.333	1.024	0.990	1.057
16	ψ	intercept	mean elevation	0.628	0.194	0.001	1.874	1.629	2.119
	ψ	elevation	1 SD of elevation	0.167	0.201	0.408	1.182	0.905	1.458
	γ	intercept	mean elev; June, December	0.224	0.136	0.099	1.251	1.065	1.437
	γ	Julian	September	-0.163	0.188	0.385	0.850	0.591	1.108
	γ	elevation	1 SD of elevation	0.427	0.122	0.000	1.533	1.371	1.694
	γ	elevation*Julian	1 SD of elev*September	0.154	0.167	0.359	1.166	0.936	1.397
	ε	intercept	mean elev; June, December	-1.346	0.090	0.000	0.260	0.174	0.347
	ε	Julian	September	0.090	0.126	0.472	1.095	0.921	1.268
	ε	elevation	1 SD of elevation	-0.161	0.083	0.052	0.851	0.737	0.965

Model	Parameter	Covariate	Covariate state	Coefficient (logit scale)	SE	P(> z)	Odds ratio	Lower 95% CI	Upper 95% CI
	ε	elevation*Julian	1 SD of elev*September	0.116	0.116	0.314	1.123	0.964	1.283
	ρ	intercept	mean elev; June, December	0.135	0.026	0.000	1.144	1.108	1.181
	ρ	Julian	September	0.608	0.037	0.000	1.836	1.789	1.884
	ρ	elevation	1 SD of elevation	0.021	0.024	0.400	1.021	0.987	1.054
	ρ	elevation*Julian	1 SD of elev*September	0.023	0.034	0.495	1.024	0.976	1.071
17	ψ	intercept	mean elevation	0.611	0.193	0.002	1.842	1.597	2.087
	ψ	elevation	1 SD of elevation	0.234	0.201	0.243	1.264	0.989	1.538
	γ	intercept	lactation	0.412	0.294	0.162	1.510	1.119	1.901
	γ	repro period	post-lactation	-0.707	0.412	0.086	0.493	-0.015	1.002
	γ	repro period	pre-pregnancy	-0.207	0.352	0.556	0.813	0.330	1.296
	γ	repro period	pregnancy	-0.079	0.386	0.838	0.924	0.390	1.458
	ε	intercept	lactation	-1.979	0.183	0.000	0.138	0.006	0.270
	ε	repro period	post-lactation	1.129	0.228	0.000	3.093	2.851	3.334
	ε	repro period	pre-pregnancy	1.017	0.256	0.000	2.765	2.481	3.049
	ε	repro period	pregnancy	0.222	0.282	0.432	1.249	0.862	1.635
	ρ	intercept	lactation	0.637	0.052	0.000	1.891	1.826	1.956
	ρ	repro period	post-lactation	-0.228	0.067	0.001	0.796	0.705	0.887
	ρ	repro period	pre-pregnancy	-1.109	0.079	0.000	0.330	0.245	0.414
	ρ	repro period	pregnancy	-0.561	0.074	0.000	0.571	0.476	0.666
18	ψ	intercept	mean elevation	0.604	0.194	0.002	1.829	1.583	2.076
	ψ	elevation	1 SD of elevation	0.185	0.200	0.356	1.203	0.928	1.478
	γ	intercept	mean elev; lactation	0.405	0.303	0.182	1.499	1.095	1.902
	γ	repro period	post-lactation	-0.631	0.425	0.138	0.532	-0.004	1.068
	γ	repro period	pre-pregnancy	-0.159	0.362	0.660	0.853	0.354	1.351
	γ	repro period	pregnancy	0.094	0.395	0.811	1.099	0.553	1.645
	γ	elevation	1 SD of elevation	0.400	0.117	0.001	1.492	1.336	1.648
	ε	intercept	mean elev; lactation	-1.937	0.182	0.000	0.144	0.010	0.278
	ε	repro period	post-lactation	1.118	0.228	0.000	3.059	2.816	3.302
