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Ecological features and ranging patterns at a chimpanzee release site on Rubondo Island, Tanzania

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ABSTRACT

This study examines the behavioral ecology of a chimpanzee population on Rubondo Island in Lake Victoria, Tanzania, over 40 years after chimpanzees were first introduced to the island from captivity. Despite little pre-release habitat assessment, rehabilitation, or post-release monitoring, these chimpanzees are one of the only released populations to survive over decades without provisioning. We surveyed habitat structure and plant composition to gain insights into ecological features that have supported this self-sufficient chimpanzee population for over 40 years. We also examined possible ecological sources of chimpanzee ranging patterns on the island. We surveyed woody plant composition, and quantified densities of species producing large fleshy fruits and confirmed chimpanzee fruit foods across three chimpanzee ranging areas, each separated by several kilometers. We used non-metric multidimensional scaling (NMS) ordination to compare community-level patterns of plant composition across regions. The densities of trees and lianas producing fleshy fruits were high in comparison with similar measures at endemic chimpanzee study sites. There were major differences in the composition of tree species, including species of chimpanzee fruit foods, across the three regions. In contrast, liana species composition was similar across regions, and was characterized by a few super-abundant species, including one chimpanzee fallback food. The wide-ranging patterns of chimpanzees do not appear to be influenced by localized tree fruiting patterns, but may be facilitated by the wide-spread distribution of an important fallback food. In comparison with other endemic and release sites, the relatively low ecological population density of chimpanzees, the high density of both trees and lianas producing large fleshy fruits and the presence of a high-quality, widely-distributed fallback food are factors that likely contributed to the success of Rubondo chimpanzees in reverting to natural foraging behaviors after their release.

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1. Introduction

Wild chimpanzee (*Pan troglodytes* sp.) populations have suffered drastic declines in recent decades (Butynski, 2003; Campbell et al., 2008), stemming from human population growth and resulting habitat loss, hunting pressures and disease transmission (Butynski, 2001). Currently chimpanzees face local extinctions in areas previously considered to be their last strongholds (Walsh et al., 2003; Campbell et al., 2008; Greengrass, 2009). Given the severity of threats to wild populations a diverse range of conservation approaches should be considered. Reintroduction of chimpanzees from captivity is one strategy to help restore dwindling wild populations (Goossens et al., 2005; Beck et al., 2007).

In recognition of the potentially important role of release efforts from captivity for the conservation of chimpanzees and other great apes, the International Union for the Conservation of Nature (IUCN) has recently published updated guidelines for reintroductions of great apes (Beck et al., 2007). Reintroductions typically refer to attempts to re-establish a species within its historic range, in an area where it is locally extinct (Beck et al., 2007). Other strategies, including the introduction of a taxon to an ecologically-appropriate habitat outside of its recorded distribution, are also recognized as potential conservation tools, with success of any effort measured by the establishment of a nutritionally self-sufficient population (Beck et al., 2007). Evaluations of previous and on-going release efforts will help in developing guidelines to insure the long-term viability of released populations, before this knowledge

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may become critical to protect chimpanzees from extinction (Goossens et al., 2005).

To date, there have been at least nine documented releases of chimpanzees from captivity to free-ranging conditions (reviewed in: Hannah and McGrew, 1991; Farmer et al., 2006). The subjects of releases are typically wild-born chimpanzees that have spent varied periods of time in captivity, either in sanctuaries after being rescued from the live trade market (e.g. Tutin et al., 2001), in zoos (e.g. Borner, 1985) or in research laboratories (e.g. Hladik, 1977). Many releases have been motivated by welfare concerns for captive chimpanzees housed in increasingly over-crowded and under-funded sanctuaries (Farmer, 2002a). Welfare-motivated releases have often occurred on islands, where released chimpanzees are safe from anthropogenic activity and also from potentially fatal encounters with aggressive and territorial conspecifics (Brewer Marsden et al., 2006). At most island release sites chimpanzees have required indefinite provisioning, due to inadequate space and natural resources to sustain populations over the long-term (reviewed in Hannah and McGrew, 1991). The IUCN has suggested that such outcomes may be best characterized as semi-naturalistic sanctuaries (Beck et al., 2007).

Of the previous chimpanzee releases, only two meet one of the IUCN's main criteria for evaluating the success of a reintroduction effort: the establishment of viable, self-sustaining populations over the long-term (Beck et al., 2007; Soorae, 2008). Between 1996–2005, Habitat Ecologique et Liberte des Primates (HELP), re-introduced 37 wild-born, orphaned chimpanzees to the Conkouati-Douli National Park, Republic of Congo (Tutin et al., 2001; Farmer et al., 2006). Most of the chimpanzees originated in the same region as the park (Farmer, 2002b). The reintroduction occurred in a three-step process during which chimpanzees were first rehabilitated in a sanctuary adjacent to the park, then moved to small forested islands that contained microhabitats of the release site flora, and eventually released to the 'Triangle', a 21 km^2 area bordered by rivers and a lagoon and connected to the 5400 km^2 national park by a series of natural bridges (Tutin et al., 2001). At most recent report, at least 62% (and up to 86%) of the released chimpanzees have survived, and the majority have been observed in association with wild chimpanzee groups for varying periods of time (Goossens et al., 2005). The success of this project in establishing a self-sustaining population is attributed to the pre-release rehabilitation process and extensive post-release monitoring (Tutin et al., 2001; Goossens et al., 2005).

