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Roosting behavior and roost selection by Epomophorus gambianus (Pteropodidae) in a West African rural landscape

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Dr. Jenifer Powers

The Editor-in-chief

BIOTROPICA

Dear Editor,

Submission of Revision: Manuscript ID BITR-21-303 entitled "Roosting behavior and roost selection by *Epomophorus gambianus* (Pteropodidae) in a West African rural landscape"

We wish to express our appreciation for the consideration of our manuscript, and giving us

the opportunity once again to resubmit a revised version of this manuscript. We appreciate the time and effort that you, the subject editor and the reviewers dedicated to providing feedback helpful comments on our manuscript and are grateful for the valuable comments on and improvements to the manuscript.

In this revised version, we have addressed all reviewers' comments, and issued raised by the reviewers. Please see below, for a point-by-point response to the Reviewers' comments. Responses to reviewer comments are in *italics.* All line numbers refer to the revised manuscript file.

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We trust that the revisions in the manuscript and our accompanying responses are adequate and hope that the revised manuscript is accepted for publication in BIOTROPICA.

We appreciate your time and look forward to your response.

Yours faithfully,

Kofi Amponsah-Mensah and co-authors.

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Subject Editor

Thank-you for your thorough revision of the manuscript. Both reviewers are happy with the new version and the comments made by them are very minor. One of the issues raised by Reviewer 2 involved clarity of the terms related to roosting trees, and so I thought you should have the chance to check this comment and consider changing the terms to ensure there is no confusion for the readers.

Thank you very much for your comment and for the chance to respond to issues raised once again.

I also found an error on L72: I assume pubs should be pups.

Thank you for picking up this error. "Pubs", corrected to "pups" (Line 72).

Reviewer 1

Dear authors,

Thank you for the polite and detailed response to my comments. I am very happy to see this come out and look forward to spreading it among interested readers.

Well done.

Thank you for your kind words and also for your initial comments in the first review which we agree have helped improve the manuscript.

Reviewer 2

The changes made to this revision of the manuscript have addressed my concerns from the first review. I have only a couple of very minor wording suggestions for clarity. See attached. Congratulations on this important contribution to the fruit bat research literature.

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Thank you for your kind words and also for your initial comments in the first review which we agree have helped improve the manuscript. We appreciate the suggestions and comments provided in this revision and believe these will help improve the manuscript.

Edits:

Line 124 Capitalize “Old World”

“old world” capitalised to “Old World” as suggested. (Line 124)

Lines 246-256 Apologies for complicating the idea of avoidance in my previous reviewer comments. I recognize that Preferred vs. Avoided are the common terms in this type of analysis, and I hope my concerns about “avoided” trees actually being used did not confuse the revision of this part of the study. I think the use of “less preferred” might work, although preferred still suggests some selectivity for these trees, when in fact, these trees are less chosen than even the “random” trees. I do not have an alternate term to suggest, but I do think it should be made clear that trees are used relative to their availability in this order: preferred, random, or “less preferred”. Hope that makes sense. Other terms that might work for “less preferred” are: 1) infrequently selected, 2) selected against if the authors would like to consider a different term that excludes the word “preferred”

Thank you again for the concerns raised particularly on clarifying the terms “less preferred”. To further reduce any confusion that may arise to the readers, we have adopted the suggested term “infrequently selected” to replace the term “less preferred”. (Line 246-257). We have also modified line 247-248 to show that use of tree speies relative to their availability was in the order: preferred, random, or infrequently selected.

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Subsequently all use of the term "less preferred" pertaining to selection by E. gambianus has been replaced by "infrequently selected" in the manuscript. (Lines 427, 501, table 2)

Line 289 remove "only" (40 of 60 bats being redetected is actually pretty high)

Agreed. "only" deleted (Line 290)

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TITLE PAGE

LRH and RRH: AMPONSAH-MENSAH et al.

Roosting behavior and roost selection by *Epomophorus gambianus* (Pteropodidae) in a West African rural landscape

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ABSTRACT PAGE

Urbanization is driving many species to inhabit modified landscapes, but our understanding of how species respond to this remains limited. Bats are particularly vulnerable due to their life-history traits but have received little attention. We describe the roosting behavior and roost site selection, including maternity roosts, for the Gambian epauletted fruit bat (*Epomophorus gambianus*) within a modified forest-savannah transition ecological zone in Ghana, West Africa. We compared characteristics of roost and non-roost sites to test the hypotheses that roost site selection is non-random and that maternity roost site selection differs from non-maternity roosts. Male bats were more likely to switch roost (mean= 0.49 ± 0.23 bat days, *N*=23) than females (mean= 0.33 ± 0.18 bat days, *N*=7) while linear distances between roosts used by males (255 ± 254 m) were significantly longer than for females (102 ± 71m) ($t = 4.50$, $df = 86$, $P < 0.0001$). Roost trees were more likely than non-roost trees to be bigger, taller, occur closer to buildings, and be in relatively open and less mature plots; maintaining such trees in modified landscapes could benefit the species. Lactating bats selected a subset of roost trees but significantly, those that contained a greater number of bats, a strategy which may reflect predator avoidance, or other social co-operation benefits. Although there was a preference for five tree species, other trees with preferred characteristics were also used. Our findings contribute to the understanding of how species utilize modified landscapes, which is important in the management of biodiversity in the Anthropocene.

KEYWORDS

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Fruit bats, Ghana, modified landscape, radiotracking, roosting ecology, tree roosts, tropical transition forest

1. INTRODUCTION

The majority of all terrestrial ecosystems have been modified by humans and this has resulted in an increasing number of species being driven to inhabit human modified landscapes (Galán-Acedo et al., 2019). Bats are particularly susceptible to anthropogenic changes because of their low reproductive rate, longevity, and high metabolic rates (Voigt & Kingston, 2016). Our understanding of how wildlife, including bats, respond to urbanization remains limited (Barclay et al., 2003). Unfortunately, the lack of information about the ecology of many bat species compounds this, making it difficult to assess potential threats or the implementation of suitable mitigation measures. The paucity of information on bat ecology is often attributed to the difficulty in conducting ecological studies on bats because of their nocturnal behavior (Limpert et al., 2007). Although advancements in telemetry have helped to gain insight into habitat use and movements by bats (Kalcounis-Rüppell et al., 2005; Mildenstein et al., 2005), many species disperse over very long distances making it difficult to track them. Flight also imposes constraints on the weight of tracking devices that bats can carry; although recent and future improvements in tag miniaturization should increase our ability to study their ecology.

Tree roosting bats are particularly vulnerable to habitat modification which presents a two-sided problem; the loss of roosting sites and the loss of suitable foraging habitat (Hayes & Loeb, 2007). Because roosts play vital roles in fitness and reproductive success (Kunz & Lumsden, 2003; Vonhof & Barclay, 1996), factors that affect roosts can have significant effects on the overall survival of bats. By selecting an optimum roosting site, bats achieve better protection from adverse weather conditions and predators, enhanced chances of

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successful mating and maternal care, increased social interactions and reduced energetic costs in commuting to foraging sites (Kunz, 1982; Kunz & Lumsden, 2003; Neuweiler, 2000; Tan et al., 1999). These benefits can be compromised if land use-changes and or other habitat modifications cause bats to select suboptimal roost sites.