	ε	repro period	pre-pregnancy	1.012	0.256	0.000	2.751	2.467	3.035

Model	Parameter	Covariate	Covariate state	Coefficient (logit scale)	SE	P(> z)	Odds ratio	Lower 95% CI	Upper 95% CI
	ε	repro period	pregnancy	0.194	0.282	0.491	1.214	0.827	1.601
	ε	elevation	1 SD of elevation	-0.150	0.080	0.062	0.861	0.750	0.971
	ρ	intercept	mean elev; lactation	0.634	0.052	0.000	1.885	1.819	1.951
	ρ	repro period	post-lactation	-0.228	0.067	0.001	0.796	0.705	0.887
	ρ	repro period	pre-pregnancy	-1.109	0.079	0.000	0.330	0.245	0.414
	ρ	repro period	pregnancy	-0.559	0.074	0.000	0.572	0.477	0.667
	ρ	elevation	1 SD of elevation	0.012	0.024	0.613	1.012	0.979	1.045
19	ψ	intercept	mean elevation	0.627	0.195	0.001	1.872	1.626	2.118
	ψ	elevation	1 SD of elevation	0.152	0.200	0.447	1.164	0.889	1.440
	γ	intercept	mean elev; lactation	0.448	0.316	0.156	1.566	1.149	1.983
	γ	repro period	post-lactation	-0.667	0.444	0.133	0.513	-0.041	1.068
	γ	repro period	pre-pregnancy	-0.229	0.372	0.538	0.795	0.286	1.304
	γ	repro period	pregnancy	0.056	0.413	0.892	1.058	0.486	1.630
	γ	elevation	1 SD of elevation	0.492	0.274	0.073	1.635	1.277	1.994
	γ	elevation*repro period	1 SD of elev*post-lactation	0.052	0.377	0.891	1.053	0.531	1.575
	γ	elevation*repro period	1 SD of elev*pre-pregnancy	-0.258	0.335	0.441	0.773	0.316	1.229
	γ	elevation*repro period	1 SD of elev*pregnancy	-0.097	0.356	0.786	0.908	0.416	1.400
	ε	intercept	mean elev; lactation	-1.917	0.183	0.000	0.147	0.011	0.283
	ε	repro period	post-lactation	1.053	0.232	0.000	2.866	2.613	3.120
	ε	repro period	pre-pregnancy	0.985	0.258	0.000	2.678	2.388	2.967
	ε	repro period	pregnancy	0.170	0.283	0.548	1.185	0.796	1.575
	ε	elevation	1 SD of elevation	-0.332	0.173	0.054	0.717	0.484	0.951
	ε	elevation*repro period	1 SD of elev*post-lactation	0.374	0.216	0.084	1.454	1.164	1.743
	ε	elevation*repro period	1 SD of elev*pre-pregnancy	0.189	0.241	0.435	1.208	0.877	1.539
	ε	elevation*repro	1 SD of elev*pregnancy	0.071	0.257	0.782	1.074	0.718	1.429

Model	Parameter	Covariate	Covariate state	Coefficient (logit scale)	SE	P(> z)	Odds ratio	Lower 95% CI	Upper 95% CI
		period							
	ρ	intercept	mean elev; lactation	0.635	0.053	0.000	1.886	1.819	1.953
	ρ	repro period	post-lactation	-0.227	0.068	0.001	0.797	0.703	0.891
	ρ	repro period	pre-pregnancy	-1.140	0.082	0.000	0.320	0.233	0.406
	ρ	repro period	pregnancy	-0.551	0.075	0.000	0.577	0.480	0.673
	ρ	elevation	1 SD of elevation	0.009	0.050	0.858	1.009	0.939	1.079
	ρ	elevation*repro period	1 SD of elev*post-lactation	-0.004	0.065	0.956	0.996	0.907	1.086
	ρ	elevation*repro period	1 SD of elev*pre-pregnancy	0.125	0.076	0.099	1.133	1.028	1.237
	ρ	elevation*repro period	1 SD of elev*pregnancy	-0.067	0.069	0.325	0.935	0.840	1.030