The only other self-sustaining chimpanzee population resulting from a release effort is on Rubondo Island National Park, Tanzania (Moscovice et al., 2007; Huffman et al., 2008). Between 1966–1969, the Frankfurt Zoological Society (FZS) released 17 chimpanzees onto the island, in the first documented release of chimpanzees from captivity to the wild (Grzimek, 1970; Hannah and McGrew, 1991, see Table 1). The chimpanzees were wild born from multiple countries, all purportedly in West Africa (Grzimek, 1970). They had been housed in private homes, circuses and zoos across Europe in environments ranging from group-living to solitary housing. Unlike the circumstances surrounding the Conkouati release, the Rubondo chimpanzees were introduced to a habitat outside of their historic distribution. In addition, FZS used a 'hard release strategy', indicating a lack of pre- or post-release efforts to facilitate adjustments to the release site (Beck et al., 2007). Rubondo chimpanzees were not rehabilitated after their time in captivity nor trained in any necessary survival skills prior to their release. After their release chimpanzees received supplemental provisioning and were monitored for only a few months, before staff were forced to leave the island due to escalated aggression by the chimpanzees (Grzimek, 1970; Borner, 1985). A brief report nearly two decades later confirmed that the remaining founders and a second generation of chimpanzees inhabited the island and had reverted to an unhabituated state (Borner, 1985). In 1997, FZS, in collaboration with Tanzania National Parks (TANAPA), initiated a habituation project. Beginning in 2001, Huffman, Moscovice and colleagues initiated research on chimpanzee behavioral ecology (Moscovice et al., 2007) and health status (Hasegawa et al., 2005; Petrzelkova et al., 2006, 2010). The current size of the semi-habituated population is estimated at 27–35 individuals, based on limited direct observations and nest counts (Moscovice et al., 2007).

Past primate reintroduction efforts highlight a range of factors that can influence long-term outcomes. Such factors include: adequate health and genetic screening of release stock (Tutin et al., 2001), the duration and conditions of captive housing prior to release (Soorae, 2008) and training in critical survival skills (Box, 1991; Beck et al., 2002). The quality of the habitat at the release site is also an important factor that can influence long-term viability (Cheyne, 2006) and expression of species-typical behaviors post-release (Le Hellaye et al., 2010). This study describes ecological features at a long-term chimpanzee release site on Rubondo Island, focusing on features of direct relevance to chimpanzee foraging and ranging patterns. Practitioners have proposed several broad ecological features that may influence release site habitat suitability for chimpanzees, including availability and abundance of a diverse range of fruit food resources, extent of seasonality in food availability and presence of adequate fallback foods (Balcomb et al., 2000; Tutin et al., 2001; Beck et al., 2007). However, there have been few publications providing quantitative data on these features from current release sites.

We focused our ecological assessment within regions of the island that were heavily utilized by chimpanzees, based on a pilot study (Moscovice, 2006). We compared plant composition across forest blocks separated by several kilometers to characterize food availability and to determine whether chimpanzee ranging patterns were influenced by regionally-distinct plant fruiting patterns, similar to findings from several endemic sites (e.g. Chapman et al., 1997; Furuichi et al., 2001). A better understanding of Rubondo chimpanzees' ranging patterns has practical implications for improving habituation and making informed management decisions.

We conclude by comparing ecological features on Rubondo Island with other endemic chimpanzee study sites, and with two other release sites where detailed ecological data are available: Ipassa Island, Gabon (Hladik, 1973, 1977; Hladik and Halle, 1973) and Conkouati Reserve, Republic of Congo (Tutin et al., 2001; Farmer, 2002b; Farmer et al., 2006). Through these comparisons we highlight specific ecological features associated with the establishment of viable, self-sustaining released chimpanzee populations.

Table 1
Background information on the 17 founder chimpanzees released to Rubondo Island. *Sources*: Grzimek (1970) and Borner (1985).

Cohort	Date of release	No. of females	No. of males	Estimated age at release (median and range)	Countries of origin
1	June, 1966	7	4	8.5 (4–11.5)	Cote d'Ivoire, Sierra Leone, Guinea, Unknown
2	October, 1966	0	1	7.5	Unknown
3	January, 1968	0	1	8.5	Unknown
4	June, 1969	2	2	9.5 (9–10)	Unknown

2. Materials and methods

2.1. Study site

Established in 1977, Rubondo Island National Park is a 240 km^2 island located in the Southwestern portion of Lake Victoria, Tanzania (2°18′S, 31°50′E), with an altitudinal range of 1134–1485 m above sea level (see Fig. 1). Up to 81% of the island consists of mid-elevation forest, based on a survey of forest cover across East Africa (Chapman and Chapman, 1996). During a 3-month pilot study, we conducted a broad survey of ecology and chimpanzee presence across the island (Moscovice, 2006). We identified six habitats using established East African vegetation types (Lind and Morrison, 1974). In evergreen forest habitats the canopy reaches 35 m, and common species include *Antiaris toxicaria* and *Lecaniodiscus fraxinifolius*. Semi-deciduous forest is primarily found on hillsides, with a canopy up to 25 m and common tree species including *Croton sylvaticus* and *Drypetes gerrardii*. In wooded grassland, trees cover <20% of the area, and typical tree species include *Parinari curatellifolia* and *Annona senegalensis*. Grassland is more common in the southern-most portion of the island and is characterized by *Loudetia simplex* and *Panicum maximum* grasses. Riparian forest occurs in close proximity to the lake shore and is dominated by *Phoenix reclinata* and *Pseudospondias microcarpa*. Papyrus swamp occurs at the shoreline, characterized by *Cyperus papyrus* and *Cyperus difformis* sedges.

During the pilot study, all direct sightings and recent indirect evidence of chimpanzees occurred within evergreen forest, semi-deciduous forest and wooded grassland habitats associated with ridges rising 1200–1400 m a.s.l. (Moscovice, 2006). Outside of these areas, the only other evidence of chimpanzees occurred in the southern portion of the island, where we found nest sites judged to be several months old based on their state of decay. Based on the more open habitat in the south, and the lack of any recent chimpanzee activity in these areas, we focused subsequent monitoring efforts on the three regions where chimpanzee evidence was concentrated.

