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Sleeping site selection by savanna chimpanzees in Ugalla, Tanzania

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Abstract We examined sleeping site selection by chimpanzees (*Pan troglodytes*) in the Ugalla savanna woodland area, western Tanzania, from 1994 to 2012. We established 488 km of line transects and recorded 379 chimpanzee beds within 30 m perpendicular to the transects. Comparisons between 60 × 60-m quadrats containing new and recent beds and the remaining quadrats without beds along the transects indicated that evergreen forests comprised disproportionately more area in quadrats with beds than in those without beds during the dry and rainy seasons, respectively. In Ugalla, chimpanzees coexist with lions (*Panthera leo*) and leopards (*Panthera pardus*). They may sleep in forests to reduce predation risk by these carnivores, as trees are dense and the canopy is high and closed. The angle of slope was steeper in quadrats containing beds than in those without beds during the dry season, whereas the angle was less steep in quadrats with beds than in those without beds during the rainy season. Additionally, fewer beds were found further from forests. The distance between beds and forests during the dry season was shorter than that during the rainy season. Chimpanzees may sleep in or near forests and on slopes because water pools in the valley forests along the slopes during the dry season. Quadrats with beds were at a slightly higher altitude than those without beds during the rainy season; however, the difference was not significant during the dry season. The number of beds found in or close to feeding trees was not related to the fruiting period. Sleeping site selection by chimpanzees may be affected by predation pressure and water availability in the savanna woodland area.

Keywords chimpanzee, sleeping site, savanna woodland, predation pressure, slope angle

Introduction

Whereas many mammals use nests and return to them daily (Hansell 2005), most diurnal primates do not construct nests and instead choose a new sleeping site each day, often sleeping in trees or on rocks along a cliff (Anderson 1998; Kappeler 1998). In addition to the distribution of trees and cliffs available for sleeping, sleeping site selection can also be affected by predation pressure, feeding efficiency, water availability, and physical comfort at the site as well as by other factors such as territorial defense and communication with group members (Anderson 1998). Primates frequently sleep in locations that are not easily accessible by predators and where they can readily see and escape from predators (Reichard 1998; Von Hippel 1998). Primates also often sleep in or near their feeding trees to increase feeding efficiency (Chapman et al. 1989; Day and Elwood 1999; Furuichi and Hashimoto 2004; Hamilton 1982). Primates in dry habitats frequently sleep at sites close to sources of drinking water (Sharman 1982). They can also often be found sleeping at comfortable sites, e.g., warm shelters that are protected from strong winds and rain (Goodall 1962; MacKinnon 1974; Wada et al. 2007). Primates also choose sleeping sites to facilitate the defense of feeding sites and territory (Basabose and Yamagiwa 2002; Smith et al. 2007). Some primates change their sleeping sites to avoid endo-parasite infection (Hausfater and Meade 1982), whereas others reuse their sleeping site repeatedly (Ogawa and Takahashi 2003).

Chimpanzees (*Pan troglodytes*) usually construct a bed in a tree by bending branches (Goodall 1962). Unlike other animals, however, chimpanzees construct a new bed every night (Goodall 1962), although they sometimes reuse the bed site, bed tree, and specific location within the tree after a certain interval of time (Hernandez-Aguilar

2006; Stewart et al. 2011).

Studies of chimpanzees in marginal and dry habitats are useful for understanding the variety and flexibility of chimpanzee adaptation and for illuminating models of early hominin behavioral ecology, as savanna woodland areas are considered to be similar to the habitats of early hominins (Itani 1979; Moore 1992). Habitat use and sleeping site selection by chimpanzees in dry habitats were studied in Senegal and Tanzania (Baldwin et al. 1981; Pruetz et al. 2008; Hernandez-Aguilar 2006, 2009; Hernandez-Aguilar et al. 2013; Ogawa et al. 2007; Stewart et al. 2011; Stewart and Pruetz 2013). Because the Ugalla area in western Tanzania is the most eastern and one of the driest and most open habitats of chimpanzees, many researchers have studied chimpanzees in this area (Hernandez-Aguilar 2006, 2009; Hernandez-Aguilar et al. 2013; Ogawa et al. 2007; Piel and Moore 2007; Stewart et al. 2011; Stewart and Pruetz 2013). Previous studies have revealed that chimpanzees in Ugalla frequently sleep in evergreen forests (Ogawa et al. 2007; Stewart and Pruetz 2013), although they extensively use woodlands as well (Hernandez-Aguilar 2006, 2009; Hernandez-Aguilar et al. 2013). However, chimpanzees in Ugalla also frequently sleep on slopes and/or in hilly areas (Hernandez-Aguilar 2006, 2009; Ogawa et al. 2007), similar to chimpanzees in other open habitats in Tanzania (Kano 1972; Suzuki 1969) and at Assirik in Senegal (Baldwin et al. 1981). However, it is not clear whether chimpanzees prefer hilly areas because they harbor valuable habitats such as valleys and ridges between the valleys, or because they simply prefer slopes. Furthermore, it is not known whether chimpanzees sleep along slopes because more evergreen forests exist there, or whether they prefer slopes. Chimpanzees may prefer slopes because predation risk might be lower if there is a paucity of grasses that could deter hunting by terrestrial carnivores (Hernandez-Aguilar 2009). Moreover,

chimpanzees may choose slopes to facilitate vocal communication with chimpanzees in other sub-groups, as sounds carry far in hilly areas (Piel and Moore 2007).

To investigate the factors affecting sleeping site selection by savanna chimpanzees, we posed five non-mutually exclusive hypotheses.

First, we hypothesized that the distribution of sleeping sites would be affected by the availability of sleeping trees. Unlike tropical rain forests, the savanna woodland habitat contains evergreen forests, deciduous woodlands, and grasslands. Few trees are found in grasslands, and fewer sleeping trees are available in deciduous woodlands than in evergreen forests during the dry season, when some deciduous trees lose their leaves. This first hypothesis predicts that chimpanzees frequently sleep in evergreen forests, and that this tendency is conspicuous during the dry season.