20	ψ	intercept	mean rain(ann)	0.600	0.192	0.002	1.822	1.578	2.066
	ψ	rain(ann)	1 SD of rain(ann)	-0.094	0.180	0.604	0.911	0.662	1.160
	γ	intercept	June, December	0.147	0.125	0.237	1.158	0.986	1.331
	γ	Julian	September	-0.215	0.175	0.219	0.807	0.567	1.046
	ε	intercept	June, December	-1.381	0.089	0.000	0.251	0.166	0.337
	ε	Julian	September	0.094	0.126	0.456	1.098	0.924	1.272
	ρ	intercept	June, December	0.138	0.026	0.000	1.148	1.112	1.184
	ρ	Julian	September	0.612	0.037	0.000	1.844	1.798	1.891
21	ψ	intercept	mean rain(ann)	0.555	0.187	0.003	1.742	1.502	1.983
	ψ	rain(ann)	1 SD of rain(ann)	-0.049	0.177	0.784	0.953	0.707	1.198
	γ	intercept	mean rain(mo)	0.449	0.195	0.021	1.567	1.310	1.824
	γ	rain(mo)	1 SD of rain(mo)	-0.143	0.089	0.110	0.867	0.743	0.990
	ε	intercept	mean rain(mo)	-1.528	0.127	0.000	0.217	0.104	0.330
	ε	rain(mo)	1 SD of rain(mo)	0.177	0.069	0.010	1.194	1.099	1.288
	ρ	intercept	mean rain(mo)	0.449	0.039	0.000	1.567	1.515	1.618
	ρ	rain(mo)	1 SD of rain(mo)	-0.167	0.022	0.000	0.846	0.816	0.877
22	ψ	intercept	mean rain(ann)	0.617	0.194	0.001	1.854	1.608	2.100

Model	Parameter	Covariate	Covariate state	Coefficient (logit scale)	SE	P(> z)	Odds ratio	Lower 95% CI	Upper 95% CI
	ψ	rain(ann)	1 SD of rain(ann)	-0.019	0.187	0.921	0.982	0.722	1.241
	γ	intercept	mean rain(mo); June, December	0.414	0.209	0.048	1.513	1.235	1.791
	γ	Julian	September	-0.238	0.179	0.183	0.788	0.544	1.033
	γ	rain(mo)	1 SD of rain(mo)	-0.166	0.097	0.085	0.847	0.714	0.980
	ε	intercept	mean rain(mo); June, December	-1.594	0.135	0.000	0.203	0.086	0.320
	ε	Julian	September	0.108	0.125	0.387	1.114	0.941	1.287
	ε	rain(mo)	1 SD of rain(mo)	0.164	0.073	0.024	1.178	1.078	1.278
	ρ	intercept	mean rain(mo); June, December	0.348	0.041	0.000	1.416	1.361	1.471
	ρ	Julian	September	0.602	0.037	0.000	1.826	1.779	1.873
	ρ	rain(mo)	1 SD of rain(mo)	-0.152	0.023	0.000	0.859	0.827	0.891
23	ψ	intercept	mean rain(ann)	0.631	0.196	0.001	1.879	1.631	2.126
	ψ	rain(ann)	1 SD of rain(ann)	0.000	0.191	0.999	1.000	0.735	1.265
	γ	intercept	mean rain(mo); June, December	0.559	0.230	0.015	1.749	1.453	2.045
	γ	Julian	September	0.144	0.317	0.649	1.155	0.718	1.592
	γ	rain(mo)	1 SD of rain(mo)	-0.252	0.111	0.024	0.777	0.626	0.929
	γ	rain(mo)*Julian	1 SD of rain(mo)*September	-0.210	0.146	0.153	0.811	0.610	1.011
	ε	intercept	mean rain(mo); June, December	-1.572	0.134	0.000	0.208	0.090	0.325
	ε	Julian	September	-0.030	0.205	0.885	0.971	0.687	1.254
	ε	rain(mo)	1 SD of rain(mo)	0.150	0.074	0.042	1.162	1.060	1.264
	ε	rain(mo)*Julian	1 SD of rain(mo)*September	0.093	0.107	0.385	1.097	0.949	1.245
	ρ	intercept	mean rain(mo); June, December	0.362	0.041	0.000	1.436	1.381	1.491