Total rainfall in 2003 (the year of this study) was 1 461 mm, with an average minimum temperature of 17.2 °C (SD 1.8) and an average maximum temperature of 29.4 °C (SD 1.1). There were two rainy seasons, from March–May and from October–December, a short dry season from January–February, and a longer dry season

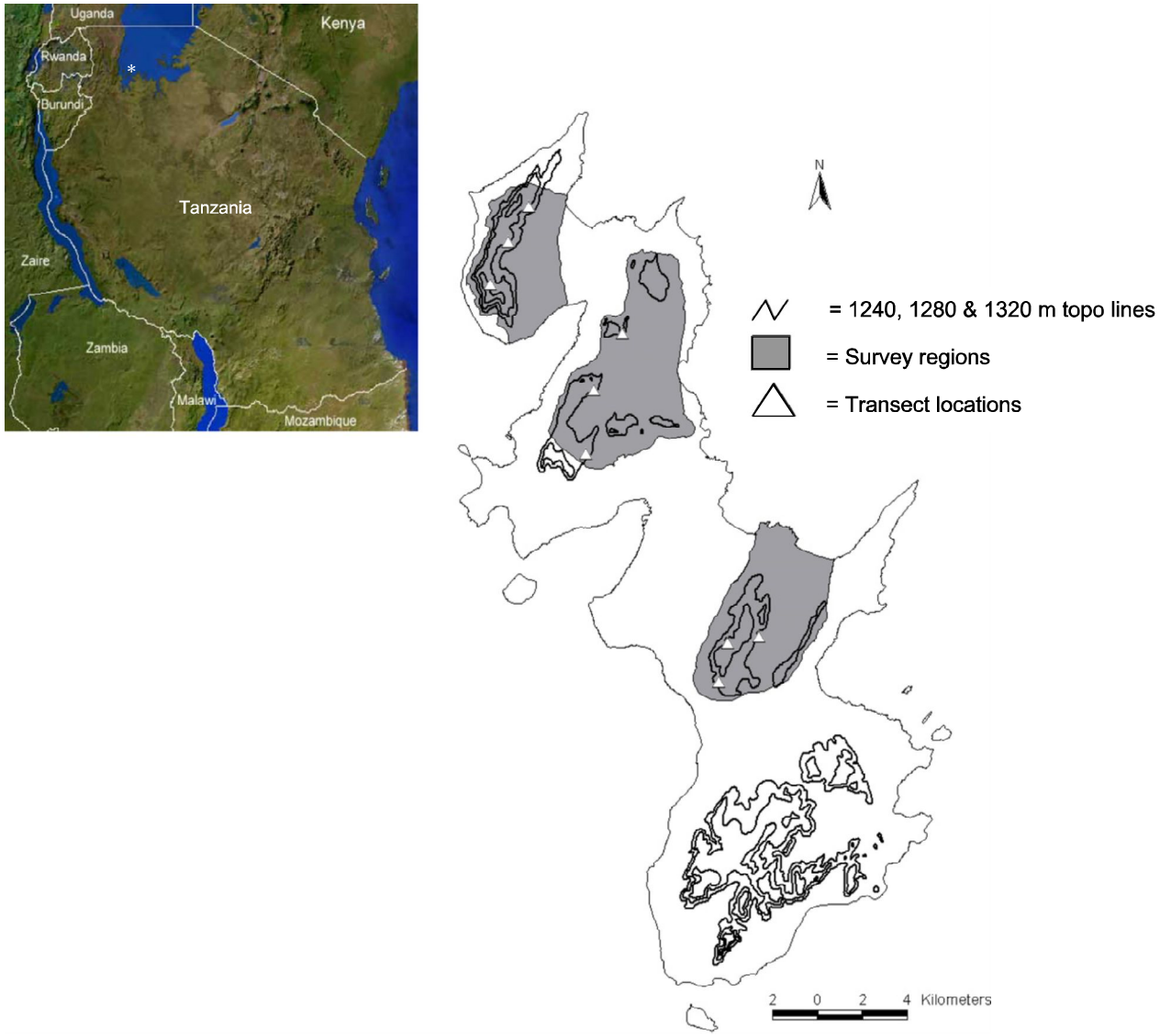


Fig. 1. Map of Tanzania and Lake Victoria, with the location of Rubondo Island indicated by an asterisk. Inset map of Rubondo Island indicates the location of transects within main chimpanzee ranging areas.

from June–September, where rainfall was below 60 mm per month (Moscovice et al., 2007). Habitat-wide tree fruit availability decreases between January–March and July–September, corresponding with the dry seasons. Liana fruiting patterns remain fairly constant across seasons (Moscovice et al., 2007). Chimpanzees increase their reliance on the fruit of a liana fallback food, *Saba comorensis*, during the long dry season (Moscovice et al., 2007).

Common large terrestrial native mammals on the island include sitatunga (*Tragelaphus spekeii*), bushbuck (*Tragelaphus scriptus*) and vervet monkeys (*Chlorocebus aethiops*). Since the 1960s, FZS has released several other non-native species to the island, including: giraffe (*Giraffa camelopardalis*), elephants (*Loxodonta africana*), suni (*Neotragus moschatus*), black and white colobus (*Colobus guereza*) and chimpanzees (Borner, 1985).

2.2. Plant survey

Building on criteria proposed by Balcomb and colleagues (2000) to characterize habitat quality for chimpanzee releases, we quantified the abundance of trees and lianas producing large, fleshy fruits (>1.5 cm in length) within main chimpanzee ranging areas. We also determined the abundance of trees and lianas producing any confirmed chimpanzee fruit foods. We established transects across the three regions of heavy chimpanzee utilization based on our pilot study (Moscovice, 2006; see Fig. 1). These regions are designated north, central and south, based on their location along the longitudinal gradient of the island, and are separated from each other by 4–16 km. Each region is between 14–23 km^2. We placed three transects, between 300–500 × 10 m in each region in a stratified random procedure, for a total tree survey area of 2.15 ha. We distinguished habitat type within 25 × 10 m quadrats on transects, based on six categories: evergreen forest, semi-deciduous forest, riparian forest, wooded grassland, grassland or papyrus swamp. We also recorded elevation with a Suunto® Electronic Altimeter/Barometer (accuracy ±10 m). All trees with ⩾10 cm diameter measured at 1.3 m above ground (diameter at breast height, DBH) were tagged, DBH was recorded and trees were identified to species level when possible.

We randomly selected six quadrats from each transect for liana monitoring, for a total liana survey area of 0.42 ha. Within these quadrats, we established a circular liana plot beginning at the center of the quadrat with a radius of 5 m (area = 78.5 m^2). We measured the DBH of lianas ⩾1 cm rooted within the circular plot and supported by tagged trees within the plot, and recorded the number of distinct lianas supported by each tree. Lianas were identified to species level when possible. Species within *Uvaria*, *Salacia* and *Capparis* genera could not be consistently identified to species level, and were grouped at the genus level for analyses.