Within the general study of habitat selection, roost site selection is particularly important to understand because roosting sites are susceptible to large scale disturbance and mortality events (O'Shea et al., 2016) where mothers and pups may be particularly vulnerable. Understanding roost selection in bats is vital to the successful management and conservation of bats, especially in modified landscapes. Available information on roost selection by bats shows a strong research bias towards cavity-roosting temperate-zone species (e.g. see Kalcounis-Rüppell et al., 2005; Lacki & Baker, 2003) for which roost selection pressures may differ from tropical tree-roosting species. For instance, temperature as a selection pressure may be more pronounced for cavity-roosting temperate-zone bat species (Willis & Brigham, 2005) but may not be as vital to tropical species where temperatures are relatively warmer and more stable throughout the year. For tropical species, roosting behavior may be more generally influenced by predators (Lima & O'Keefe, 2013).

Roost selection often depends on the characteristics of the structure being utilized, such as availability, physical structure and reliability (Kunz & Lumsden, 2003). Because factors that determine how resources are used by animals may vary depending on scale (Manly et al., 1993), roost selection is best studied at multiple spatial scales. Studies investigating selection, typically, have examined characteristics for selection at the tree-level, plot/stand level and landscape-level (e.g. Limpert et al., 2007; Lucas et al., 2015). Roost selection in bats is usually non-random, and bats require specific characteristics to suit their needs. Among tree roosting species for instance, taller trees with larger trunks are usually selected as roosts e.g., Indian flying fox *Pteropus giganteus* (Hahn et al., 2014), large flying-

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fox *P. vampyrus natunae* (Gumal, 2004), Rafinesque's big-eared bat *Corynorhinus rafinesquii* (Lucas et al., 2015) and several *Myotis* species (Kalcounis-Rüppell et al., 2005). Larger trees provide room to accommodate more bats in a single tree, which is a trait likely to be favored by gregarious species (Gumal, 2004). Larger and taller trees might also provide height for easier take-off into flight (Pierson & Rainey, 1992) and can reduce the chances of disturbance or predation, especially by ground-dwelling predators (Kunz, 1982; Lumsden & Bennett, 2006).

Similarly, in tree cavity roosting bats, taller and larger trees are often selected because they tend to be old enough to have developed suitable cavities for roosting (Sedgeley & O'Donnell, 1999, 2004), and they provide better insulation (Sedgeley, 2001). These features (larger size, greater height and bigger crowns) are characteristics of older trees which have relatively stronger branches that are less likely to break under the weight of a large number of bats compared to younger trees. Alternatively, the preference for older trees as roosts could arise from consistent usage over time of trees that have provided good conditions for roosting. Such roosts, therefore, could be selected because of historical philopatry and may be important in the maintenance and persistence of the colony. Specific tree species might be preferred (Vonhof & Barclay, 1996) because their morphology and other characteristics meet requirements for roosting space and for suitable protection through concealment.

Aside from the physical characteristics of roost trees, factors such as reproductive status, predator avoidance, and physiological demands can also influence roost selection and roosting behavior in bats (Kerth, 2008; Kunz & Lumsden, 2003). Conditions and requirements for maternity roosts, for example, often differ from those of regular roosts (Kunz & Lumsden, 2003) and may be more inclined towards minimizing energetic expenditures and maximizing the survival and growth of pups (Sedgeley, 2001), thereby influencing the choice of roost sites. Predator avoidance or disturbance, microclimate

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requirements, or changes in distance to feeding sites can cause bats to elicit roosting behaviors such as roost switching (Kunz & Lumsden, 2003; Lewis, 1995; Russo et al., 2005). This is usually common in foliage roosting bats which exhibit roosting fidelity to roosting range with several trees, rather than to a single tree (Kunz, 1982; Vonhof & Barclay, 1996).

The Gambian epauletted fruit bat (*Epomophorus gambianus*) is widespread and very common in West Africa. This species occurs in, and utilizes, a wide variety of natural habitats such as savannah woodlands and forest-savannah mosaics but also is commonly recorded in anthropogenically modified landscapes. Like most Old World fruit bats (Pteropodidae), this species plays important roles in the ecosystems in which it occurs, contributing to vital ecosystem services, such as pollination and seed dispersal (Amponsah-Mensah et al., 2019; Kunz et al., 2011). The species roosts singly or in loose colonies in foliage by hanging freely from branches in trees (Boulay & Robbins, 1989; Happold, 2013). As for other species, such as the straw-coloured fruit bat (*Eidolon helvum*), Pohle's fruit bat *Scotonycteris Ophiodon,* and the Hammer -headed fruit bat *(Hypsignathus monstrosus*), the loss of suitable habitats for both feeding and roosting has been identified as a threat to this species, resulting in range-wide declines (IUCN, 2021; Mickleburgh et al., 2002).

In this study, we describe roosting behavior and the roost site selection for both maternity and non-maternity roosts used by *E. gambianus* within a modified rural landscape in the forest-savannah transition ecological zone of Ghana, West Africa. We test the hypothesis that roost site selection by *E. gambianus* is non- random and predict that, similar to observations in other pteropod species, this species selects specific characteristics (such as bigger and taller trees) that differentiate roost sites from non-roost sites. We also test the hypothesis that maternity roost site selection differs from that for non-maternity roosts. Since the species is not known to form single-sex maternity colonies, we predict that nursing bats utilize a subset of available roosting sites, especially those that offer increased protection for

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pups. To test these predictions, we compare tree level, plot and landscape level characteristics of roost trees *vs* non-roost trees and also for maternity *vs* non-maternity roosts. By radiotracking bats, we also provide descriptions of roosting behavior of this species and predict that patterns of roost use by nursing female bats differs from those of males due to the energetic constraints associated with reproduction in females.

2. METHODS

2.1 Study site

Data for this study were collected in Ve-Golokuati, a town located in the Volta region of Ghana (6° 59' 55''N, 0° 26'18''E). This rural town occurs within the wet semi-equatorial climatic zone with rainfall occurring in a double maxima pattern (annual range 1,016–1,210 mm). The vegetation is heterogeneous with areas of regenerating secondary forest, farm bush and remnant pockets of the original forest which is a transition between semi-deciduous forest and Guinea savannah woodland forest. Changes to the original forest are mainly due to agricultural use, timber exploitation, and the expansion of human settlements within the area. A population of about 5,000 *E. gambianus* that roosts within several trees in the town (hereafter referred to as a colony) was the focus of this study. The extent of this colony (82.6 ha) was used to define the limits of the study area for the data collection.

2.2 Locating roost trees

For this study, we classify a roost as a tree within which bats were roosting. Trees within the study area were searched for the presence of roosting *E. gambianus* bats. Roosting bats were also located using radio-telemetry. Bat trapping for radio tagging was done using ground mist nets (3-5 m high above ground level, 6-18 m long) between 1800 h and 0600 h during trapping nights. All bat trapping and handling techniques followed the guidelines of the

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American Society of Mammalogists (Sikes et al., 2011). Radio tags weighed between 5.0 g and 6.3 g (mean 5.7 ± 0.3 g) and bats that were fitted with radio-tags weighed between 82 g to 150 g (mean 113 ± 16 g; Table S1). Tags were well within 5-10% of bat body mass (O'Mara et al., 2014; Sikes et al., 2011).

A total of 60 SOM-2190 radio-transmitters (Wildlife Materials International, Inc, Murphysboro, Illinois) were fitted to adult and subadult *E. gambianus* using permanent collars. Twenty bats were tagged in October 2015 and 40 bats were tagged in February 2016 (18 females; 42 males). Tagged bats were subsequently homed-in on foot during the day to their roosts using a TRX- 1000S, receiver and a 3-element directional Yagi antenna (Wildlife Materials International, Inc). For each bat, once the transmitter's signal was homed-in on its location, efforts were made to visually confirm its location in a tree. This was done to ensure that signals received from tags were coming from tags that were still attached to bats and not tags that had fallen under roosts. For each identified roost tree, the GPS location was recorded. Transmitters had an estimated battery life of between 10-12 months and radiotracking data were collected over an 11-month period (September 2015 to August 2016). Bats tagged on October 2015 were tracked for 11 months and those tagged in February 2016 were tracked for 6 months. Twenty bats were initially tracked daily up to 5 days after their initial release; subsequently, all radio-tagged bats were tracked once-monthly.