	ρ	Julian	September	0.490	0.058	0.000	1.632	1.556	1.708
	ρ	rain(mo)	1 SD of rain(mo)	-0.161	0.023	0.000	0.851	0.819	0.884
	ρ	rain(mo)*Julian	1 SD of rain(mo)*September	0.079	0.032	0.014	1.082	1.038	1.127

Model	Parameter	Covariate	Covariate state	Coefficient (logit scale)	SE	P(> z)	Odds ratio	Lower 95% CI	Upper 95% CI
24	ψ	intercept	mean rain(ann)	0.586	0.191	0.002	1.796	1.552	2.040
	ψ	rain(ann)	1 SD of rain(ann)	-0.075	0.180	0.676	0.928	0.679	1.177
	γ	intercept	lactation	0.422	0.295	0.153	1.525	1.134	1.917
	γ	repro period	post-lactation	-0.735	0.413	0.075	0.480	-0.026	0.985
	γ	repro period	pre-pregnancy	-0.213	0.353	0.547	0.808	0.325	1.292
	γ	repro period	pregnancy	-0.073	0.387	0.850	0.930	0.394	1.465
	ε	intercept	lactation	-1.972	0.182	0.000	0.139	0.007	0.271
	ε	repro period	post-lactation	1.120	0.228	0.000	3.065	2.822	3.308
	ε	repro period	pre-pregnancy	1.015	0.256	0.000	2.759	2.475	3.043
	ε	repro period	pregnancy	0.224	0.282	0.427	1.251	0.865	1.637
	ρ	intercept	lactation	0.637	0.052	0.000	1.891	1.826	1.956
	ρ	repro period	post-lactation	-0.228	0.067	0.001	0.796	0.705	0.887
	ρ	repro period	pre-pregnancy	-1.109	0.079	0.000	0.330	0.245	0.414
ρ	repro period	pregnancy	-0.561	0.074	0.000	0.571	0.476	0.666	
25	ψ	intercept	mean rain(ann)	0.604	0.193	0.002	1.829	1.584	2.075
	ψ	rain(ann)	1 SD of rain(ann)	-0.017	0.187	0.927	0.983	0.724	1.242
	γ	intercept	mean rain(mo); lactation	0.532	0.340	0.118	1.702	1.261	2.142
	γ	repro period	post-lactation	-0.646	0.425	0.128	0.524	-0.010	1.058
	γ	repro period	pre-pregnancy	-0.101	0.371	0.786	0.904	0.391	1.417
	γ	repro period	pregnancy	-0.013	0.399	0.974	0.987	0.434	1.540
	γ	rain(mo)	1 SD of rain(mo)	-0.104	0.099	0.293	0.901	0.764	1.038
	ε	intercept	mean rain(mo); lactation	-2.041	0.201	0.000	0.130	-0.011	0.271
	ε	repro period	post-lactation	1.064	0.229	0.000	2.897	2.648	3.147
	ε	repro period	pre-pregnancy	0.893	0.264	0.001	2.442	2.136	2.749
	ε	repro period	pregnancy	0.179	0.283	0.528	1.195	0.807	1.584
	ε	rain(mo)	1 SD of rain(mo)	0.091	0.076	0.231	1.095	0.990	1.201
	ρ	intercept	mean rain(mo); lactation	0.835	0.061	0.000	2.305	2.233	2.377
	ρ	repro period	post-lactation	-0.228	0.067	0.001	0.796	0.704	0.888
	ρ	repro period	pre-pregnancy	-1.070	0.080	0.000	0.343	0.257	0.429

Model	Parameter	Covariate	Covariate state	Coefficient (logit scale)	SE	P(> z)	Odds ratio	Lower 95% CI	Upper 95% CI
	ρ	repro period	pregnancy	-0.589	0.074	0.000	0.555	0.460	0.650
	ρ	rain(mo)	1 SD of rain(mo)	-0.145	0.023	0.000	0.865	0.833	0.897
26	ψ	intercept	mean rain(ann)	0.630	0.198	0.001	1.878	1.628	2.128
	ψ	rain(ann)	1 SD of rain(ann)	0.023	0.196	0.909	1.023	0.751	1.294