Second, we hypothesized that chimpanzees would select sleeping sites that would maximize predator avoidance (Hernandez-Aguilar 2006, 2009; Hernandez-Aguilar et al. 2013; Ogawa et al. 2007; Pruetz et al. 2008; Stewart and Pruetz 2013). Because chimpanzees are larger bodied than most other primates, few studies have examined predation pressure on chimpanzees (Baldwin et al. 1981; Pruetz et al. 2008; Zuberbühler and Jenny 2002). Although few direct observations have been recorded, however, Tsukahara (1993) documented that chimpanzees have been eaten by lion(s) (*Panthera leo*) in Mahale, Tanzania, whereas others have been killed by leopards (*Panthera pardus*) in Mahale, Tanzania (Nakazawa et al. 2013), in Tai, Côte d'Ivoire (Boesch 1991; Zuberbühler and Jenny 2002), and in Lope, Gabon (Hanschell et al. 2005). Chimpanzees in the Ugalla savanna woodland area of western Tanzania coexist with lions, leopards, and other potential predators such as hyenas (*Crocuta crocuta*) and African wild dogs (*Lycaon pictus*) (Hernandez-Aguilar 2009; Ogawa et al. 2007). In the

Ugalla woodlands, trees are scattered, the canopy is open (Hernandez-Aguilar 2006, 2009), and tree height is no more than 25 m (Ogawa unpublished data); thus, chimpanzees may have difficulty escaping into tall trees when they encounter predators in this area. If the carnivore can climb trees, chimpanzees may have difficulty passing through the branches. Thus, this vegetation can be dangerous for chimpanzees both in the daytime and at night. In contrast to woodlands, forests may provide chimpanzees with better sites for sleeping in terms of predator avoidance (Hernandez-Aguilar 2006, 2009; Ogawa et al. 2007; Stewart and Pruetz 2013) for reasons similar to those pertaining to the grassland-forest mosaic area in Fongoli and Assirik, Senegal (Pruetz et al. 2008). A comparison between trees with beds and trees without beds at Issa in Ugalla showed that chimpanzees made their beds in taller trees with a larger diameter and crown height and a higher first branch (Hernandez-Aguilar 2006, 2009; Hernandez-Aguilar et al. 2013). Moreover, they chose trees with more leaves and thicker horizontal branches (Hernandez-Aguilar 2006, 2009; Hernandez-Aguilar et al. 2013). A comparison between Issa and Fongoli, where predator pressure is low, showed that chimpanzees at Issa made higher beds at more peripheral places along horizontal branches in the tree (Stewart and Pruetz 2013). These observations indicate that chimpanzees chose safer trees and safer places within the trees. However, chimpanzees may also choose a sleeping site in their home range, depending on the ranging pattern for a particular day. Our second hypothesis also predicted that chimpanzees frequently sleep in forests. However, fewer trees are available in woodlands because tree density is low and some trees in woodlands are deciduous. Therefore, the question of which vegetations chimpanzees select as their sleeping sites when controlling for the availability of sleeping trees remains unanswered. Unlike the first hypothesis, our

second hypothesis predicts that chimpanzees would sleep in forests more frequently than expected according to the number of available sleeping trees.

Third, we hypothesized that chimpanzees would choose their sleeping sites to increase their feeding efficiency (Furuichi and Hashimoto 2004; Stanford and O'Malley 2008). Because one of the best choices to maximize the feeding efficiency is sleeping in their feeding trees, chimpanzees may frequently make their beds in the tree of which they eat fruits and other parts during the period, as observed in *Pan paniscus* in Lomako, Zaïre (Democratic Republic of the Congo) (Badrian et al. 1981). When they do not choose the feeding trees, they may sleep close to the trees. This hypothesis leads to the expectation that chimpanzees sleep in or close to their feeding trees more frequently than expected.

Fourth, chimpanzees are expected to select sleeping sites located close to water. This hypothesis predicts that chimpanzees sleep in or near evergreen forests and on slopes, because water is more likely to accumulate at the valley evergreen forests along the slopes. The tendency to choose this environment should be more conspicuous during the dry season in Ugalla, when most drinking water is restricted to the valley forests. The second and the fourth hypotheses predicted that many beds are found in forests. Unlike the second hypothesis, however, the fourth hypothesis predicts that, even when chimpanzees sleep in woodlands, they sleep close to forests, especially during the dry season.

Finally, we hypothesized that chimpanzees would choose comfortable sites for sleeping (Koops et al. 2012), just as primates in temperate forests choose warm sites to facilitate thermoregulation (Wada et al. 2007). In contrast to tropical rainforests in the low flatlands of central Africa, savanna woodland areas are distributed in highlands and

hilly areas in eastern Africa. Because low altitude sites generally provide warmer temperatures (Salomons 2001), although this remains to be tested in Ugalla, our final hypothesis predicts that chimpanzees sleep at low altitude for thermoregulation.

To examine these five hypotheses, we conducted field surveys in the Ugalla area and performed geographic information system (GIS) analyses. The main objectives of this study were to examine habitat use by chimpanzees in terms of sleeping sites in the Ugalla area, to examine factors affecting sleeping site selection, and to discuss the adaptive strategies of savanna chimpanzees.

Methods

Study Area

Location Eastern chimpanzees (*Pan troglodytes schweinfurthii*) are distributed in the DRC, Uganda, Rwanda, Burundi, and Tanzania (Inskipp 2005). In Tanzania, they are distributed in western regions along the eastern shore of Lake Tanganyika (Kano 1972). We studied wild chimpanzees in the Ugalla area, Tanzania (5°09'–5°57'S, 30°23'–31°01'E). This area is 3352 km² with an elevation of 980–1712 m and is surrounded by the Ugalla River to the east, the Malagarasi River to the north, Uvinza-Mpanda Road to the west, and the Niamansi Basin to the south (Kano 1972; Hernandez-Aguilar 2006, 2009; Ogawa et al. 2007; Stewart et al. 2011; Fig. 1).

Climate Mean annual rainfall was 980 mm (750–1350 mm) from 1973 to 2005, as recorded by the Tanzanian Directorate of Meteorology at Uvinza (5°06'S, 30°23'E), at

the northwest edge of the Ugalla area (Ogawa et al. 2007). No rain fell between June and August during 16 of the 31 years recorded. Average monthly rainfall between May and October was 21 mm, and that between November and April was 148 mm. Because of this extended dry season and the local geographical and geological features (Sutton and Roberts 1968), most streams in Ugalla dry up during the dry season. In the present study, we divide the year into four equal periods, May–July, August–October, November–January, and February–April, for phenology surveys, and we consider the May–October and November–April periods to be the dry and the rainy seasons, respectively. Hernandez-Aguilar (2006, 2009) recorded daily maximum and minimum temperatures at the Issa site (05°25'S, 30°35'E) in the central Ugalla area from August 2002 to June 2003. These data showed that average daily maximum temperature was highest in August (34°C) and lowest in November (28°C), whereas the average daily minimum temperature was highest in January (17°C) and lowest in August (14°C).

Geography and Vegetation The Ugalla area consists two plains, plateaus in southwest Ugalla and basins in northeast Ugalla, intersected by slopes with steep scarps and valleys (Fig. 1). In Ugalla, there are three types of evergreen forests: small patchy forests at springs under cliffs and escarpments in slopes; valley forests along flowing water in slopes; and flat riverine forests in flatlands. While flat riverine forests are narrow and not necessarily continuous along streams, as most streams in flatlands dry up during the dry season, some of wide valley forests along slopes and patchy forests under escarpments keep water until the end of the dry season (Itani 1979; Kano 1972; Moore 1992, 1994; Ogawa et al. 1999, 2007). While the evergreen forests comprise only 2% and grasslands comprise 12 % of the area (Ogawa et al. 2007), most of the

Ugalla area is composed of savanna woodlands locally called “miombo” woodlands (Hernandez-Aguilar 2006, 2009; Itani 1979; Kano 1972; Moore 1992, 1994; Ogawa et al. 2007). Unlike evergreen forests, the ground of savanna woodlands is covered by C4 grasses. The woodlands in Ugalla are dominated by deciduous trees of *Brachystegia* and *Julbernardia*. Some trees in the woodlands lose their leaves during the dry season; however, leaf loss and flushing patterns vary so that some trees have leaves throughout the year.