2.3 Roosting behavior

Epomophorus gambianus bats could be easily observed and counted in roosting trees once roosts were identified. To describe roosting behavior, the number of bats per tree was counted monthly by a single observer (KAM) over a 32-month period. During this period, any newly identified bat roost within the study area was recorded. Roosting behavior was described using the mean monthly number of bats per roost tree, the maximum number of bats recorded in each roost tree, and how frequently roost trees were utilized as roosts by bats. In addition,

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the roosting behavior of radio-tagged bats was monitored, including the number of different roosts used and the frequency with which bats switched roosts between monthly detections. Frequency of roost switching was estimated as the number of times a bat changed roost trees divided by the total number of times the bat was detected.

Lactating *E. gambianus* females carrying pups could be identified easily in roost trees during bat roost monitoring. All roosts that were observed to have at least one female bat carrying a pup during the study period were delineated as maternity roosts and those in which no nursing females were seen were delineated as non-maternity roosts. Once pups were weaned it became difficult to visually distinguish female bats from sexually immature males of similar sizes within the roost trees. Hence our designation of roosts as maternity roost is based solely on the presence of lactating females with pups at roosts. This categorization of maternity and non-maternity roosts allows for the comparison of the characteristics of roost sites used by *E. gambianus* for both purposes. This distinction is important as any observed differences in features selected could have implications for differences in management strategies for the conservation of the species.

For each bat roost found, the tree species was identified and measurements of the tree height (HT), trunk diameter at breast height (DBH) and the crown diameter (CD) were taken. These parameters were chosen as they are commonly used to assess the structural characteristics of tree roosts (Hahn et al., 2014; Lucas et al., 2015; Sedgeley & O'Donnell, 2004). Tree height was measured using a Nikon® Forestry Pro laser rangefinder, DBH was measured at 1.4 m above the ground and crown diameter was measured as the longest on-the-ground extent across the crown of each tree using a tape measure. The Global Positioning System (GPS) locations for all roosts and non-roost trees and for all buildings (houses, homesteads and shops) within the study area were recorded. GPS coordinates were uploaded into PC-GPS software Garmin BASECAMP version 4.6.2 (Garmin Ltd) for spatial analysis

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in Quantum GIS software (QGIS version 2.12.2-Lyon). Distance from trees to buildings (DB) were extracted using the linear distance matrix in QGIS. A 17.8 m radius circular buffer (ca 0.1-ha area) was delineated around each roost tree to create roost plots. For each plot, the total tree basal area "BA" (m^2/ha) and the tree density "TD" (trees/ha) per plot were calculated using the "points in polygon" tool in QGIS.

For comparison, we selected all trees within the study area (N = 957) with DBH > 0.1 m and height > 4.2 m that were not used as roosts. These minimum heights and DBH criteria were chosen because they were the minimum recorded for roost trees. All trees not used as roosts that were selected for comparison (comparison trees) and their corresponding plots were assessed for the same characteristics as roost trees and roost plots.

2.4 Data analysis

2.4.1 Roosting behavior and tree characteristics

We combined radiotracking data obtained from bats initially tracked daily together with those tracked monthly. Hence radio-tracking data was standardized as bat-days (1 bat day =1day of radiotracking data from 1 bat). Frequency of roost switching was estimated as number of switches made by a bat between successive detections divided by the total number of bat-days it was detected. Frequency of switching was estimated for only tagged bats that were located at least two times during the study (N =30).

Univariate analysis (Mann-Whitney U test for 2 independent samples) was used to compare differences in roosting behavior of radio-tagged bats, roost tree versus non-roost tree characteristics, and for maternity roosts versus non-maternity roosts. For roost trees and non-roost trees, comparisons were made for differences in tree height, DBH, crown diameter, distance to nearest building, plot tree density and plot total basal area. Comparisons were also made for differences in the mean monthly number of bats per tree (AvN), maximum number of bats recorded at roost (MaxB), frequency of occupancy of roost (FO) and the distance to

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the nearest neighboring roost tree (DNR) for maternity and non-maternity roost trees. Parameters of bat roosting behavior are reported with descriptive statistics and where appropriate, means ± *SD*.

2.4.2 Preference for tree species as roosts

To test if there was a preference of tree species used as roosts by the bats, a binomial exact test was used to compare the use of each roost tree species that was identified, relative to their availability in this order: preferred, random, or infrequently selected. Comparison trees were combined together with roost trees to establish availability of all tree species for this analysis. If the proportion of a tree species used was significantly greater than expected based on its availability, the species was described as "Preferred". If there was no significant difference in the relative use and availability, the species was described as being used at "Random". However, if a tree species' use was significantly less than expected based on its availability, it was considered as "Infrequently selected" (Hahn et al., 2014; Neu et al., 1974; Sedgeley & O'Donnell, 2004). Exact tests were performed in Minitab statistical package (version 16.1) and all tests were conducted with a 95% CI. We also used this approach when considering the characteristics of maternity roost and non-maternity roosts.

2.4.3 Roost selection

Logistic regression was used to determine which of the tree variables measured best differentiated characteristics of roost and non-roost trees and to predict roost selection by *E. gambianus*. Seven variables were included in the global model (full model) and subset models were obtained using the dredge function in the "MuMIn" package (Bartoń, 2009). Model selection was based on AIC values. Model averaging of the best models (delta AIC≤ 2) was done to obtain parameter estimates, unconditional standard errors of the predictor variables and their 95% CI. The relative importance of each parameter was assessed using the "importance" function in the "MuMIn" package (Bartoń, 2009). We considered a predictor

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variable as having a significant effect on roost selection if the associated 95% CI did not overlap with zero.

Similarly, we ran a logistic regression on tree characteristics for maternity and non-maternity roost trees to identify roost tree variables that were important for maternity roost selection. Eight parameters were included in the global model; the maximum number of bats per tree (MaxN) and plot basal area (BA) were collinear to mean monthly number of bats per roost and plot tree density respectively and hence were excluded from the global model. Subset models of the global model were ranked by AICc. Selection of best models, model averaging and parameter significance followed a similar procedure to that conducted for the roost tree selection.

3. RESULTS

3.1 Roosting behavior

A total of 152 roost trees were identified; 139 from roost searches and an additional 13 from tracking radio-tagged bats to their roosts. Seventy-seven of these roost trees were utilized as maternity roosts. Between one to 1,122 bats were recorded at roost trees with mean of 80 bats per tree. The mean monthly number of bats per roost tree ranged from one to 256 bats per tree over the monitoring period (Figure 1a). The frequency of occupancy of roosts ranged from 3.1% to 100% (Figure 1b). Roosts were typically made up of a mix of both males and females. *Epomophorus gambianus* co-roosted with Peter's lesser epauletted fruit bat (*Micropteropus pusillus*) at twenty-six of these roosts, however both species were spatially separated within the roost tree and never mixed.

Out of the 60 bats that were radio-tagged, 40 (28 males, 12 females) were re-detected during the study period. Radio-tagged bats were successfully located on 139 bat days at 51

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different roosts, 19 of which were used by more than one radio-tagged bat (Figure 2). The frequency of switching roosts varied from 0 to 0.86 bat days (*N*=30 bats). Frequency of switching was higher in males (mean= 0.49 ± 0.23 bat days, *N*=23) than in females (mean= 0.33 ± 0.18 bat days, *N*=7) suggesting that males were more likely than females to switch roosts. On average, there was a 93% chance of a bat switching to a previously unused roost when switching. The mean linear distance between roosts used by male bats (255 ± 254 m) was significantly longer than that for female bats (102 ± 71m) ($t = 4.50$, $df = 86$, $P < 0.0001$). Roost sharing by both sexes of radio-tagged bats was observed at five different roost trees and up to seven radio-tagged bats of both sexes shared the same roost on three different occasions.