	γ	intercept	mean rain(mo); lactation	0.777	0.554	0.161	2.175	1.506	2.844
	γ	repro period	post-lactation	-0.729	0.764	0.340	0.482	-0.454	1.419
	γ	repro period	pre-pregnancy	-0.635	0.664	0.339	0.530	-0.307	1.367
	γ	repro period	pregnancy	-0.076	0.686	0.912	0.927	-0.023	1.876
	γ	rain(mo)	1 SD of rain(mo)	-0.283	0.265	0.285	0.753	0.393	1.113
	γ	rain(mo)*repro period	1 SD of rain(mo)*post- lactation	0.094	0.355	0.792	1.098	0.607	1.589
	γ	rain(mo)*repro period	1 SD of rain(mo)*pre- pregnancy	0.322	0.311	0.301	1.379	0.959	1.800
	γ	rain(mo)*repro period	1 SD of rain(mo)*pregnancy	0.067	0.341	0.845	1.069	0.597	1.541
	ε	intercept	mean rain(mo); lactation	-2.017	0.258	0.000	0.133	-0.050	0.316
	ε	repro period	post-lactation	0.984	0.342	0.004	2.675	2.291	3.059
	ε	repro period	pre-pregnancy	1.105	0.400	0.006	3.019	2.590	3.447
	ε	repro period	pregnancy	0.069	0.441	0.875	1.072	0.461	1.682
	ε	rain(mo)	1 SD of rain(mo)	0.107	0.144	0.456	1.113	0.914	1.312
	ε	rain(mo)*repro period	1 SD of rain(mo)*post- lactation	0.020	0.195	0.918	1.020	0.750	1.290
	ε	rain(mo)*repro period	1 SD of rain(mo)*pre- pregnancy	-0.164	0.206	0.426	0.848	0.565	1.132
	ε	rain(mo)*repro period	1 SD of rain(mo)*pregnancy	0.045	0.267	0.867	1.046	0.676	1.416
	ρ	intercept	mean rain(mo); lactation	0.815	0.080	0.000	2.259	2.164	2.354
	ρ	repro period	post-lactation	-0.295	0.105	0.005	0.745	0.603	0.887
	ρ	repro period	pre-pregnancy	-0.848	0.128	0.000	0.428	0.278	0.579
	ρ	repro period	pregnancy	-0.570	0.114	0.000	0.566	0.420	0.712

Model	Parameter	Covariate	Covariate state	Coefficient (logit scale)	SE	P(> z)	Odds ratio	Lower 95% CI	Upper 95% CI
	ρ	rain(mo)	1 SD of rain(mo)	-0.131	0.044	0.003	0.877	0.816	0.938
	ρ	rain(mo)*repro period	1 SD of rain(mo)*post- lactation	0.049	0.059	0.408	1.050	0.968	1.131
	ρ	rain(mo)*repro period	1 SD of rain(mo)*pre- pregnancy	-0.142	0.068	0.037	0.868	0.775	0.961
	ρ	rain(mo)*repro period	1 SD of rain(mo)*pregnancy	-0.016	0.069	0.819	0.984	0.889	1.080
27	ψ	intercept	mean temp(ann)	0.562	0.189	0.003	1.754	1.511	1.997
	ψ	temp(ann)	1 SD of temp(ann)	-0.165	0.195	0.398	0.848	0.579	1.116
	γ	intercept	mean temp(mo)	1.536	0.505	0.002	4.646	4.197	5.095
	γ	temp(mo)	1 SD of temp(mo)	-0.718	0.251	0.004	0.488	0.179	0.797
	ε	intercept	mean temp(mo)	-1.489	0.220	0.000	0.226	0.026	0.425
	ε	temp(mo)	1 SD of temp(mo)	0.136	0.117	0.248	1.146	0.984	1.307
	ρ	intercept	mean temp(mo)	-0.437	0.095	0.000	0.646	0.520	0.772
	ρ	temp(mo)	1 SD of temp(mo)	0.360	0.051	0.000	1.433	1.365	1.501
28	ψ	intercept	mean temp(ann)	0.612	0.193	0.002	1.844	1.599	2.089
	ψ	temp(ann)	1 SD of temp(ann)	-0.189	0.198	0.342	0.828	0.556	1.100