Study Subjects

Chimpanzees live in a fission–fusion society of a multi-male and multi-female unit group (community) and form temporal sub-groups (parties) (Nishida 1968). Previous bed surveys have estimated that a total of 200–300 chimpanzees inhabit Ugalla, with a density of 0.07–0.09 individuals/km² (Ogawa et al. 2007; Yoshikawa et al. 2008). Genetic identification techniques have revealed that the size of a unit group at Issa was a minimum of 67 individuals (Rudicell et al. 2011). At Nguye, the largest sub-groups were composed of 14 individuals (determined by direct observation) and 23 individuals (determined by bed count) (Ogawa et al. 2007). At Issa, the largest sub-group was 26 individuals (determined by bed count; Stewart and Pruetz 2013), suggesting that chimpanzees in Ugalla formed small temporal sub-groups. Previous observations and bed counts have estimated that chimpanzees at Nguye and Bhukalai in Ugalla form temporal sub-groups of 2.0 individuals in the daytime and sub-groups of 5.0 individuals at night during the dry season (Ogawa et al. 2007).

Data Collection

Study Periods Ogawa, Yoshikawa, and/or Idani stayed in the Ugalla area for a total of 480 days from 1994 to 2012: 324 days during the dry season in 1994–1997, 1999, 2001, 2003, 2007, 2008, and 2010–2012, and 156 days during the rainy season in 1995, 2007, 2008, 2010, and 2011. We conducted line transect bed surveys, and line transect and quadrat vegetation surveys during certain portions of the study periods (Table 1).

Bed Survey We made line transects for bed surveys at the Mfuwazi, Nguye, Mufombosi, Bhukalai (Mogogwesi), Mtongesi, Bukombe, Shangwa, Issa Basin, Nkondwe, and Niamansi sites in the Ugalla area (Fig. 1, Table 1). Before each daily walk, we planned the transect for that day. We usually made a round trip from our riverside base camp to a plateau or a ridge between valleys. Using a 1/50,000 (1 cm to 0.5 km) map, a compass, and a global positioning system (GPS), we walked on not only traditional paths but also paths made by wild animals and off-paths along the nearly straight-line transects. When we found chimpanzee beds along the line transects, we recorded 1) species of the bed tree and 2) age class of the bed, categorized as new (all leaves were green), recent (some leaves were green), old (all leaves were not green), and disintegrating (no leaves). We also recorded 3) the perpendicular distance between the bed and the transect. We measured this distance using the footsteps of local guides, and after 2007, using a laser range finder (Nikon Laser 550AS).

We found chimpanzee beds when we were conducting surveys other than line transects. For example, when we were following or looking for chimpanzees, we found some beds along the non-transect walking routes. When we found beds along the line

transect and went there, we sometimes found additional beds. In these cases, we recorded the same information, with the exception of 3) the perpendicular distance between the bed and the transect.

Because several chimpanzees typically sleep together, we defined a bed cluster as ≥ 1 bed(s) located within 20m of the closest bed that appeared to have been made on the same day. When we found beds, we stood at the center of the bed cluster, at the midpoint between the edge of the beds, and recorded vegetation and location using GPS. Prior to 2003, we did not record the locations of some bed clusters by GPS but instead marked them on a 1/50,000 map.

We and our local assistants monitored two 5-km line transects at Nguye every 2 weeks for 1 year and recorded the presence of chimpanzee beds (Table 1). These two transects were also used as line transects for phenology surveys (see the next section).

Vegetation Survey We conducted vegetation surveys within 50×50 -m or 100×100 -m quadrats (2500 m^2 or $10,000 \text{ m}^2$) in a woodland and in a flat riverine evergreen forest at Nguye and in a evergreen forest dominated by *Monopetalanthus richardsiae* at Bhukalai (Ogawa et al. 2007; Table 1). Furthermore, we conducted vegetation surveys along straight 2-, 4-, or 5-km line transects (4-m wide) at Mfuwazi, Nguye, Bhukalai, Shangwa, Issa basin, Nkondwe, and Niamansi (Table 1). We established perpendicular transects across the river. We recorded species name, DBH, and the height of all trees that were ≥ 5 cm in DBH in the quadrats and transect areas. We used the line transects for vegetation and bed surveys.

Phenology survey Because all chimpanzee beds in Ugalla were made in trees with

mature unwithered leaves, and 99.8% of the beds were in trees of ≥ 5 -cm DBH (Ogawa et al. 2007), we regarded these trees as available trees for sleeping. We and our local assistants estimated the number of available trees by recording the leaves of each tree of ≥ 5 -cm DBH every 2 weeks for 1 year along two 5-km line transects at Nguye (Table 1). We recorded the proportion of mature unwithered leaves: 0 (<5%), 25%, 50%, 75%, and 100%. Based on these data, we calculated the relative amount of leaves that were available for sleeping using the following formula: (amount available leaves in forests) : (amount available leaves in woodlands) = (area [m^2] $\times$ tree density [trees/ m^2] $\times$ average proportion of mature unwithered leaves in each tree [%] in forests) : (area [m^2] $\times$ tree density [trees/ m^2] $\times$ average proportion of mature non-withered leaves in each tree [%] in woodlands).

Data Analysis

GIS Analysis by Vegetation and Topological Map We performed geographic information system (GIS) analyses using satellite images and 1/50,000 topological maps. We classified vegetation into four types: savanna woodland, evergreen forest, grassland, and other (which included areas such as cultivated fields and human settlements). When at a location where the vegetation appeared typical of the area, we recorded the vegetation and its location (longitude and latitude) using GPS to generate a vegetation map during the survey from 1999 to 2008. We recorded 349 points in savanna woodlands, 122 points in evergreen forests, 80 points in grasslands, 30 points in cultivated fields and human settlements. We generated a vegetation map of chimpanzee habitats in Tanzania using ERDAS Imagine (LGGM) based on satellite images (ETM+)

recorded on 1 November 2001 and 22 May 2002. Using a 90-m SRTM digital elevation model, we measured the angle (slope) of the ground. We also calculated the distance between each bed cluster and the edge of the nearest forest whose area was $\geq 10,000 \text{ m}^2$, using ArcGIS (ArcView 9.3.1) (ESRI).

Factor Analysis We used generalized linear mixed models (GLMM) and two-tailed, non-parametric statistical tests at a significance level of $p = 0.05$. We used R software 2.13.10 (R Development Core Team, 2011) and SPSS Statistics 19. Data are shown as means $\pm$ standard deviations (*SDs*) (minimum–maximum).