3.2 Roost characteristics and selection

A total of 1,109 (roost and comparison) trees were identified and assessed within the study area. However, due to tree losses during the study period, not all trees could be assessed for all parameters. Binomial exact tests indicated that roost selection with respect to tree species was non-random. Neem (*Azadirachta indica*), mango (*Mangifera indica*), fig (*Ficus sp.*), Indian mast (*Polyalthia longifolia*) and African tulip (*Spathodea campanulata*) trees were used as roosts in significantly higher proportions than they were available (Table 2). These five preferred species made up only 31% of the total number of trees assessed in the study area but constituted 57% of all roost trees. Bats showed less preference for oil palm trees (*Elaeis guineensis*), soursop (*Annona muricata*), coconut (*Cocos nucifera*) and the African copaiba balsam (*Daniellia oliveri*) trees. Twenty-four other tree species were used at random as the proportion of their use was not significantly different to their availability. Fifty-seven tree species were not used, but there was no evidence to indicate that these trees were actively avoided. Tree species used as maternity roosts did not differ from those utilized as non-maternity roosts.

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With the exception of tree plot basal area, all other roost tree characteristics differed significantly from non-roost (comparison) trees. Roost trees were significantly taller ($P < 0.0001$), had significantly larger DBH ($P < 0.0001$), larger crown diameters ($P < 0.0001$), lower plot tree densities ($P < 0.0001$) and were closer to buildings ($P < 0.0001$) compared to non-roost tree characteristics (Table 1). For tree species that were identified as preferred, species-level comparisons (using effect size estimates based on Wendt, 1972's rank biserial formula) for characteristics of roost and non -roost trees showed similar results (Table S2).

Six parameters were present in the top model set for the model averaging for roost selection (Table S3). Tree height, crown diameter, distance to building, DBH, and plot total basal area had the highest relative importance compared to plot tree density (19% relative importance). Based on calculated 95% CI, all the variables, with the exception of plot tree density, were significant predictors of roost selection (Table 3). A one-unit increment in height, DBH and crown diameter of a tree increased the odds of being utilized as a roost by 1.2, 13.3 and 1.1 respectively; trees that had bigger trunk diameters, larger crowns and were taller were more likely to be used as roosts. Plot total basal area and distance to building had inverse effects on selection; increase in plot basal area reduced probability of selection and trees closer to buildings were more likely to be used as a roost.

3.3 Maternity roost characteristics and selection

Univariate analysis indicated differences in characteristics of maternity and non-maternity roost trees. Maternity roost trees were significantly bigger DBH ($P = 0.03$) and were located in plots with significantly fewer trees ($P = 0.04$) compared to non-maternity roost trees. Maternity roosts were more-frequently occupied by bats ($P < 0.0001$), had a higher average monthly number of bats ($P < 0.0001$), and higher maximum number of bats ($P < 0.0001$)

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compared to non-maternity roosts (Table 4). Other characteristics did not differ significantly between the two groups.

Tree height, crown diameter and frequency of occupancy were not present in the best models (Table S4) indicating that these parameters were poor predictors of maternity roost selection. Model averaged estimates of parameters indicated that the mean monthly number of bats recorded was the single most important parameter and the only significant predictor of maternity roost selection. All other parameters that were present in the best models had confidence intervals that included zero, indicating little support that these parameters affected maternity roost selection (Table 5).

4. DISCUSSION

4.1 *Epomophorus gambianus* roosting behavior and roost selection

Epomophorus gambianus is often described as roosting in loose colonies of individuals or a few individuals, with large colonies, comprising multiple roosts, containing up to a few hundred individuals (Boulay & Robbins, 1989; Marshall & McWilliam, 1982; Rosevear, 1965; Thomas & Fenton, 1978). Although we report similar roosting behavior in this species in the current study, we also show that single roosts can be much larger, containing over a thousand individuals, and that colonies can be five times as big as these large roosts. Our observation of *E. gambianus* co-roosting with *M. pusillus*, has been reported previously (Boulay & Robbins, 1989) and suggests that both species have similar roosting requirements.

Although the frequency of occupancy at roost sites was generally high, fidelity to specific roost trees was rather low, with bats utilizing several roosts and switching frequently between them. An earlier study reported similar behavior in this species, with bats switching between several roosts almost each day (Thomas & Fenton, 1978). In a review of site fidelity

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by bats (Lewis, 1995), *E. gambianus* was described as a species that frequently changed roosts. Generally, roost switching is known to be high among tree roosting bats (Kunz, 1982; Menzel et al., 1998), and this has been documented for several species, including, Wahlberg's epauletted fruit bat *Epomophorus wahlbergi* (Fenton et al., 1985), *Hypsignathus monstrosus* (Bradbury, 1977), fringed myotis *Myotis thysanodes* (Lacki & Baker, 2007), lesser long-eared bat *Nyctophilus geoffroyi* (Lumsden & Bennett, 2006), big brown bat *Eptesicus fucus* (Vonhof & Barclay, 1996), and greater short-nosed fruit bat *Cynopterus sphinx* (Storz et al., 2000).

For tree roosting species, fidelity to an area, rather than to a single tree, is common (Hein et al., 2008; Kunz, 1982; Vonhof & Barclay, 1996) for reasons including decreased predation, decreased disturbance, reducing ectoparasite loads, familiarity with different roost microclimates, and reducing commuting costs to foraging sites (Kunz & Lumsden, 2003; Lewis, 1995). Patterns of roost switching and aggregation among radio-tagged bats, together with the observed variation in mean numbers and frequency of roost occupancy, suggest a fission-fusion behavior in *E. gambianus.* Although this behavior is widespread in bats, much remains to be understood and future studies on this could help in understanding the complex social structures, group decision making, and cooperation among bats (Kerth, 2008; Kerth & Barbara, 1999).

As we hypothesized, roost selection by *E. gambianus* was not random. Collectively, *E. gambianus* roost trees were bigger and taller, had larger crown diameters, were closer to buildings, and located in plots with lower tree densities than trees that were not used as roosts. Logistic regression indicated tree trunk size (DBH), tree height, crown diameter, plot basal area and distance to nearest building as the most important factors that differentiated roost trees from non-roost trees and these parameters predicted roost selection for *E. gambianus*. These predictor variables occurred at different scales; at the tree scale (height,

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DBH, crown diameter), plot scale (plot basal area), and landscape scale (distance to buildings). This suggests that *E. gambianus* selects roosts by considering factors from different spatial scales, supporting the view that resource selection occurs at multiple scales (Limpert et al., 2007; Lucas et al., 2015; Manly et al., 1993). Although very few landscape-level factors were considered in this study owing to the relatively small study area, we anticipate that, at a much larger scale, the effects of other landscape factors, such as distance to water and feeding areas (e.g. Kalcounis-Rüppell et al., 2005), might also influence roost selection.

The occurrence of roost trees was higher in plots that had lower basal area and lower tree density, although we found little support for the latter. This suggests a preference for roosting in bigger and taller trees located in relatively open and less mature plots rather than in mature, dense plots. Management efforts targeted at trees within such plots could be important for the conservation of the species. We also found significant support for the selection of trees closer to buildings as roosts by *E. gambianus*. The formation of roosts in close proximity to humans is very common among pteropodid bats. *Eidolon helvum* and several *Pteropus* species form very large colonies in urban centres (Hahn et al., 2014; Pierson & Rainey, 1992; Rosevear, 1965). The reason for this behavior is unclear for some species like *Eidolon helvum* which forage over large distances (Calderón-Capote et al., 2020).