	γ	intercept	June, December	0.146	0.125	0.243	1.157	0.985	1.330
	γ	Julian	September	-0.212	0.175	0.225	0.809	0.569	1.049
	ε	intercept	June, December	-1.382	0.089	0.000	0.251	0.166	0.336
	ε	Julian	September	0.096	0.126	0.445	1.101	0.927	1.275
	ρ	intercept	June, December	0.138	0.026	0.000	1.148	1.112	1.184
	ρ	Julian	September	0.612	0.037	0.000	1.844	1.798	1.891
29	ψ	intercept	mean temp(ann)	0.608	0.195	0.002	1.837	1.589	2.084
	ψ	temp(ann)	1 SD of temp(ann)	-0.173	0.200	0.389	0.841	0.566	1.116
	γ	intercept	mean temp(mo); June, December	1.467	0.563	0.009	4.336	3.820	4.853
	γ	Julian	September	-0.137	0.178	0.442	0.872	0.626	1.118
	γ	temp(mo)	1 SD of temp(mo)	-0.701	0.273	0.010	0.496	0.158	0.834
	ε	intercept	mean temp(mo); June,	-1.570	0.238	0.000	0.208	0.000	0.416

Model	Parameter	Covariate	Covariate state	Coefficient (logit scale)	SE	P(> z)	Odds ratio	Lower 95% CI	Upper 95% CI
			December						
	ε	Julian	September	0.001	0.127	0.993	1.001	0.825	1.177
	ε	temp(mo)	1 SD of temp(mo)	0.149	0.128	0.244	1.161	0.985	1.337
	ρ	intercept	mean temp(mo); June, December	-0.125	0.100	0.213	0.882	0.744	1.021
	ρ	Julian	September	0.584	0.038	0.000	1.793	1.745	1.842
	ρ	temp(mo)	1 SD of temp(mo)	0.147	0.054	0.007	1.158	1.084	1.233
30	ψ	intercept	mean temp(ann)	0.605	0.194	0.002	1.831	1.585	2.078
	ψ	temp(ann)	1 SD of temp(ann)	-0.172	0.200	0.389	0.842	0.567	1.117
	γ	intercept	mean temp(mo); June, December	1.871	0.565	0.001	6.495	6.065	6.924
	γ	Julian	September	0.739	0.731	0.312	2.094	1.200	2.987
	γ	temp(mo)	1 SD of temp(mo)	-0.884	0.272	0.001	0.413	0.096	0.730
	γ	temp(mo)*Julian	1 SD of temp(mo)*September	-0.428	0.349	0.220	0.652	0.189	1.114
	ε	intercept	mean temp(mo); June, December	-1.746	0.237	0.000	0.174	-0.017	0.366
	ε	Julian	September	-1.397	0.456	0.002	0.247	-0.184	0.679
	ε	temp(mo)	1 SD of temp(mo)	0.184	0.125	0.142	1.202	1.030	1.374
	ε	temp(mo)*Julian	1 SD of temp(mo)*September	0.762	0.237	0.001	2.143	1.855	2.430
	ρ	intercept	mean temp(mo); June, December	-0.125	0.100	0.215	0.883	0.744	1.021
	ρ	Julian	September	0.561	0.140	0.000	1.752	1.571	1.932
	ρ	temp(mo)	1 SD of temp(mo)	0.146	0.054	0.007	1.157	1.082	1.232
	ρ	temp(mo)*Julian	1 SD of temp(mo)*September	0.013	0.075	0.866	1.013	0.908	1.117
31	ψ	intercept	mean temp(ann)	0.604	0.193	0.002	1.829	1.584	2.075
	ψ	temp(ann)	1 SD of temp(ann)	-0.199	0.199	0.317	0.820	0.546	1.093
	γ	intercept	lactation	0.419	0.294	0.154	1.521	1.130	1.911

Model	Parameter	Covariate	Covariate state	Coefficient (logit scale)	SE	P(> z)	Odds ratio	Lower 95% CI	Upper 95% CI
	γ	repro period	post-lactation	-0.734	0.412	0.075	0.480	-0.024	0.984
	γ	repro period	pre-pregnancy	-0.214	0.352	0.544	0.808	0.325	1.290