From February–December 2003, we conducted phenological monitoring of trees and lianas on the subset of quadrats where both plant types were measured. We counted the number of trees in fruit and also counted the number of liana fruit patches, defined as a tagged tree supporting fruiting lianas. We combined measures of ripe and unripe fruit, due to difficulty distinguishing between different maturation stages for some species. For further details on transects and phenological monitoring refer to Moscovice and colleagues (2007). F.M. made plant identifications based on on-site classifications and vouchers analyzed at the University of Dar es Salaam Herbarium. Plant classifications follow Beentje (1994, 2002). Moscovice and colleagues (2007) identified fruits eaten by chimpanzees based on limited direct observations and fecal analyses.

2.3. Chimpanzee evidence

From January–December 2003, chimpanzee tracking occurred on 22.1 (SD 4.7) days per month. Between one to three teams, consisting of L.M. and trained assistants, were distributed across the three regions on each tracking day. The available teams alternated regions across days and attempted to evenly monitor all three regions within each month. During tracking, the location of any fresh chimpanzee evidence was recorded to within 10–50 m accuracy using Garmin© e-trex Global Positioning System (GPS) units. Fresh chimpanzee evidence consisted of any of the following: direct sightings, vocalizations without sightings, fresh nests (determined to be between 0–2 days old based on the abundance of fresh leaves in the nest) and other fresh traces, including chimpanzee feces, tracks and/or food remains estimated to be between 0–2 days old.

Consistent with other chimpanzee studies, we define home range as the fraction of the entire range that is habitually used (e.g. Newton-Fisher, 2002; Amsler, 2009). We used the minimum convex polygon (MCP) method to estimate home range, considered the most reliable method for inter-site comparisons of ranging area (Newton-Fisher, 2002). An MCP is the smallest area polygon to encompass all location points (Rodgers and Carr, 1998). Occasional excursions outside of the main ranging area are not considered representative of home range (Newton-Fisher, 2002), but can strongly influence MCP estimates (Rodgers and Carr, 1998). As a result, many chimpanzee home range estimates use an adjusted 95–99% MCP (e.g. Herbinger et al., 2001; Williams et al., 2004), based on exclusion of a subset of data points furthest from the arithmetic center of all x and y coordinates. We calculated MCPs based on location data from all fresh chimpanzee evidence (n = 455), using the home range extension for ArcView 3.2 (Rodgers and Carr, 1998). For the minimum home range estimate, we calculated 99% MCPs in each of the three survey regions, summed these MCPs and added an additional 9 km^2, for the minimum number of sq. km grid cells that must be crossed to move across the three regions. For the maximum home range estimate, we calculated one 99% MCP that connected independent chimpanzee locations across the entire study site, subtracting the area of the resulting polygon that was outside of the island boundaries.

Most daily chimpanzee evidence within a region was found within a relatively short distance and likely represented repeated evidence from the same chimpanzee group. Inclusion of non-independent location data collected at short time intervals can improve the accuracy of home range estimates such as the MCP (Amsler, 2009), but violates assumptions of independence for statistical analyses. For all statistical analyses of ranging, we included a maximum of one location of confirmed chimpanzee evidence per region per tracking day (n = 168). We also conducted an analysis using a larger data set of all daily chimpanzee evidence that could not be directly attributed to a continuous follow of the same chimpanzee group (n = 257). The results of the two tests were the same, and we report only the results of statistical tests using the smaller data set including a maximum of one location per region per tracking day.

2.4. Analyses

We used one-way analysis of variance (ANOVA) with posthoc Tukey's HSD tests to compare broad-scale habitat features across regions, and chi-square tests to compare chimpanzee habitat utilization across seasons. We used the non-metric multidimensional scaling (NMS) ordination analysis (Kruskal, 1964) to examine community-level patterns of tree and liana species composition on transects. NMS ordinations extract the strongest patterns of inter-correlation in biological data and produce a plot in multiple dimensions representing the degree of similarity in the data, with axes that can be related to measured environmental variables. The goodness of fit of the final model is determined by the stress, a measure of the degree of departure from monotonicity in the data.

Stress ranges from 0–100, with smaller values indicating a more stable configuration of the data.

We performed two NMS ordinations, one on tree species abundance on transects and one on liana species abundance on transects, using the PC-ORD software package, and the Sorensen distance measure to compute floristic similarities among transects (McCune and Grace, 2002). We stipulated 100 runs with the data, with iterations from four dimensions to one dimension. The number of dimensions with the lowest stress was selected for the final model. We also ran a Monte Carlo test using 100 runs with randomized data, to test whether the observed ordination structure provided a better fit to the data than expected by chance (McCune and Grace, 2002). We overlaid regional categories on the final plot, and used joint plots, or fitted vectors, to examine how elevation and the densities of specific tree and liana species related to the ordination axes. The length and direction of a joint plot is based on the strength of the correlation between a variable and the ordination axes (McCune and Grace, 2002). Variables with the strongest patterns of correlation with the ordination structure, based on Pearson r^2 values >0.55 with one or more of the axes, were further tested for statistical differences among regions using one-way ANOVAs with posthoc Tukey's HSD tests.

Trees not identified to species level and lianas not identified to genus level were omitted from ordinations and calculations of species diversity, but were included in measures of tree and liana abundance. ANOVAs and chi-square tests were performed with SPSS© version 16. Results are presented as X (SD). All tests are two-tailed with $\alpha = 0.05$.

3. Results

3.1. Habitat type and elevation

The dominant habitat type across all transects was semi-deciduous forest, which occurred on 87.2% ($n = 75$) of quadrats. The other less common habitat types on transects were: evergreen forest, found mainly in valleys between ridges ($n = 4$ quadrats) and wooded grassland, typically found on hilltops ($n = 7$ quadrats). There were significant differences in mean quadrat elevation on transects in different regions ($F_{2,6} = 8.38$, $p = 0.018$). Transects in the northern region occurred at higher mean elevations (1261 m a.s.l., SD 13.1) than transects in the central region (1215 m a.s.l., SD 20.7) or in the southern region (1217.3 m a.s.l., SD 11.1, Tukey's HSD test, $p = 0.032$).

3.2. Tree species density and distribution

We measured 1096 trees, representing 53 species, 50 genera and 32 families (see supplementary material, Appendix A). There were 506.7 trees ha^{-1} (SD 45) and tree basal area was 27.3 m^2 ha^{-1} (SD 9.9). Tree density and basal area did not vary significantly across regions ($F's_{2,6} = 1.12–1.32$, $p's = 0.335–0.387$).