We analyzed conditions in the areas that contained one or more chimpanzee beds. Along the line transects drawn on a map, we drew a 30 + 30-m wide belt transects. This size was used because the detection rate of a chimpanzee bed was constant within 30 m from the line transect. We further divided the belts into 60 m from the start to the end of the transect for each day and drew 60×60 -m quadrats (3600 m^2). We omitted the fraction of the area at the end of the transect for each day as well as the overlapping areas where the transects crossed. Some of the transects were excluded from the GIS analysis because, prior to 2003, a GPS was not always taken on the walks, and the exact transects could not be determined. We then calculated a) the proportion of the area covered by forests, b) the average slope of the ground, and c) the average altitude in each 60×60 -m quadrat. For factor analyses, we conducted GLMM, for which we chose a), b), and c) as predictor variables, the number of beds as a response variable, and a Poisson distribution as the family of distribution. We also compared indices a), b), and c) in quadrats that contained ≥ 1 bed and in quadrats without beds.

Along the two 5-km bed and vegetation line transects at Nguye, we established a 30

+ 30-m wide belt, upon which we overlaid 166 60×60 -m quadrats. We compared the number of chimpanzee feeding trees within the transects (4-m wide) in quadrats with beds with those in quadrats without beds during each period.

Results

Bed Distribution and Bed Site Condition

We recorded a total of 1512 beds in 491 bed clusters, including 379 beds in 172 clusters within the quadrats (<30 m from the line transects) and the remaining 1133 beds in 319 bed clusters outside of the quadrats and along non-transect walking routes. All beds were located in trees, and no beds were found on the ground.

Along the line transects, we drew 8126 quadrats, for a total analysis of 487.6 km of belts in 29.3 km^2 . Because the quadrats were individually hand drawn on the map, the area of each quadrat was not exactly 3600 m^2 but rather $3564.7 \pm 508.1 \text{ m}^2$. In each quadrat, deciduous woodland occupied $90.3 \pm 21.9\%$ (0–100%), evergreen forest occupied $5.6 \pm 17.4\%$ (0–100%), and grassland occupied $4.1 \pm 15.0\%$ (0–100%) of the area. The slope of the ground was $5.7 \pm 5.1^\circ$ (0.01 – 33.5°), and the altitude was $1209 \pm 21.9 \text{ m}$ (1041 – 1621 m).

Within the belts, we found 379 beds in 172 bed clusters across 93 quadrats, whereas 8033 quadrats contained no beds. GLMM indicated that the proportion of evergreen forest had the strongest effect on the number of beds within quadrats, followed by slope of the ground and altitude. The model including the proportion of evergreen forests and slopes was selected as the best model ($AIC = 3500.5$, likelihood ratio χ^2 index = 462.9, p

< 0.05; Table 2), indicating that both variables affected bed distribution, although the slope angle was slightly correlated with the proportion of evergreen forest (Kendall rank correlation test, $n = 8126$, $\tau = 0.05$, $z = 7.3$, $p < 0.05$).

During the dry season, 52 beds in 17 bed clusters were new and recently made in 11 of 5844 quadrats. We analyzed each effect of the proportion of forest, slope of the ground, and altitude, because the interaction among them in GLMM was not significant. Comparisons of the conditions in quadrats with beds and without beds revealed that evergreen forest comprised more area in quadrats with beds ($41.8 \pm 49.4\%$ [0–100%]) than in those without beds ($3.7 \pm 14.3\%$ [0–100%]) (Mann-Whitney U test with Bonferroni adjustment, $n_1 = 11$, $n_2 = 5833$, $z = 4.0$, $p < 0.05/3 = 0.017$; Fig. 2a). The angle of the ground was steeper in quadrats with beds ($9.8 \pm 4.7^\circ$ [2.5–17.6°]) than in those without beds ($4.8 \pm 4.6^\circ$ [0.0–32.5°]) (Mann-Whitney U test with Bonferroni adjustment, $n_1 = 11$, $n_2 = 5833$, $z = 3.6$, $p < 0.017$; Fig. 2b). Altitude did not significantly differ between quadrats with beds (1205 ± 92.7 m [1096–1392 m]) and those without beds (1200 ± 120.0 m [1041–1549 m]) (Mann-Whitney U test with Bonferroni adjustment, $n_1 = 11$, $n_2 = 5833$, $z = 0.6$, n.s.; Fig. 2c).

During the rainy season, 109 beds in 56 bed clusters were new and recently made in 38 of 2282 quadrats. We analyzed each effect of the proportion of forest, slope of the ground, and altitude, because the interaction among them in GLMM was not significant. Similar to the dry season, evergreen forests comprised more of the area in quadrats with beds ($29.8 \pm 33.3\%$ [0–100%]) than in quadrats without beds ($4.5 \pm 115.3\%$ [0–100%]) (Mann-Whitney U test with Bonferroni adjustment, $n_1 = 38$, $n_2 = 2,244$, $z=9.4$, $p < 0.017$; Fig. 2a). In contrast to the dry season, the angle of the ground was less steep in quadrats with beds ($5.7 \pm 6.3^\circ$ [0.6–25.4°]) than in those without beds ($8.0 \pm 5.5^\circ$ [0.4–

33.5°]) (Mann-Whitney U test with Bonferroni adjustment, $n_1 = 38$, $n_2 = 2,244$, $z = -3.7$, $p < 0.017$; Fig. 2b). Altitude was higher in quadrats with beds (1246 ± 61.6 m [1150–1435 m]) than in those without beds (1236 ± 97.0 m [1103–1621 m]) (Mann-Whitney U test with Bonferroni adjustment, $n_1 = 38$, $n_2 = 2,244$, $z = 2.7$, $p < 0.017$; Fig. 2c).

The vegetation of some bed trees was not clear, because we could not identify the species of some bed trees, and some bed clusters straddled two vegetations. However, vegetation was clearly identified in 321 beds of 150 bed clusters within the quadrats. Of those beds, 175 (54.5%) were located in forests and 146 (45.5%) were in woodlands. If the grassland area was excluded, the proportions of forest and woodland in the remaining areas were 5.8% and 94.2%, respectively, indicating that more beds were located in forests than expected given the proportion of the forest area (χ^2 -test, $df = 1$, $\chi^2 = 1394.4$, $p < 0.05$). In addition, 135 new and recently made beds in 65 bed clusters revealed that more beds were located in forests than expected during both the dry (χ^2 test, $df = 1$, $\chi^2 = 504.6$, $p < 0.05$) and rainy (χ^2 test, $df = 1$, $\chi^2 = 888.4$, $p < 0.05$) seasons (Fig. 3).