E. gambianus might roost closer to urban and peri-urban areas because household backyard gardens offer an oasis of fruit diversity and alternative food sources, especially as natural food resources diminish due to foraging habitat loss and agricultural intensification (Hahn et al., 2014; Kessler et al., 2018; Plowright et al., 2014). Unfortunately, foraging distances for *E. gambianus* and the feeding habits of this species are not well known (but see Amponsah-Mensah et al., 2019; Thomas & Fenton, 1978), and further work is required to verify this assumption. *Epomophorus gambianus* exhibited preference for trees which were

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closer to buildings. This could be because predation risk might be reduced if natural predators avoid areas close to human habitation (Voigt et al., 2015) except where significant hunting by humans or predation by domestic animals (e.g., cats; see Ancillotto et al., 2013) occurs. Trees close to buildings are commonly planted as ornamental trees and to provide shade within the compounds of houses or of several households, or as fruit trees. The utilization of roosts close to human habitation could be the result of loss of suitable bat roosting and feeding habitat or the encroachment of humans into bat habitat. Habitat loss has been identified as one of the leading problems bats face globally, driving population declines of several species (Kunz et al., 2011; Mickleburgh et al., 1992, 2002).

The use of tree species for roosting by *E. gambianus* was not at random; this bat species preferred neem, mango, African tulip tree, Indian mast tree, and fig trees over other tree species even though the preferred species made up less than 32% of all trees within the area. Oil palm, soursop, coconut and African copaiba balsam trees were infrequently selected and many other species were not used as roosts by bats in this study. Although we identified a preference for specific tree species, our findings also indicates that other tree species can be utilized by the species. Preference for specific tree species has been reported previously (e.g. Vonhof & Barclay, 1996) but, as in this study and others (e.g. Sedgeley & O'Donnell, 1999), preference can be an artefact of the physical, plot or landscape level characteristics and not just the species per se. Tree species that typically attain physical characteristics or occur in plots that make them suitable for roosting by bats, may be preferred over others. Hence, where these tree species are not available or do not meet preferred characteristic requirements, other species may be utilized as roosts. Elsewhere in Ghana, *E. gambianus* has been reported to roost in neem and fig trees but also in mahogany (*Khaya senegalensis*) trees (Ayensu, 1974; Baker & Harris, 1957; Marshall & McWilliam, 1982) and outside Ghana, in sausage tree *Kigelia africana* and *Cola* sp. (Rosevear, 1965; Thomas & Fenton, 1978).

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In addition to the morphological features of trees measured in this study, other features of trees such as shape, canopy cover (see Kalcounis-Rüppell et al., 2005), or fruiting phenology could potentially influence roost tree selection by bats. For instance, Marshall & McWilliam (1982) described *E. gambianus* roosting high up in "umbrella shaped trees" and Boulay & Robbins (1989) described the species hanging from branches in trees well shaded by foliage. This suggests that shape of tree, canopy cover or degree of shade provided by trees could influence their selection for roosting. Tree-roosting bat species are known to switch or abandon roosts when roosts are defoliated, hence tree species that lose their leaves (e.g., deciduous species) may be avoided or less preferred (Kunz, 1982). The preferred tree species identified as being used by *E. gambianus* in this study are evergreen or semi-evergreen species, which might also influence their selection.

4.2 Sex related and maternity roost selection

As predicted, maternity roosts were a subset of all roost trees, most significantly, those roosts that contained a higher number of bats. Since maternity roosts are only a subset of all roost trees, we propose that reproductive females of this species may exhibit aggregation patterns at large roost where they may form mixed-sex aggregations rather than single-sex maternity roosts during reproduction seasons. Our observation of some radio-tagged bats aggregating at some roosts in this study provides anecdotal evidence for this and further studies will be required to provide more insight.

On the basis that *E. gambianus* roost in loose colonies where individuals are well spaced from each other (Happold, 2013), the selection of large colonies by nursing female bats is likely a predator avoidance strategy rather than for physiological benefits such as thermoregulation, which often explains aggregation in temperate zone species. An advantage of selecting large roosts is that nursing females and their young are more likely to be better protected from predation by decreasing the risk of attack of any individual (Fenton et al.,

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1994; Wilkinson & South, 2002) or by providing increased vigilance (Klose et al., 2009). Alternatively, the selection of roosts with more bats may also reflect social co-operation needs, such as offering the opportunity for young bats to learn and socialize with each other (Kerth, 2008) which is likely to be important in such a social and colonial roosting species. Hence trees that contain large roosts could be vital to the sustainability of the colony and should be prioritized in conservation management practices.

The use of a smaller roosting area by female bats has been hypothesized to be a strategy for reducing the energetic constraints when roost-switching while carrying pups (Henry & Kalko, 2007). This is consistent with our observation of shorter distances between roosts used by radio-tagged female bats compared to male bats. Utilizing a smaller roosting area and travelling shorter distances between roosts also has the advantage of reducing the risk of detection by predators. Although the extent of predation was not assessed during the current study, some observations were made of pied crows (*Corvus albus*) attacking juvenile bats in roosts. Also, the yellow-billed kite (*Milvus migrans*) and shikra (*Accipiter badius*) were seen to attack bats in flight when roosts were disturbed. The extra weight of carrying a pup can reduce the agility and maneuverability needed to evade an aerial attack by predators. Roosts used by male bats might be dispersed over a larger area due to their propensity to utilize multiple roosts compared to female bats and their use of calling roosts for courtship displays.

In conclusion, our study confirms that roost selection by *E. gambianus* is not random as the species selects trees with characteristics that differentiate roost trees from non-roost trees. Trees used as roosts were more likely to be closer to buildings and to occur in open and less mature plots than non-roost trees, thus highlighting the species' ability to persist in human modified landscapes and in close proximity to people. Based on our findings, ensuring the preservation of large roosts can be important for maintaining maternity roosts whilst

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management practices that preserve trees with the preferred characteristics in open and less mature plots can provide roosting opportunities for *E. gambianus* within modified landscapes. Our findings contribute knowledge of how wildlife utilize human-modified landscapes which is vital to better predict and improve the management of biodiversity in the Anthropocene.

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TABLES

Table 1. Differences in characteristics between roost and non-roost trees. Comparisons were made using Mann-Whitney U tests. Seven roost trees which were lost before some parameters could be measured are not included.

	Roost, *N* =145		**Non roost *N* =957**		
Roost Parameter	**median**	**IQ range**	**median**	**IQ range**	***P***
Tree Height (m)	10.4	8.80-12.40	7.8	6.2-10	<0.0001
Tree DBH (m)	0.48	0.35-0.71	0.3	0.24-0.09	<0.0001
Tree Crown diameter (m)	10.25	7.5-13.1	7.6	5.4-9.9	<0.0001
Plot tree density (Trees/ha)	40	20-70	60	30-90	<0.0001
Plot basal area (m^2/ha)	7.2	3.5-11	7.4	3.2-13	0.66
Distance to nearest building (m)	12.529	6.4-23	17.0	10.36-27.28	0.0001

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Table 2. Roost tree selection by *E. gambianus* showing preferred, random, and infrequently selected species. Selection is based on the use of a tree species as a roost compared to its abundance within the study area. Tests are based on binomial exact tests. Only species with abundance ≥4 are shown. Fifty-seven tree species unused by bats for roosting are not included here.