There were 207.7 trees ha^{-1} (SD 70.8) that produced large fleshy fruits, representing 37.7% ($n = 20$) of the monitored tree species. There were no differences in the density of trees producing large fleshy fruits between regions ($F_{2,6} = 1.012$, $p = 0.418$). There were 338.1 trees ha^{-1} (SD 90.2) of confirmed chimpanzee fruit foods, representing 41.5% ($n = 22$) of the monitored tree species. There were significant differences in the density of trees producing chimpanzee fruit foods across the three regions ($F_{2,6} = 5.197$, $p = 0.049$), due to higher densities of fruit food trees in the southern region compared with the northern region (230.7 trees ha^{-1} (SD 101.5) vs. 166.7 trees ha^{-1} (SD 34.5), Tukey's HSD test, $p = 0.047$).

The tree ordination was based on 53 species and nine transects. The best model was a two-dimensional solution with a final stress of 6.48. This solution had significantly less stress than expected by chance, based on a Monte Carlo test with randomized data ($p = 0.04$). The cumulative coefficient of determination for the two axes was 89.5%, indicating that the final model incorporated most of the variance from the original data. Transects were grouped by region in the ordination plot, suggesting greater similarity in tree species composition within regions than among them (inset Fig. 2). Transects in the northern region occurred at higher

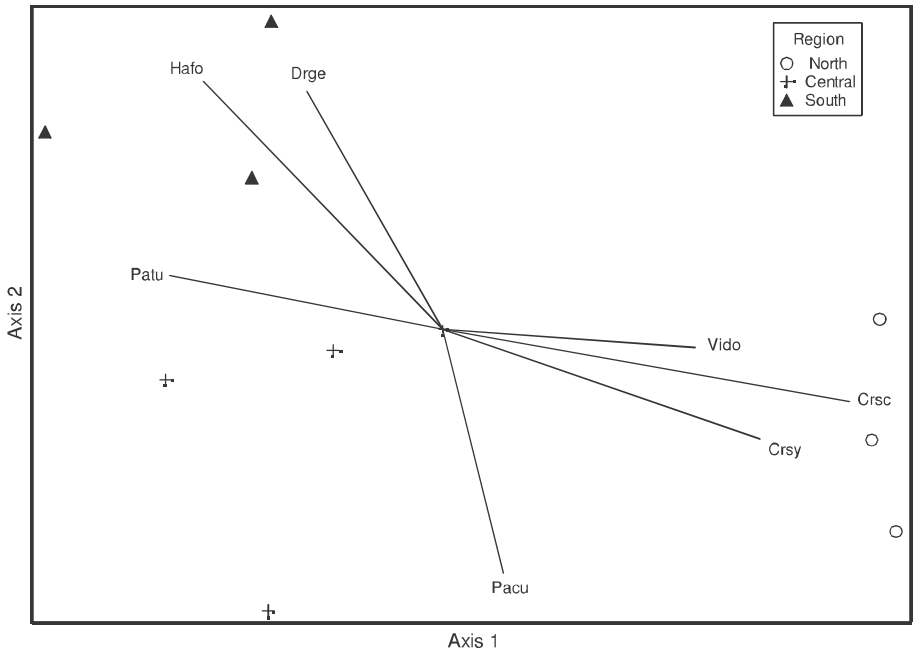


Fig. 2. Two-dimensional NMS ordination of tree species composition on transects. The coefficient of determination for axis 1 is 71.9% and for axis 2 is 17.6%. Points represent tree species composition values for each transect. ○ = Northern region transects ($n = 3$); + = central region transects ($n = 3$); Δ = southern region transects ($n = 3$). Joint plots indicate the strength and direction of the correlation of individual tree species with Pearson r^2 values > 0.55 with one or more of the axes. Tree species: *Craterispermum schweinfurthii* (Crsc), *Croton sylvaticus* (Crsy), *Drypetes gerrardii* (Drge), *Haplocoelum foliolosum* (Hafo), *Pancovia turbinata* (Patu), *Parinari curatellifolia* (Pacu) and *Vitex doniana* (Vido).

Table 2
Mean (±SD) regional densities for seven species that had the strongest correlations with the axes in the two-dimensional NMS ordination of tree species on transects. Pearson correlation coefficients indicate the strength and direction of the relationship of each species with the ordination axes. Results of one-way ANOVA tests for differences in regional densities of each tree species are included. For posthoc tests see text.

Tree species	North (No. ha^{-1})	Central (No. ha^{-1})	South (No. ha^{-1})	Axis 1, r^2	Axis 2, r^2	$F_{(2,6)}$	P value
Craterispermum schweinfurthii	139 (±5)	4 (±7)	0	0.98	−0.41	808.69	0.001
Croton sylvaticus	80 (±4)	49 (±18)	27 (±21)	0.86	−0.51	8.28	0.019
Drypetes gerrardii	1 (±2)	0	119 (±42)	−0.57	0.75	24.03	0.001
Vitex doniana	55 (±34)	4 (±8)	7 (±6)	0.77	−0.21	6.37	0.038
Haplocoelum foliolosum	0	33 (±29)	61 (±33)	−0.75	0.76	4.47	0.065
Pancovia turbinata	0	106 (±66)	120 (±100)	−0.8	0.36	2.34	NS
Parinari curatellifolia	7 (±8)	8 (±5)	0	0.38	−0.76	1.96	NS

values on axis 1 relative to transects in the central and southern regions. Transects in the southern region occurred at higher values on axis 2 than transects in the central region. Elevation was mildly correlated with axis 1 (Pearson $r^2 = 0.51$). Joint plots indicated strong correlations between the axes and the transect densities of seven tree species: *Craterispermum schweinfurthii*, *Croton sylvaticus*, *Drypetes gerrardii*, *Haplocoelum foliolosum*, *Pancovia turbinata*, *Parinari curatellifolia* and *Vitex doniana* (see Fig. 2), suggesting that differences in densities of these species were driving the separation of transects by region in the ordination.