However, the proportion of beds in forests during the rainy season was not greater than that during the dry season (χ^2 test, $df = 1$, $\chi^2 = 1.9$, n.s.). Additionally, we compared the actual and expected number of beds during each season based on leaf availability. The density of trees with a DBH ≥ 5 cm was 0.09 trees/m² in forests and 0.02 trees/m² in woodlands (see below). The proportion of mature unwithered leaves in each tree with DBH ≥ 5 cm was 77.7% in forests and 87.9% in woodlands during the rainy season, and 66.0% in forests and 86.2% in woodlands during the dry season. These findings indicate that (amount available leaves in forests) : (amount available leaves in woodlands) = 24.6% : 75.4% during the dry season, and 22.0% : 78.0% during the rainy

season, respectively. Comparison between the ratio of number of beds to the amount available leaves in forests and woodlands revealed that more beds were located in forests than expected during both the dry (χ^2 test, $df = 1$, $\chi^2 = 88.3$, $p < 0.05$) and rainy (χ^2 test, $df = 1$, $\chi^2 = 169.5$, $p < 0.05$) seasons (Fig. 3).

Among the bed clusters in woodlands, the farthest one was 614 m from the nearest evergreen forest. We found more bed clusters at the site closer to the forest (Kendall rank correlation test, $n = 7$, $\tau = -0.67$, $z = -2.1$, $p < 0.05$; Fig. 4). The distance between bed clusters and the nearest evergreen forest during the dry season (92 ± 74 m [7–313 m]) was shorter than that during the rainy season (184 ± 121 m [16–614 m]) (Mann-Whitney U test, $n_1 = 37$, $n_2 = 30$, $z = -3.8$, $p < 0.05$; Fig. 5).

Feeding Tree and Sleeping Tree

Table 3 shows data on the feeding and sleeping trees of chimpanzees. We identified the species of 719 sleeping trees in which beds were new and recently made. Chimpanzees made beds in 28 different tree species. Of these, they fed on fruits or legumes of 14 species, based on direct observation and fecal analyses (Yoshikawa and Ogawa unpublished data). If we divide the year into four periods according to the phenology of fruits and legumes, chimpanzees made 593 beds in feeding trees when they fed on the fruits or legumes of that tree; however, this number did not significantly differ from that expected by chance (χ^2 test, expected number = 573.4, $df = 1$, $\chi^2 = 3.3$, n.s.).

Along two 5-km bed and vegetation line transects at Nguye, we recorded 16 chimpanzee beds in seven quadrats during the 1-year monitoring period. Among the 664

quadrats ($166 \times$ four periods), the number of feeding trees within the vegetation transect line in quadrats with beds (2.7 ± 2.5 [0–4]) did not significantly differ from the number found in quadrats without beds (3.0 ± 2.7 [0–18]) (Mann-Whitney U test, $n_1=7$, $n_2=657$, $z=-0.98$, n.s.).

Vegetation

We recorded 443 trees with a DBH ≥ 5 cm in two 50×50 -m quadrats in forests at Bhukalai and Nguye and 232 trees in 100×100 -m quadrats in a woodland at Nguye (Ogawa et al. 2007). After reanalyzing the data, we found that trees in forests were denser (0.09 trees/m²) than those in woodlands (0.02 trees/m²) (χ^2 test, $df = 1$, $\chi^2 = 22.7$, $p < 0.05$). Additionally, trees ≥ 10 m in height were denser in forests (0.05 trees/m²) than in woodlands (0.02 trees/m²) (χ^2 test, $df = 1$, $\chi^2 = 101.1$, $p < 0.05$). Trees ≥ 20 m in height were also denser in forests (0.02 trees/m²) than in woodlands (0.01 trees/m²) (χ^2 test, $df=1$, $\chi^2 = 16.4$, $p < 0.05$), although the average tree height in forests (14.1 ± 7.9 m [3–35 m]) was shorter than was that in woodlands (17.9 ± 6.1 m [2–25 m]) (Mann-Whitney U test, $n_1 = 356$, $n_2 = 195$, $z = 6.9$, $p < 0.05$).

We recorded 3815 trees with a DBH ≥ 5 cm in 104,000 m² on slopes at Nguye, Bhukalai, and Nkondwe, and 1976 trees in 48,000 m² in flatlands at Shangwa, Mfuwazi, and Issa Basin (Table 1). Deciduous woodlands, evergreen forests, and grasslands occupied 91.2%, 3.2%, and 5.6% of the transect area, respectively. Trees on slopes (0.037 trees/m²) were less dense than were those in flatlands (0.041 trees/m²) (χ^2 test, $df = 1$, $\chi^2 = 17.7$, $p < 0.05$). However, trees on slopes (9.4 ± 6.5 m [1–32]) were taller than were those in flatlands (8.8 ± 5.3 m [1–34]) (Mann-Whitney U test, $n_1 = 3815$, $n_2 =$

1976, $z = 2.7$, $p < 0.05$). Additionally, trees ≥ 10 m in height were denser on slopes (0.014 trees/m²) than in flatlands (0.013 trees/m²) (χ^2 test, $df = 1$, $\chi^2 = 5.8$, $p < 0.05$). Trees ≥ 20 m were also denser on slopes (0.003 trees/m²) than in flatlands (0.002 trees/m²), but the difference was not significant (χ^2 test, $df = 1$, $\chi^2 = 0.5$, n.s.).

Discussion

Quadrats with chimpanzee beds contained a higher proportion of forest than did quadrats without beds. In addition, chimpanzees made beds in forests at a disproportionately high frequency given the overall percentage of the area that was covered by forests, similar to previous studies in Ugalla (Ogawa et al. 2007; Stewart and Pruetz 2013). Although some deciduous trees lose their leaves during the dry season, however, the proportion of beds in forests during the rainy season was not greater than that during the dry season. Moreover, the comparison of available sleeping trees according to tree density and seasonal change of mature unwithered leaves showed that chimpanzees slept in forests more frequently than expected during both the dry and rainy seasons. This finding indicates that the following factors other than the availability of sleeping trees might influence the distribution of chimpanzee beds. One of the possible factors is that chimpanzees may have slept in forests more often because forests are safer than woodlands. It may be also possible that chimpanzees select forests because they had more preferred tree species or because forest trees had more desirable sleeping locations, as chimpanzees chose certain tree species and certain locations in the trees for sleeping (Hernandez-Aguilar 2006, 2009; Hernandez-Aguilar et al. 2013; Ogawa et al. 2007).

485

486 In areas with few to no predators, chimpanzees sometimes construct ground beds
 487 (Koops et al. 2012). However, chimpanzees in Ugalla did not construct beds on the
 488 ground (Hernandez-Aguilar 2006, 2009; Ogawa et al. 2007), suggesting that the
 489 predation risk was high in this area. If chimpanzees on the ground in woodlands
 490 encounter carnivores in the daytime and evening before arriving at a sleeping site, they
 491 may have to run away on the ground due to low density and wide spaces between trees.
 492 Furthermore, it may be more difficult for chimpanzees to monitor the movements of
 493 terrestrial carnivores in the woodlands because of the high and abundant grasses; for
 494 example, lions can hide in bushes when they hunt (Ogutu and Dublin 2004). Woodlands
 495 would also likely be dangerous at night. This is supported by the fact that chimpanzees
 496 in Ugalla form larger sub-groups at night than in the daytime (Ogawa et al. 2007),
 497 assuming that chimpanzees form large sub-groups to reduce predation risk, although
 498 several other factors, such as food patch size and number of estrous females, may affect
 499 sub-group size (Matsumoto-Oda et al. 1998). If a carnivore can climb a tree,
 500 chimpanzees have difficulty passing through branches because the canopy is open in
 501 woodlands.