Plant species	**Proportion of all trees**	**Proportion of roost trees**	***P***	**Preference**
Anacardium occidentale	0.004	0	1.0	Random
Annona muricata	0.03	0	0.041	Infrequently selected
Azadirachta indica	0.07	0.15	0.001	Preferred
Carica papaya	0.009	0.0	0.62	Random
Ceiba petandra	0.004	0.007	0.46	Random
Citrus sp.	0.01	0	0.61	Random
Cocos nucifera	0.05	0	0.002	Infrequently selected
Crescentia cujete L.	0.004	0	1.0	Random
Daniellia oliveri	0.04	0	0.011	Infrequently selected
Delonix regia	0.04	0.021	0.35	Random
Elaeis guineensis	0.11	0.007	0	Infrequently selected
Eucalyptus sp.	0.01	0	0.39	Random
Ficus spp	0.02	0.083	0.001	Preferred
Gliricidia sepium	0.04	0.021	0.35	Random
Gmelina arborea	0.04	0.041	0.82	Random
Mangifera indica	0.20	0.28	0.022	Preferred
Milicia spp	0.005	0.007	0.52	Random

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Millettia thonningii	0.005	0.014	0.19	Random
Morinda lucida	0.005	0.007	0.52	Random
Moringa oleifera	0.004	0	1.0	Random
Newbouldia laevis	0.04	0.048	0.48	Random
Persia americana	0.005	0	1.0	Random
Pithecellobium dulce	0.005	0	1.0	Random
Polyalthia longifolia	0.02	0.062	0.003	Preferred
Psidium guajava	0.01	0	0.63	Random
Senna siamea	0.08	0.097	0.52	Random
Spathodea campanulata	0.006	0.028	0.03	Preferred
Spondias mombin	0.03	0.014	0.31	Random
Sterculia rhinopetala	0.004	0.014	0.15	Random
Tectona grandis	0.04	0.028	1.0	Random
Unidentified sp12	0.006	0.021	0.10	Random
Unidentified sp6	0.004	0	1.0	Random
Vitex doniana	0.007	0.014	0.33	Random

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506 Table 3. Model average estimates of parameters for top models (ΔAIC <2) showing the effect
507 of each parameter on roost selection and their relative importance.

Parameter	Estimate	Odds	*SE*	CI (95%)	Relative importance
Intercept	-4.1	0.02	0.37	-4.83, -3.37	
Plot Total Basal Area	-0.06	0.94	0.02	-0.10, -0.002	1
Crown Diameter	0.07	1.08	0.03	0.01, 0.13	1
Distance to Building	-0.06	0.94	0.01	-0.08, -0.04	1
DBH	2.6	13.3	0.6	1.41, 3.77	1
Tree Height	0.21	1.24	0.03	0.15, 0.28	1
Plot Tree Density	-0.002	0.1	0.003	-0.013, 0.004	0.19

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Table 4. Differences in characteristics of maternity and non-maternity roosts. Comparisons were made using Mann-Whitney U tests. Different *N* for different characteristics as a result of roost loss within study area.

	Maternity roosts			Non maternity roost			
Roost Parameter	***N***	**median**	**IQ range**	***N***	**median**	**IQ range**	***P***
Tree Height (m)	70	10.5	9.15 - 12.60	75	10.2	8.40 - 12.40	0.28
Tree DBH (m)	70	0.53	0.38 - 0.76	75	0.45	0.30 - 0.67	0.03
Tree Crown diameter (m)	70	11	8.24 - 13.3	75	9.6	6.6 -12.8	0.07
Average monthly no. of bats per tree	77	7.65	2.62 - 26.95	49	1.67	0.56 -5.06	0.0001
Maximum number of bats per tree	77	40	13 - 141.5	49	15	3.5 - 30	0.0001
Frequency of occupancy (%)	77	52	28 - 91	49	25.00	12.5 - 50	0.0001
Plot tree density (Trees/ha)	70	30	20 - 60	75	50	30 - 80	0.04
Plot basal area (m^2/ha)	70	7.3	3.85 - 11.23	75	7.2	3.20 - 11.70	0.1
Distance to nearest roost tree (m)	70	14.36	10.24 - 31.41	75	13.27	7.56 - 26.24	0.4
Distance to nearest building (m)	70	13.52	7.37 - 22.38	75	12.32	5.53 - 22.77	0.7

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513 Table 5. Model average estimates of parameters for top models (ΔAICc<2) showing the
514 effect of each parameter on maternity roost selection by *E. gambianus*.

Parameter	Estimate	*SE*	CI (95%)	Relative importance
Intercept	-0.39	0.79	-1.96, 1.18	
Average monthly number of bats	0.24	0.073	0.09, 0.38	1
Distance to building	0.02	0.026	-0.01, 0.08	0.6
DBH	-1.05	1.13	-3.65, 0.38	0.64
Plot tree density	-0.0005	0.003	-0.02, 0.014	0.09
Distance to nearest roost	-0.0006	0.005	-0.03, 0.02	0.09

515

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FIGURE LEGENDS

Figure 1. Map of trees (green dots) within the study site showing (a) frequency of occupancy of trees by bats (b) mean monthly number of bats recorded and (c) maximum number of bats recorded for trees utilized as roosts.

Figure 2. Roosts used by individual radio-tagged *Epomophorus gambianus* bats in (a) male bats, (b) female bats**.** Figures represent individual bat IDs and lines indicate roosts used by same individual for bats that used more than one roost.

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FIGURES

Figure 1.