There were significant differences in regional transect densities of four of the seven tree species indicated in the ordination, confirmed by ANOVAs (see Table 2). *C. schweinfurthii* densities were higher in the northern region than in the central and southern regions (Tukey's HSD test, $p < 0.001$). *C. sylvaticus* densities were higher in the northern region than in the southern region (Tukey's HSD test, $p = 0.016$), and *V. doniana* densities tended to be higher in the northern region than in the central or southern regions (Tukey's HSD test, $p = 0.061$). In contrast, *D. gerrardii* densities were higher in the southern region than in either the northern or central region (Tukey's HSD test, $p = 0.002$).

Of the tree species with significant differences in regional presence, *C. sylvaticus*, and *V. doniana* are confirmed chimpanzee foods and *D. gerrardii* is among the top 10 most heavily utilized foods, based on occurrence in fecal samples (Moscovice et al., 2007). These three species had distinct fruiting patterns (inset Fig. 3a–c). *C. sylvaticus* and *V. doniana* fruiting peaks occurred during the first wet season, from March–May, while *D. gerrardii* fruit was most abundant during the second wet season, from October–December.

3.3. Liana species density and distribution

We measured 1063 lianas, occurring on 80.9% ($n = 191$) of trees $\geqslant$10 cm DBH within the liana survey plots. There were 4.5 lianas per tree (SD 5.12). Identified lianas represented 16 species, 16 genera and 14 families (see supplementary material, Appendix B). There were 2507.7 lianas ha^{-1} (SD 657.4) and liana basal area was 2.1 m^2 ha^{-1} (SD 0.6). Liana density and basal area did not differ across regions ($F's_{2,6} = 0.526–1.005$, $p's = 0.616–0.420$). There were 1981.6 lianas ha^{-1} (SD 526.2) producing large fleshy fruit, representing 75% ($n = 12$) of the monitored species. There were 1958 lianas ha^{-1} (SD 495.6) producing confirmed chimpanzee fruit foods, representing 81.2% ($n = 13$) of the monitored species. There were no differences in regional transect densities of lianas producing large fleshy fruits, or producing confirmed chimpanzee fruit foods ($F's_{2,6} = 0.608–0.971$; $p's = 0.431–0.575$).

The liana ordination was based on 16 species and nine transects. The best model was a four-dimensional solution, with a final stress of 0.002. The solution was more stable than expected by chance, based on the Monte Carlo test with randomized data ($p = 0.02$). Transects did not group by region on any axes of the liana ordination. The only species with a strong pattern of correlation with the ordination plot was *Strychnos lucens* (axis 3, $r^2 = 0.70$).

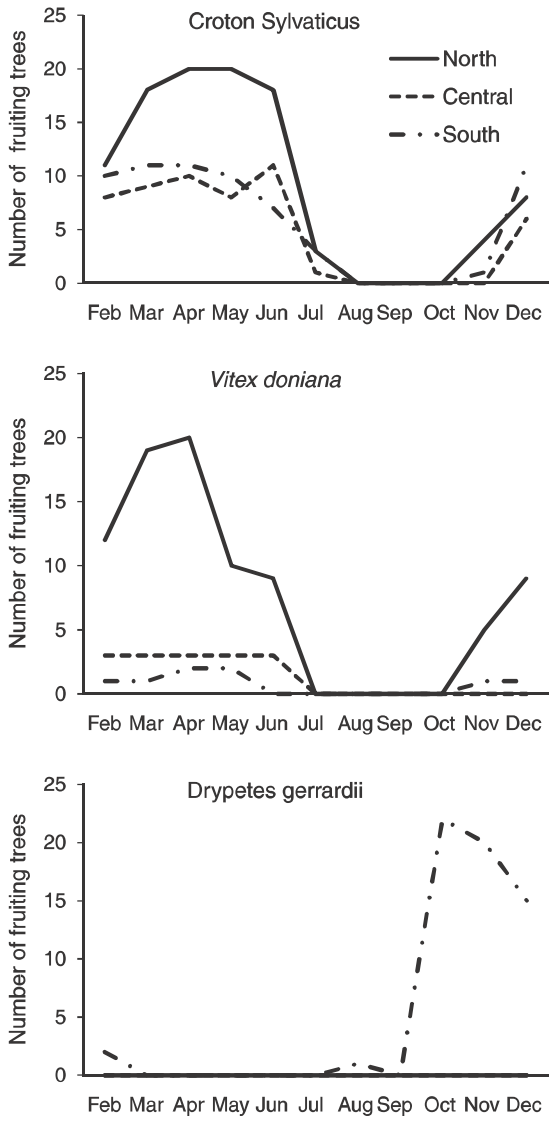


Fig. 3. (a–c) Monthly fluctuations in fruit availability for three species of confirmed chimpanzee fruit foods with regionally-distinct distributions based on the NMS ordination and supported by statistical analyses. For figures b and c, refer to the legend in figure a.

However *S. lucens* densities did not differ significantly across regions ($F_{2,6} = 1.054$, $p = 0.405$).

3.4. Chimpanzee habitat utilization across seasons

We encountered fresh chimpanzee evidence (including nests, feces, vocalizations or direct sightings) during 39.2% (SD 8.1) of

Table 3
Percent of overlap in presence and utilization of confirmed Rubondo chimpanzee plant foods at study sites in East Africa (Gombe, Tanzania; Mahale, Tanzania; Budongo Forest, Uganda), Central Africa (Lope, Gabon; Kahuzi-Biega, Democratic Republic of Congo) and West Africa (Bossou, Guinea). See main text for references.

Percent overlap	Gombe, Tanzania	Mahale, Tanzania	Budongo, Uganda	Lope, Gabon	Kahuzi, DRC	Bossou, Guinea
Genera of confirmed Rubondo foods	70.5	72.7	70.5	63.6	40.9	47.7
Species of confirmed Rubondo foods	40.9	38.6	43.2	9.1	13.6	9.1
Species of Rubondo foods that are present and also eaten	77.8	76.4	31.4	49.4	50	100

tracking days per season. There were no differences in the regional proportion of encounters with chimpanzee evidence during any of the four seasons (mean proportion of encounters in each region during: first dry season = 42.8% (SD 7.3), χ^2 (2, n = 43) = 0.634, p = 0.728; first wet season = 42.8% (SD 2.4), χ^2 (2, n = 95) = 0.192, p = 0.909; long dry season = 33.8% (SD 8.8), χ^2 (2, n = 114) = 2.063, p = 0.356; second wet season = 38.2% (SD 12.0), χ^2 (2, n = 98) = 3.140, p = 0.208). Daily utilization of regions by chimpanzees did not appear to be influenced by seasonal or regional differences in tree fruit availability.