502 In contrast to the woodlands, the forests had more trees with $DBH \geq 5$ cm, more
 503 trees with $DBH \geq 5$ cm and ≥ 10 m in height, and more trees with $DBH \geq 5$ cm and ≥ 20 m
 504 in height. The intervals between trees were narrow, and the canopy was closed. If a
 505 carnivore climbs a tree containing sleeping chimpanzees in a forest, the chimpanzees
 506 are likely to pass through branches more easily and escape from the carnivore.
 507 Chimpanzees make higher tree beds if the predation risk is high (Pruetz et al. 2008),
 508 which is similar to other primates (Reichard 1998; Von Hippel 1998). Chimpanzees at

Issa in Ugalla made beds higher and at more peripheral locations within the tree than did chimpanzees in Fongoli that had no predators (Stewart and Pruetz 2013). These observations suggest that chimpanzees may choose safer places to reduce predation risk. As well as choosing safer places in a tree, chimpanzees may choose forests for their sleeping sites to reduce predation risk because forests should be safer than woodlands; thus supporting the predation pressure hypothesis. Direct evidence of predation pressure in the forests and woodlands in future studies can contribute to a better understanding of the predation pressure hypothesis.

Feeding efficiency is another potential factor affecting the choice of chimpanzee sleeping sites. Chimpanzees in Ugalla chose *Monopetalanthus richardsiae*, *Brachystegia bussei*, and *Pterocarpus tinctorius* as sleeping trees more frequently than expected from the density of the trees, and chimpanzees also feed on legumes of these trees (Ogawa et al. 2007). However, our study did not show that chimpanzees made more beds in or near their feeding trees during the period in which they actually fed on the fruits or legumes of that tree. Chimpanzees in Ugalla were more likely to sleep in forests, but they ate fruits and other parts of plants in both woodlands and forests (Hernandez-Aguilar 2006; Schoeninger et al. 1999; Yoshikawa and Ogawa unpublished data). Thus, the present study did not provide evidence to support the feeding efficiency hypothesis. This may be because the selection of sleeping sites is heavily influenced by predation pressure, as the predation risk is high in Ugalla. However, lack of evidence supporting the feeding efficiency hypothesis does not necessarily mean that the distribution of food resources is unrelated to sleeping site selection. An examination of feeding trees within a wider area around the sleeping trees

may reveal a relationship between sleeping trees and feeding trees, as previously reported (Furuichi and Hashimoto 2004).

The fact that chimpanzees made more beds in forests than expected indicates that water availability influenced the distribution of sleeping sites, as most available water in Ugalla was found in the evergreen forests along streams. Additionally, water is not readily available in the flatlands, and is restricted to the valley forests along slopes and the small patchy forests under escarpments in slopes during the dry season, whereas numerous pools exist in the woodlands and grasslands of the flatlands during the rainy season (Itani 1979; Kano 1972; Moore 1992, 1994; Ogawa et al. 1999, 2007). Although beds were not aggregated close to water pools at Issa (Hernandez-Aguilar 2006, 2009), when chimpanzees constructed beds in woodlands, more beds were located in woodlands that were closer to forests, and chimpanzees made beds closer to the forest during the dry season than during the rainy season. Furthermore, quadrats containing beds were located along steeper slopes than quadrats without beds during the dry season. These results indicate that chimpanzees preferred to sleep in or near forests and on slopes to obtain water from the forest valleys during the dry season.

The low correlation between the proportion of forests and slope of the ground and the best model in the GLMM analysis indicated that the fact that the chimpanzees frequently slept along slopes was not a byproduct of more forests being present along slopes and chimpanzee preference for forests. Similarly, chimpanzees did not shun flatland sleeping sites because of human activities, as chimpanzees also made few beds in the flatlands at Mfuwazi and Issa Basin, where permanent human habitation is absent. Chimpanzees may have chosen slopes as sleeping sites to reduce the risk of predation

because trees on the slopes were taller, and trees with ≥ 10 m in height were denser than trees in the flatlands. Chimpanzees may sleep along slopes to facilitate vocal communication with other chimpanzees (Piel and Moore 2007). During the rainy season, however, chimpanzees slept in gently sloping locations rather than along steep slopes. Neither the predation pressure hypothesis nor the vocal communication hypothesis could explain the seasonal differences in the relation between bed sites and slopes. Seasonal changes in the relationship between bed sites and slopes is best explained by the water availability hypothesis, although more direct data on water availability are needed to confirm this hypothesis.

Previous studies have shown that chimpanzees adjusted the height of themselves and their beds in trees according to the temperature of the air (Samson and Hunt 2012; Takemoto 2004). However, we found no significant relationship between bed sites and altitude during the dry season, and the altitude in quadrats with beds was 10 m higher than that in quadrats without beds during the rainy season. High altitude sites generally provide warmer temperatures (Salomons 2001), although there is no data in Ugalla. Thus, our evidence did not support the hypothesis that chimpanzees selected warm sleeping sites within their home range to facilitate thermoregulation. Data on temperature, humidity, and other factors are needed to test the physical comfort hypothesis.

Our findings provide insight into the possible habitat use of early hominins as they likely faced problems similar to those faced by chimpanzees in the savanna woodland areas (Moore 1992). Early hominins were under constant threat of predation pressure by

carnivores (Hart and Sussman 2005). Although habitat use in woodlands is also important, forests provide crucial vegetation for chimpanzees in open habitats (e.g., both the savanna woodland area in Tanzania and the grassland-forest mosaic area in Senegal) (McGrew et al. 1981; Moore 1992; Pruetz and Bertolani 2009; Stewart and Pruetz 2013). The habitats of hominins preceding *Homo erectus* also included forests (White et al. 2009). As long as early hominins constructed beds in trees, as do chimpanzees (Sept 1998), they may have used forests as safe sleeping sites, possibly to avoid the risk of predation. Moreover, early hominins may have preferred to live in or near forests and on slopes, possibly to obtain water from the valleys. Until hominins began to use vessels or other inventions to keep or obtain drinking water, they could not have changed their ranging patterns, similar to savanna chimpanzees.

Factors affecting sleeping site selection by chimpanzees vary with the conditions of each study site (Basabose and Yamagiwa 2002; Furuichi and Hashimoto 2004; Koops et al. 2012; Pruetz et al. 2008; Stanford and O'Malley 2008; Stewart et al. 2007). Although the present study found no evidence to support the feeding efficiency and physical comfort hypotheses, our findings supported the predation pressure and water availability hypotheses. Chimpanzees selected forests as their sleeping sites, possibly to reduce the risk of predation. Chimpanzees preferred to sleep in or near forests and on slopes during the dry season, possibly to obtain drinking water. Although further surveys are needed to provide more direct evidence, our findings on the distribution of chimpanzee beds suggests that predation pressure and water availability are important factors in the selection of sleeping site by chimpanzees in the Ugalla savanna woodland area.