	γ	repro period	pregnancy	-0.074	0.386	0.848	0.929	0.395	1.463
	ε	intercept	lactation	-1.977	0.182	0.000	0.138	0.007	0.270
	ε	repro period	post-lactation	1.124	0.228	0.000	3.077	2.835	3.319
	ε	repro period	pre-pregnancy	1.016	0.256	0.000	2.762	2.478	3.046
	ε	repro period	pregnancy	0.231	0.281	0.411	1.260	0.876	1.644
	ρ	intercept	lactation	0.637	0.052	0.000	1.891	1.826	1.956
	ρ	repro period	post-lactation	-0.228	0.067	0.001	0.796	0.705	0.887
	ρ	repro period	pre-pregnancy	-1.110	0.079	0.000	0.330	0.245	0.414
	ρ	repro period	pregnancy	-0.561	0.074	0.000	0.571	0.476	0.666
32	ψ	intercept	mean temp(ann)	0.608	0.196	0.002	1.837	1.588	2.086
	ψ	temp(ann)	1 SD of temp(ann)	-0.180	0.201	0.370	0.835	0.559	1.112
	γ	intercept	mean temp(mo); lactation	1.803	0.768	0.019	6.068	5.465	6.671
	γ	repro period	post-lactation	-0.733	0.448	0.102	0.480	-0.068	1.029
	γ	repro period	pre-pregnancy	-0.300	0.402	0.455	0.741	0.196	1.286
	γ	repro period	pregnancy	-0.128	0.429	0.765	0.880	0.288	1.472
	γ	temp(mo)	1 SD of temp(mo)	-0.698	0.303	0.021	0.498	0.123	0.873
	ε	intercept	mean temp(mo); lactation	-1.898	0.271	0.000	0.150	-0.054	0.353
	ε	repro period	post-lactation	0.961	0.227	0.000	2.613	2.356	2.870
	ε	repro period	pre-pregnancy	0.885	0.248	0.000	2.423	2.135	2.712
	ε	repro period	pregnancy	0.072	0.280	0.798	1.074	0.687	1.462
	ε	temp(mo)	1 SD of temp(mo)	0.050	0.133	0.709	1.051	0.867	1.235
	ρ	intercept	mean temp(mo); lactation	0.326	0.116	0.005	1.385	1.228	1.543
	ρ	repro period	post-lactation	-0.218	0.067	0.001	0.804	0.712	0.896
	ρ	repro period	pre-pregnancy	-1.044	0.082	0.000	0.352	0.262	0.442
	ρ	repro period	pregnancy	-0.555	0.074	0.000	0.574	0.479	0.669
	ρ	temp(mo)	1 SD of temp(mo)	0.161	0.054	0.003	1.175	1.100	1.249
33	ψ	intercept	mean temp(ann)	0.638	0.196	0.001	1.893	1.646	2.140

Model	Parameter	Covariate	Covariate state	Coefficient (logit scale)	SE	P(> z)	Odds ratio	Lower 95% CI	Upper 95% CI
	ψ	temp(ann)	1 SD of temp(ann)	-0.113	0.202	0.576	0.893	0.614	1.172
	γ	intercept	mean temp(mo); lactation	2.986	1.715	0.082	19.800	19.046	20.555
	γ	repro period	post-lactation	-1.033	2.104	0.623	0.356	-1.962	2.674
	γ	repro period	pre-pregnancy	-1.986	1.888	0.293	0.137	-1.221	1.495
	γ	repro period	pregnancy	-1.084	2.008	0.589	0.338	-1.830	2.507
	γ	temp(mo)	1 SD of temp(mo)	-1.192	0.775	0.124	0.303	-0.497	1.104
	γ	temp(mo)*repro period	1 SD of temp(mo)*post- lactation	0.060	0.968	0.950	1.062	-0.278	2.403
	γ	temp(mo)*repro period	1 SD of temp(mo)*pre- pregnancy	0.755	0.881	0.392	2.128	1.056	3.199
	γ	temp(mo)*repro period	1 SD of temp(mo)*pregnancy	0.381	0.927	0.681	1.463	0.223	2.703
	ε	intercept	mean temp(mo); lactation	-1.511	0.272	0.000	0.221	-0.024	0.465