Of the three male chimpanzees that were individually identifiable during the study period, all were observed in all three of the surveyed regions on multiple occasions (Moscovice, 2006). Furthermore, based on characteristics of party size and composition during sightings, we strongly suspect that the entire chimpanzee population utilized all three of the survey areas. The minimum population home range estimate, considering only the three survey areas and the straight-line distance required to travel across them, was 43 km^2. The maximum home range estimate, including the survey areas and all intervening habitat, was 82 km^2.

3.5. Overlap in plant composition with endemic chimpanzee study sites

We examined whether confirmed Rubondo chimpanzee plant foods were also present and consumed at endemic chimpanzee study sites, using comprehensive plant lists from three long-term study sites in East Africa (Gombe, Tanzania: Clutton-Brock and Gillett, 1979; Mahale, Tanzania: Nishida and Uehara, 1981, 1983; Budongo Forest, Uganda: Synnott, 1985), two sites in Central Africa (Lope, Gabon: Tutin et al., 1994; Kahuzi, DRC: Yumoto et al., 1994) and one site in West Africa (Bossou, Guinea: Sugiyama and Koman, 1987, 1992). There was similarity in the percentage of Rubondo plant food genera and species that were also present at the three East African sites. A smaller percentage of Rubondo plant foods were also present at the Central and West African chimpanzee study sites (see Table 3). Considering the species of Rubondo chimpanzee plant foods that were also present at endemic sites, between 31–100% (median 50%) were also consumed by chimpanzees at those sites, based on long-term, comprehensive food lists (Gombe, Tanzania: Michael Wilson, personal communication; Mahale, Tanzania: Nishida and Uehara, 1983; Budongo Forest, Uganda: Reynolds, 2005, Appendix B1; Newton-Fisher, 1999; Lope, Gabon: Tutin et al., 1994; Kahuzi, DRC: Basabose, 2002; Bossou, Guinea: Sugiyama and Koman, 1987, 1992, see Table 3).

4. Discussion

Releases of chimpanzees to islands have potentially important roles in improving the welfare of sanctuary-housed chimpanzees (Farmer, 2002a; Carter, 2003) and as illustrated by the HELP Project, as intermediate steps in conservation-motivated reintroductions of chimpanzees to mainland sites (Farmer et al., 2006). This research identified ecological features at an island release site that may have helped to promote a natural behavioral repertoire in chimpanzees post-release. In addition to appropriate habitat, there are many other variables that influence the outcome of a chimpanzee release effort, including the age and health status of released individuals, the amount of time spent in captivity, the extent of rehabilitation prior to release and the composition of released social groups (Tutin et al., 2001; Farmer et al., 2006; Beck et al., 2007). Unfortunately, there are few records of chimpanzee behavior and health status prior to or immediately following the release to Rubondo Island, to examine how these variables may have contributed to the long-term success of the release effort. Since the chimpanzees were introduced to a habitat outside of their historic range and did not receive extensive rehabilitation or provisioning, an emphasis on ecological features that may have facilitated their adjustment to a novel habitat is especially warranted. Conservation introductions should be considered only as last resort measures (Beck et al., 2007). However, given the severity of current threats to West African chimpanzee populations *in situ* (e.g. Walsh et al., 2003), there is practical conservation value in assessing the extent of behavioral flexibility in adapting to an environment outside of the historic range of the subspecies.

Our plant surveys were based on sampling predominantly semi-deciduous forest habitat with a dense liana understory. Based on direct sightings and indirect evidence, chimpanzees heavily utilized this habitat type within our survey areas, and transects surveyed all but 15.2% (n = 7) of confirmed chimpanzee foods. Ecological features within the survey areas are especially relevant for understanding how this introduced chimpanzee population has survived and become self-sufficient.

4.1. Habitat use in relation to fruit availability and distribution

Across regions, tree density was similar but there were distinct differences in tree species dominance and distribution, based on the NMS ordination and supported by statistical comparisons. Differences in regional tree composition may be due to differences in elevation among regions, or possibly to the impact of the introduced elephant population on the island. At Kibale National Park, differences in tree species composition across neighboring forest tracts were linked to patterns of elephant land-use and their destruction of preferred feeding trees (Chapman et al., 1997). Detailed monitoring of elephant ranging and habitat utilization is necessary to determine their impact on regional plant composition on Rubondo Island.

Results from the tree ordination can be combined with data on phenology and chimpanzee dietary selection to make predictions about seasonal patterns of chimpanzee habitat utilization. Given their dietary preference for *D. gerrardii* fruit (Moscovice et al., 2007), which is found almost exclusively in the Southern region, it is likely that chimpanzees will spend more time in the Southern region during the October–December wet season, coinciding with the *D. gerrardii* fruiting period (see Fig. 3c). In contrast, chimpanzees may prefer the Northern region during the March–May wet season, coinciding with the fruiting periods of two food species that occur at higher densities in this region (see Fig. 3a and b). However, the percentage of encounters with fresh chimpanzee evidence was similar across regions in every season, suggesting that regionally-distinct tree fruiting patterns had little impact on habitat utilization. These results contrast with data from several endemic sites, where seasonal preferences for specific habitat types have been linked to local

concentrations of important food resources (e.g. Chapman et al., 1997; Furuichi et al., 2001).

Considering the semi-habituated state of the Rubondo chimpanzees and difficulties with systematically covering their large ranging area, it is possible that our ranging data were not precise enough to identify temporal shifts in regional habitat use. Systematic data on nesting patterns over a longer time period will help to additionally test whether patterns of chimpanzee ranging relate to the regionally-distinct fruiting patterns identified here. It is also possible that Rubondo chimpanzee ranging patterns may be less influenced by regionally-distinct fruiting patterns in comparison with several endemic sites, due to a relatively high density and even distribution of high-quality fruit foods. Similarly, at the resource rich Ngogo forest within Kibale National Park, Uganda, monthly variability in range use by chimpanzees is not influenced by the distribution of preferred fruit foods that are available during periods of habitat-wide fruit abundance (Potts, 2008).