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Fig. 1 The Ugalla study area in Tanzania

Fig. 2 Conditions in quadrats containing chimpanzee beds in Ugalla

Figure legend

(a) Percentage of evergreen forest area, (b) slope angle of the ground, and (c) altitude are compared between the 60×60-m quadrats containing new or recently made chimpanzee beds and the quadrats without beds. Dry: during the dry season. Rainy: during the rainy season. With beds: quadrats containing beds. Without beds: quadrats without beds. Asterisks indicate significance at $p < 0.05$.

Fig. 3 Number of beds in forests and woodlands in Ugalla

Figure legend

Recorded: number of beds recorded by bed surveys. Expected: number of beds expected based on relative leaf availability estimated by area, tree density (trees/m²), and proportion of mature unwithered leaves in each tree in forests and woodlands (see text). Forest: beds in forests. Woodland: beds in woodlands. Dry: during the dry season. Rainy: during the rainy season. Asterisks indicate significance at $p < 0.05$.

Fig. 4 Location of bed clusters in woodlands in Ugalla

Figure legend

Numbers of bed clusters in woodlands are shown with the distance between each bed

cluster and the edge of the nearest evergreen forest with area $\geq 10,000 \text{ m}^2$.

Fig. 5 Distance between bed clusters and the nearest forest in Ugalla

Figure legend

The distance (m) between bed clusters and the nearest evergreen forest during the dry season and the rainy season are shown. Dry: during the dry season. Rainy: during the rainy season. An asterisk indicates significance at $p < 0.05$.

Table 1 Study sites and surveys in the Ugalla area

Site name	Location		Bed line transect		Vegetation line transect					
	Latitude	Longitude	Distance (km)	Date (dd/mm/yy)	Area	Vegetation ⁽¹⁾	Altitude		Topography ⁽²⁾	Date (dd/mm/yy)
							Lowest	Highest		
Mfuwazi	05°12' S	30°38' E	28.0	09/08/1995 & 09-11/08/2008	2km×4m	W & F	1,040	1,050	F	10/08/2008
Nguye (Ngya)	05°13' S	30°28' E	153.8	23-29/07/2001, 31/07-20/08/2003, 25/12/2007-04/01/2008, & 31/12/2010-09/03/2011	5km×4m	W & F	1,120	1,260	H	25-29/12/2007 ⁽³⁾
					5km×4m	W & F	1,120	1,260	H	30/12/2007-04/01/2008 ⁽³⁾
					100m×100m	W	1,140	1,140	H	18/08/1997
					50m×50m	F	1,110	1,110	H	01-04/11/1995
Mufombosi	05°15' S	30°39' E	40.7	02-05/08/1997	-	-	-	-	-	-
Bhukalai (Mogogwesi)	05°27' S	30°44' E	47.8	02-26/08/1996	4km×4m	W & F	1,240	1,370	H	23-30/08/1995
					4km×4m	W & F	1,260	1,400	H	07-08/08/1996
					50m×50m	F	1,300	1,300	H	01-04/09/1995
Mtongesi	05°28' S	30°48' E	52.6	11-13/08/1997	-	-	-	-	-	-
Bukombe	05°32' S	31°00' E	55.7	08-10/08/1997	-	-	-	-	-	-
Shangwa	05°36' S	30°45' E	43.4	10-14/08/1996	4km×4m	W & F	1,490	1,510	F	11-13/08/1996
Issa Basin	05°38' S	30°46' E	52.1	23-27/02/2003 & 11-13/08/2008	2km×4m	W & F	1,100	1,110	F	12/08/2008
Nkondwe	05°56' S	30°57' E	13.3	20-22/08/2008	4km×4m	W & F	1,170	1,320	H	15-16/08/1996
					4km×4m	W & F	1,170	1,380	H	23-26/08/2008
Niamansi ⁽⁴⁾	05°57' S	30°58' E	8.5	31/08-02/09/2005	4km×4m	W & F	1,120	1,180	F	31/08-01/09/2005
					4km×4m	W & F	1,140	1,200	F	25-26/08/2008

(1) W: Woodland, F: Forest

(2) F: Flatland, H: Hill

(3) Along these transect lines, we monitored chimpanzee beds for 1 year beginning on 4th Jan. 2008, and seasonal changes in leaves for 1 year beginning on 1st Sept. 2010.

(4) The bed and vegetation transects in Niamansi were not included in the analysis, because this area is outside the distribution of chimpanzees.

Table 2 Factors affecting sleeping site selection by chimpanzees in Ugalla

Predictor variable	Coefficient	SE	Wald χ^2 index	<i>p</i> value	Coefficient*	SE*
% of evergreen forest	0.480	0.201	568.1	<0.05	0.468	0.063
Angle of the ground	0.332	0.041	65.4	<0.05	0.373	0.020
Altitude	0.286	0.052	30.3	<0.05	-	-

*: Coefficient and standard error (SE) in the selected model

Table 3 Sleeping trees and feeding trees of chimpanzees in the Ugalla area

Species	Feeding part	Number of sleeping trees				Total
		Dry season		Rainy season		
		May-July	Aug.-Oct.	Nov.-Jan.	Feb.-April	
<i>Albizia glaberrima</i> and/or <i>amara</i>			3	8		11
<i>Anisophyllea pomifera</i> and/or <i>boehr</i>	Fruit		<u>1</u>			1
<i>Brachystegia boehmii</i>			1		4	5
<i>Brachystegia bussei</i>	Legume	<u>0</u>	19	5	1	25
<i>Brachystegia spiciformis</i>	Legume	<u>0</u>	17			17
<i>Combretum moll</i>					1	1
<i>Combretum zeyheri</i>					2	2
<i>Craibia grandiflora</i> and/or <i>microcarpa</i>			4		4	8
<i>Ficus</i> spp.	Legume	<u>0</u>	<u>3</u>	<u>0</u>	<u>0</u>	3
<i>Garcinia huillensis</i>	Fruit		<u>1</u>			1
<i>Garcinia volkensii</i>	Fruit		<u>2</u>			2
<i>Isobertlinia angolensis</i>	Legume	<u>0</u>	5			5
<i>Julbernardia paniculata</i>			3			3
<i>Julbernardia unijugata</i>	Legume	<u>65</u>	<u>182</u>	6	4	257
<i>Maesa lanceolata</i>			7			7
<i>Markhamia obtusifolia</i>				1		1
<i>Monopetalanthus richadsiae</i>	Legume	<u>37</u>	<u>281</u>	17		335
<i>Multidentia crassa</i>	Fruit	<u>0</u>	<u>1</u>	<u>0</u>	<u>0</u>	1
<i>Pachystela brevipes</i>			5			5
<i>Parinari curatellifolia</i>	Fruit	<u>0</u>	<u>4</u>	<u>0</u>	<u>0</u>	4
<i>Pericopsis angolensis</i>			3			3
<i>Pseudospondias microcarpa</i>	Fruit		<u>0</u>	<u>0</u>	1	1
<i>Pterocarpus tinctorius</i>	Legume	<u>0</u>	<u>1</u>	<u>2</u>	1	4
<i>Syzygium guineense</i>	Fruit		<u>7</u>	<u>6</u>		13
<i>Techlea trichocarpa</i>			1			1
<i>Temnocalyx</i> sp.			1			1
<i>Trichilia dregeana</i>			1			1
<i>Vitex ferruginea</i>			1			1
Total		102	554	45	18	719

The number of trees in which beds were new or recently made are listed.