	ε	repro period	post-lactation	-0.384	0.629	0.541	0.681	-0.160	1.522
	ε	repro period	pre-pregnancy	0.169	0.718	0.814	1.184	0.196	2.173
	ε	repro period	pregnancy	-0.083	0.883	0.925	0.920	-0.301	2.142
	ε	temp(mo)	1 SD of temp(mo)	-0.234	0.161	0.146	0.791	0.571	1.012
	ε	temp(mo)*repro period	1 SD of temp(mo)*post- lactation	0.763	0.332	0.021	2.145	1.743	2.548
	ε	temp(mo)*repro period	1 SD of temp(mo)*pre- pregnancy	0.451	0.452	0.318	1.570	0.974	2.166
	ε	temp(mo)*repro period	1 SD of temp(mo)*pregnancy	0.157	0.474	0.740	1.170	0.517	1.823
	ρ	intercept	mean temp(mo); lactation	-0.724	0.245	0.003	0.485	0.184	0.785
	ρ	repro period	post-lactation	1.005	0.297	0.001	2.731	2.401	3.062
	ρ	repro period	pre-pregnancy	1.124	0.321	0.000	3.077	2.736	3.418
	ρ	repro period	pregnancy	-0.055	0.329	0.867	0.946	0.491	1.402
	ρ	temp(mo)	1 SD of temp(mo)	0.710	0.126	0.000	2.034	1.879	2.190
	ρ	temp(mo)*repro period	1 SD of temp(mo)*post- lactation	-0.642	0.153	0.000	0.526	0.334	0.719

Model	Parameter	Covariate	Covariate state	Coefficient (logit scale)	SE	P(> z)	Odds ratio	Lower 95% CI	Upper 95% CI
	ρ	temp(mo)*repro period	1 SD of temp(mo)*pre- pregnancy	-1.298	0.185	0.000	0.273	0.090	0.456
	ρ	temp(mo)*repro period	1 SD of temp(mo)*pregnancy	-0.257	0.169	0.130	0.774	0.543	1.004
34	ψ	intercept	mean wind	0.595	0.191	0.002	1.813	1.570	2.056
	ψ	wind	1 SD of wind	0.126	0.199	0.525	1.134	0.860	1.409
	γ	intercept	June, December	0.149	0.125	0.234	1.161	0.988	1.333
	γ	Julian	September	-0.209	0.175	0.230	0.811	0.571	1.051
	ε	intercept	June, December	-1.381	0.089	0.000	0.251	0.166	0.336
	ε	Julian	September	0.096	0.126	0.444	1.101	0.927	1.275
	ρ	intercept	June, December	0.138	0.026	0.000	1.148	1.112	1.184
	ρ	Julian	September	0.612	0.037	0.000	1.844	1.798	1.891
35	ψ	intercept	mean wind	0.585	0.191	0.002	1.795	1.551	2.039
	ψ	wind	1 SD of wind	0.127	0.199	0.524	1.135	0.861	1.410
	γ	intercept	lactation	0.419	0.295	0.155	1.521	1.129	1.913
	γ	repro period	post-lactation	-0.725	0.413	0.079	0.484	-0.023	0.991
	γ	repro period	pre-pregnancy	-0.215	0.353	0.543	0.807	0.323	1.291
	γ	repro period	pregnancy	-0.068	0.386	0.860	0.934	0.400	1.469
	ε	intercept	lactation	-1.975	0.182	0.000	0.139	0.007	0.270
	ε	repro period	post-lactation	1.123	0.228	0.000	3.074	2.832	3.316
	ε	repro period	pre-pregnancy	1.014	0.256	0.000	2.757	2.473	3.041
	ε	repro period	pregnancy	0.228	0.281	0.419	1.256	0.872	1.641
	ρ	intercept	lactation	0.637	0.052	0.000	1.891	1.826	1.956
	ρ	repro period	post-lactation	-0.228	0.067	0.001	0.796	0.705	0.887
	ρ	repro period	pre-pregnancy	-1.110	0.079	0.000	0.330	0.245	0.414
	ρ	repro period	pregnancy	-0.561	0.074	0.000	0.571	0.476	0.666