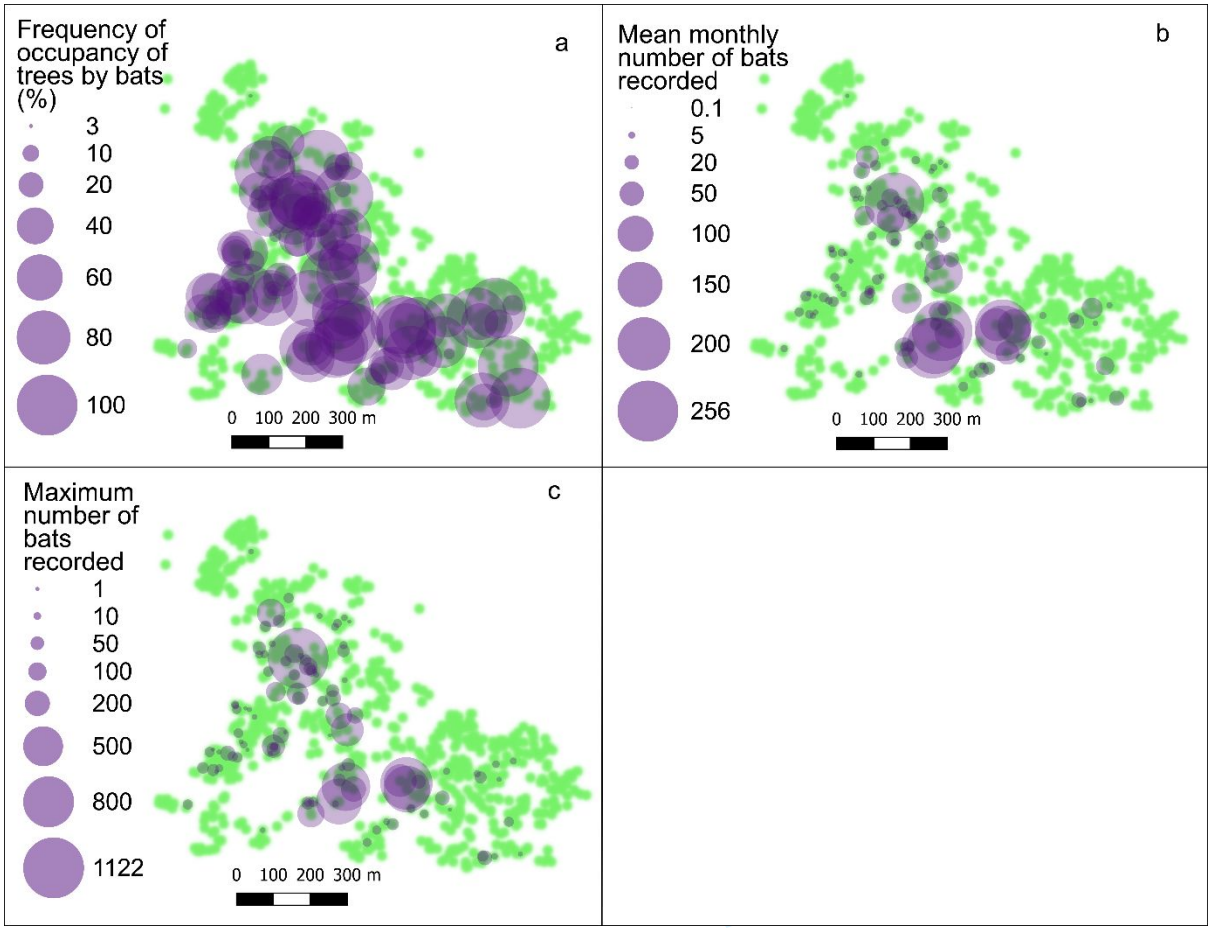
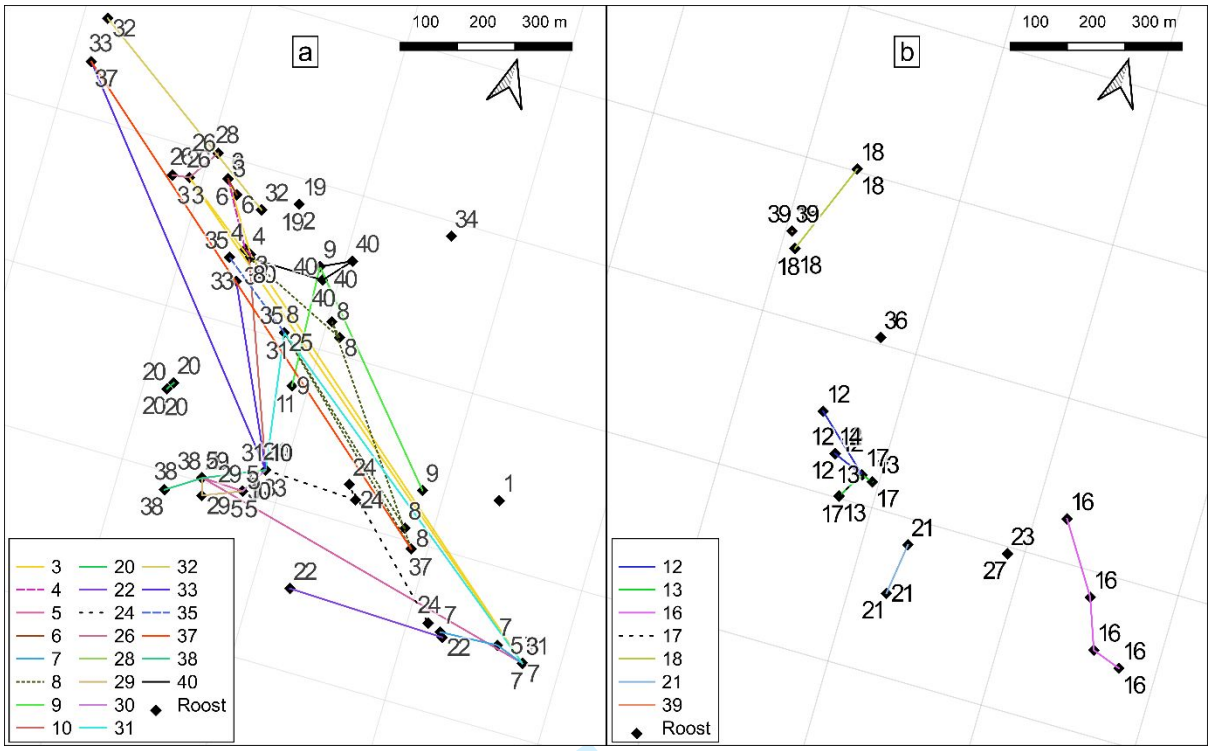


Figure 2



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AUTHOR CONTRIBUTION STATEMENT

YNB and KAM conceived the research ideas and designed methodology; KAM conducted the investigations and led the field data collection; KAM and JLNW analyzed the data; KAM led the writing of the manuscript; YNB, AAC, and JLNW obtained the funding, supervised the research, reviewed and edited the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

DISCLOSURE STATEMENTS

The corresponding author confirms on behalf of all authors that there have been no involvements that might raise the question of bias in the work reported or in the conclusions, implications, or opinions stated.

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Supporting Information

Table S1. Capture data of Epomophorus gambianus bats tagged with radio-tags and corresponding tags fitted to bats.

No.	Bat ID	Sex	Age	Forearm (mm)	Bat weight (g)	Date of tagging	Tag ID	Tag weight (g)
1	4402063	Male	Subadult	85.7	110	20 September 2015	105	5.5
2	4426720	Male	Subadult	88.4	124	21 September 2015	005	6.1
3	4403776	Male	Subadult	88.4	116	21 September 2015	035	5.9
4	4410728	Male	Adult	91.6	144	21 September 2015	065	6.3
5	4404830	Male	Subadult	92.3	114	21 September 2015	135	5.9
6	4432302	Male	Subadult	90.6	110	22 September 2015	155	5.9
7	4433569	Male	Adult	90.5	134	22 September 2015	165	6.1
8	4425864	Male	Subadult	86.3	100	22 September 2015	246	5.7
9	4436503	Male	Adult	88.0	122	23 September 2015	195	6.1
10	3702622	Male	Subadult	91.7	114	23 September 2015	265	6.0
11	3702299	Female	Adult	87.4	104	23 September 2015	335	5.2
12	3581362	Female	Adult	85.9	110	23 September 2015	354	5.3
13	4399184	Female	Adult	83.0	100	23 September 2015	395	5.0
14	4424584	Male	Subadult	89.9	116	23 September 2015	515	6.1
15	4420680	Male	Adult	95.2	136	23 September 2015	655	6.3
16	3705052	Female	Adult	83.8	102	24 September 2015	435	5.1
17	3706803	Male	Subadult	90.3	112	24 September 2015	545	6.2
18	3705875	Female	Adult	82.3	101	25 September 2015	285	5.8