Old and disintegrating beds were also recorded in *Albizia versicolor*, *Annona senegalensis*, *Brachystegia microcarpa*, *Brachystegia microphylla*, and *Embelia schimperi*.

Underlined: The period when chimpanzees fed on fruits or legumes of the tree.

[illegible]

Fig. 2 Conditions in quadrats containing chimpanzee beds in Ugalla

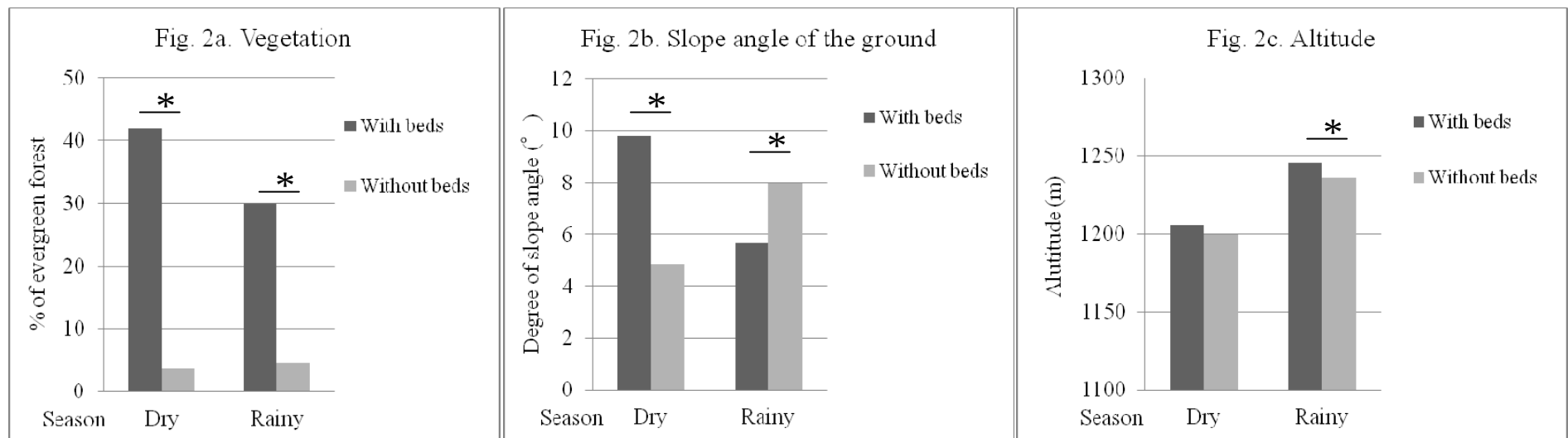


Fig. 3 The number of beds in forests and woodlands in Ugalla

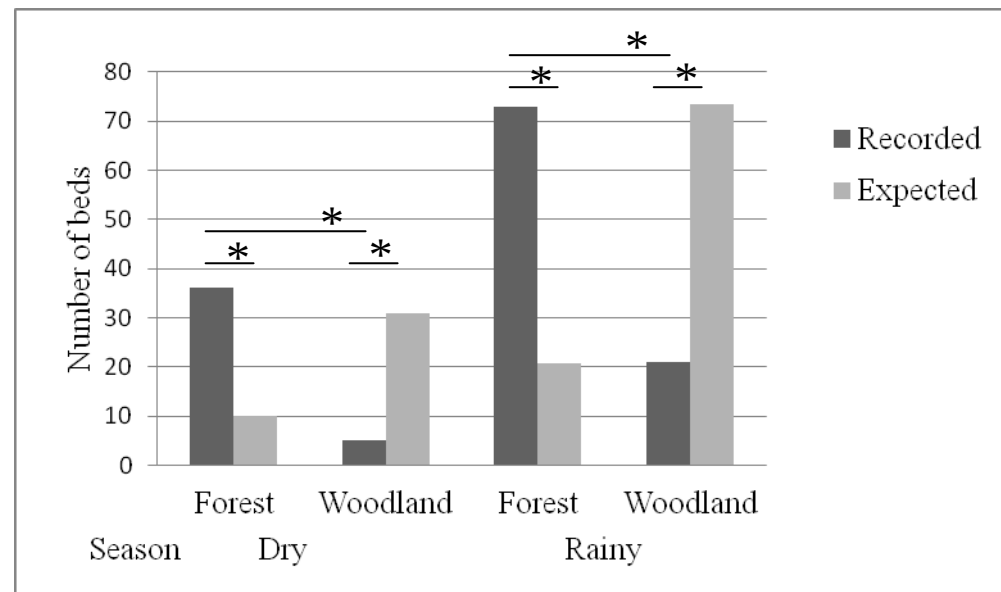


Fig. 4 Location of bed clusters in woodlands in Ugalla

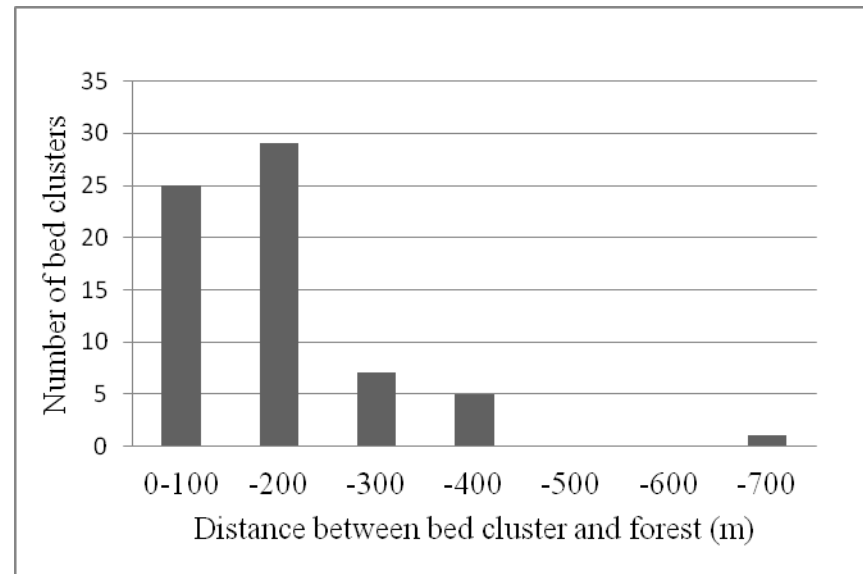


Fig. 5 Distance between bed clusters and the nearest forest in Ugalla