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19	3704115	Male	Adult	90.6	126	25 September 2015	675	6.2
20	3706053	Male	Subadult	86.5	115	26 September 2015	485	6.1
21	4409084	Female	Adult	82.1	100	25 February 2016	425	5.1
22	4401763	Male	Subadult	88.8	108	25 February 2016	445	5.3
23	3487312	Female	Adult	84.7	102	25 February 2016	465	5.4
24	4433230	Female	Adult	85.4	110	25 February 2016	524	5.5
25	4435993	Female	Adult	83.6	92	25 February 2016	535	5.4
26	4407464	Male	Subadult	78.3	82	25 February 2016	555	5.6
27	4410452	Male	Subadult	85.4	100	25 February 2016	845	5.8
28	4415162	Female	Adult	85.4	108	25 February 2016	855	5.6
29	4423253	Male	Subadult	90.5	108	25 February 2016	865	5.9
30	4434144	Male	Subadult	81.8	88	25 February 2016	885	5.9
31	4411486	Male	Subadult	85.3	112	25 February 2016	815	6.0
32	4411661	Male	Adult	86.5	126	25 February 2016	685	6.1
33	3483933	Male	Subadult	84.6	98	25 February 2016	715	6.1
34	4398727	Male	Adult	91.4	146	25 February 2016	764	6.1
35	4412199	Male	Subadult	86.7	98	26 February 2016	345	5.5
36	3472448	Female	Adult	83.5	112	26 February 2016	455	5.6
37	4422423	Male	Subadult	88.7	104	26 February 2016	505	5.7
38	4426106	Female	Adult	81.9	100	26 February 2016	575	5.5
39	4425813	Male	Subadult	85.0	98	26 February 2016	615	5.6
40	4399273	Male	Subadult	79.5	88	26 February 2016	635	5.4
41	4426768	Male	Subadult	85.0	112	26 February 2016	835	5.8
42	4421126	Male	Subadult	87.2	120	26 February 2016	785	5.8
43	4424752	Female	Adult	84.3	110	26 February 2016	795	5.2

For Peer Review Only

44	4408765	Male	Adult	88.3	132	26 February 2016	805	6.0
45	4401242	Male	Subadult	89.7	114	26 February 2016	825	5.6
46	4428923	Female	Adult	88.6	106	26 February 2016	695	5.6
47	4425480	Male	Adult	87.3	126	26 February 2016	705	5.6
48	4421639	Male	Adult	88.3	130	26 February 2016	725	5.7
49	4428079	Male	Subadult	89.7	120	26 February 2016	735	5.9
50	4411571	Male	Adult	91.2	146	26 February 2016	745	5.9
51	4399990	Male	Subadult	87.8	118	26 February 2016	755	5.9
52	4416122	Male	Subadult	86.9	110	26 February 2016	775	5.7
53	A05046	Female	Subadult	77.6	82	27 February 2016	385	5.5
54	A05053	Female	Adult	84.7	104	27 February 2016	415	5.6
55	A05050	Female	Adult	84.8	110	27 February 2016	604	5.6
56	A05047	Male	Adult	90.4	136	27 February 2016	225	5.7
57	A05052	Male	Adult	90.0	150	27 February 2016	255	5.7
58	A05045	Female	Subadult	81.5	92	27 February 2016	315	5.4
59	A05048	Male	Subadult	88.8	112	27 February 2016	045	5.8
60	A05043	Male	Adult	92.7	144	27 February 2016	084	5.7

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Table S2 Probability of superiority (or common language effect size) estimation for species-level comparisons of roost and non -roost tree characteristics for preferred tree species. *r* is rank biserial correlation based on Wendt (1972)'s formula (*r* =1 – (2U)/ (n1 * n2); n1, n2= sample sizes of the 2 groups, *U*=Mann Whitney *U*. *Pa>b* is the probability of superiority or common language effect size and gives the percentage of occasions when a randomly sampled member of the distribution with the higher median will have a higher score than a randomly sampled member of the other distribution. Higher median values for each pair of comparisons are shown in bold.

		Tree Height					**Tree DBH**			
		Median (IQR)					Median (IQR)			
Tree species	*N*	Roost	*N*	Non roost	***r***	***Pa>b***	Roost	non roost	***r***	***Pa>b***
Azadirachta indica	22	**10.1 (9.4-10.65)**	51	9.2 (7.9-10.4)	0.28	63.9	**0.4 (0.31-0.51)**	0.34 (0.22-0.48)	0.23	61.6
Ficus spp	12	**9.5 (7.05-11.45)**	15	6.8 (6-7.8)	0.49	74.4	**0.645 (0.49-0.76)**	0.31 (0.22-0.48)	0.84	91.9
Mangifera indica	41	**9.4 (8.2-11)**	177	7.0 (5.7-8)	0.67	83.6	**0.64 (0.41-0.89)**	0.33 (0.25-0.46)	0.65	82.5
Polyalthia longifolia	9	**14.2 (12.24-15.09)**	10	10.0 (8.15-14.7)	0.44	72.2	**0.27 (0.25-0.43)**	0.33 (0.25-0.40)	0.09	54.4
Spathodea campanulata	4	**15.6 (10.55-17.5)**	3	8.0 (7.2-14.8)	0.67	83.3	**0.89 (0.74-0.99)**	0.28 (0.27-0.53)	1.00	100.0

Tree species	**Tree crown Diameter**	**Plot Tree density**

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	Median (IQR)				Median (IQR)			
	Roost	non roost	*r*	***Pa>b***	Roost	non roost	*r*	***Pa>b***
Azadirachta indica	**10.3 (7.71-12.35)**	8.4 (5.74-12)	0.17	58.6	**60 (30-82.5)**	50 (30-90)	0.05	52.5
Ficus spp	**12.57 (7.42-15.65)**	7.8 (6-8.8)	0.54	77.2	40 (12.5-80)	**60 (20-90)**	0.30	65.0
Mangifera indica	**10.25 (8.5-12.88)**	8 (5.97-10)	0.43	71.6	20 (20-45)	**40 (20-70)**	0.34	67.1
Polyalthia longifolia	**4.4 (2.5-7.8)**	3.6 (2.23-5.62)	0.13	56.7	30 (20-60)	**60 (42.5-70)**	0.34	67.2
Spathodea campanulata	**12.6 (11.73-13.4)**	7.4 (5.6-12.4)	0.75	87.5	20 (10-67.5)	**50 (40-70)**	0.50	75.0

Distance to nearest building

	Median (IQR)			
Tree species	Roost	non roost	*r*	***Pa>b***
Azadirachta indica	12.81 (7.13-25.4)	**20.56 (13.52-29.59)**	0.33	66.7
Ficus spp	19.03 (8.46-33.91)	**20.92 (12.91-28.11)**	0.06	52.8
Mangifera indica	**13.43 (6.38-19.2)**	13.04 (8.65-22.30)	0.13	56.3
Polyalthia longifolia	7.42 (3.96-18.04)	**9.21 (7.21-14.88)**	0.18	58.9
Spathodea campanulata	**18.84 (10.37-22.88)**	17.8 (11.5-30.05)	0.17	58.3

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Table S3. Model parameters, AIC values, Aikaike weights and model weights for top models ($\Delta AIC \leq 2$) that explained roost site selection of *E. gambianus*. BA is plot total basal area, CD is crown diameter, DB is distance to building, DBH is tree diameter at breast height, Ht is Tree height, and TD is plot tree density.

Model number	**Model parameters**	***df***	**Log Likelihood**	**AIC**	**ΔAIC**	**Model weight**
1	BA, CD, DB, DBH, Ht	6	-345.3	702.6	0	0.63
2	BA, CD, DB, DBH, Ht, TD	7	-344.9	703.7	1.09	0.37

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Table S4. Model parameters, AICc values, Aikaike weights and model weights for candidate models that explained maternal roost selection in *E. gambianus*. DBH-diameter at breast height; AvN -Average monthly number of bats; DNR-distance to nearest roost, DB-distance to building; TD- plot tree density

Model Components	*df*	Log Likelihood	AICc	ΔAICc	model weight
AvN, DB, DBH,	4	-47.1	102.7	0	0.25
AvN, DBH	3	-48.4	103	0.35	0.21
AvN	2	-49.5	103.2	0.54	0.19
AvN, DB	3	-48.6	103.5	0.81	0.17
AvN, DB, DBH, TD	5	-47.0	104.6	1.94	0.09
AvN, DB, DBH, DNR	5	-47.0	104.7	2	0.09

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