Our interpretation of resource abundance on Rubondo Island is consistent with a previous finding that Rubondo chimpanzees maintained similar sub-group sizes across months and seasons (Moscovice et al., 2007). In contrast at many endemic study sites chimpanzees form smaller sub-groups during seasonal periods of fruit scarcity, which is viewed as a strategy to reduce feeding competition (reviewed in Wrangham, 2000). The combined evidence from ranging and grouping patterns is consistent with lower levels of intraspecific feeding competition on Rubondo Island relative to many endemic sites. Our estimate that the population has doubled in size since the initial release (Moscovice et al., 2007), is further consistent with our assessments of a high-quality habitat on Rubondo Island.

4.2. Comparison of ecological features at long-term release sites

We highlight several factors that influence food abundance, quality and distribution on Rubondo Island, and compare our results with available data from endemic chimpanzee study sites, and from two other release sites with published ecological data: Conkouati Reserve, Republic of Congo, the only other release site with a self-sustaining chimpanzee population, and Ipassa Island, Gabon, a release site that maintained a provisioned population for 10 years (see Table 4).

4.2.1. Characteristics of preferred and fallback foods

Across endemic chimpanzee study sites, ripe fruits constitute the greatest proportion of total diet (Goodall, 1986; Conklin-Brittain et al., 1998; Furuichi et al., 2001), and are consistently

Table 4
Comparison of ecological features at three chimpanzee release sites.

Release site	Rubondo Island, Tanzania	Triangle, Conkouati Reserve, Congo	Ipassa Island, Gabon
Size (km^2)	240	21	0.65
No. of released chimpanzees	17	37	8
Duration of chimpanzee presence post-release	1966-Present	1996-Present	1968–1978
Habituation status of chimpanzees	Semi-habituated	Fully habituated	Fully habituated
Extent of provisioning	Minimal, for 2 months post-release only	Minimal, accounting for 0.79% of feeding time	Significant, accounting for 30% of diet for duration of release
Home range (km^2)	43–82	>21	<0.65
Ecological population density (individuals/km^2 ranging area)[a]	0.33–0.81	1.3–1.5	12.3
Dominant habitat	Evergreen and semi-deciduous primary forest	Primary, seasonally inundated and swamp forest	Riparian forest
Percent forested habitat	81	62 (includes swamp forest)	na
Annual rainfall (mm)	1461	1610	1755
No. of dry months per year (rainfall < 60 mm)[b]	4	4	3
No. of months of habitat-wide fruit scarcity[c]	3	3	4
No. of surveyed plant species at release site	>115	>605	>900
No. of tree species accounting for 50% of total surveyed population	5	na	15
No. of woody plant species in diet[d]	>41	>56	>99
No. of fruit species accounting for >0.5% of diet[e]	18	18	na
Fallback foods (utilized during periods of habitat-wide food scarcity)[f]	Fruits of *Saba comorensis*	Fruits of *Staudia gabonensis*, *Vitex* sp. and *Elaeis guinnensis*	Leaves of *Baphia leptobotrys* and stems of *Hypselodelphis violacea* (Marantaceae)
Percent of plant food species also consumed by endemic chimpanzees in same region[g]	14–32	5–37	29
Citations	Grzimek (1970), Borner (1985), Chapman and Chapman (1996), Moscovice et al. (2007) and this study	Tutin et al. (2001), Farmer (2002b), Farmer et al. (2006) and Goossens et al. (2005)	Hladik (1973, 1974, 1977) and Hladik and Halle (1973)

[a] Rubondo calculation based on population size estimate of 27–35 idds (Moscovice et al., 2007); Triangle calculation from Goossens and colleagues (2005); Ipassa calculation based on population size of 8 (Hladik, 1977).
[b] Rubondo data based on Fig. 1, Moscovice et al. (2007); Triangle data based on Fig. 6.2, Farmer (2002b); Ipassa data based on Fig. 3, Hladik (1973).
[c] Rubondo data based on Fig. 1, Moscovice et al. (2007); Triangle data based on Farmer (2002b); Ipassa data based on Fig. 10, Hladik (1973) and Fig. 4, Hladik (1977).
[d] Includes only woody plants identified to species level. Rubondo data based on Table 1, Moscovice et al. (2007); Triangle data based on Appendix E, Farmer (2002b); Ipassa data based on Table 1, Hladik (1973).
[e] Rubondo data based on percent occurrence in feces (Moscovice, unpublished data); Triangle data based on percent feeding time (Table 8.8, Farmer, 2002b).
[f] Rubondo data from Moscovice and colleagues (2007); Triangle data from Table 8.16, Farmer (2002b); Ipassa data from Figs. 10 and 16, Hladik (1973).
[g] Comparison of foods identified to species level. Rubondo dietary species compared with Gombe, Tanzania, Mahale, Tanzania and Budongo, Uganda, for citations see text; Triangle dietary species compared with Lope, Gabon, Nouabale-Ndoki, Republic of Congo and Kahuzi-Biega, Democratic Republic of Congo (from Appendix E, Farmer, 2002b); Ipassa dietary species compared with complete food list from Lope, Gabon (Tutin et al., 1994).

the most preferred dietary food items, selected disproportionately to their abundance (e.g. Wrangham et al., 1996). Density estimates of woody plants producing large fleshy fruits are important indicators of food availability for chimpanzees that can be readily compared across sites. The density of fleshy-fruit producing trees in our survey areas are at the high end of similar estimates collected from six different sites within the range of endemic chimpanzees in Kibale, Uganda (Balcomb et al., 2000). There are few comparable data on the density of fleshy-fruit producing lianas at other chimpanzee study sites. However, total liana density on Rubondo Island is between four to nine times higher than comparable measures from three different Ugandan chimpanzee study sites (270–625 lianas $\geqslant$ 1 cm DBH ha^{-1}, Eilu, 2000) and is also higher than values from several other African survey sites (Gentry, 1991). Our findings are consistent with other vegetation surveys noting a high abundance and diversity of lianas within the Lake Victoria region (Jackson and Gartlan, 1965; Lind and Morrison, 1974). Considering that 75% of the liana species on the island produce large fleshy fruits, the density of fleshy-fruit producing lianas on Rubondo Island is also likely to be greater than densities at many endemic sites. There are no published data on densities of fleshy-fruit producing tree or liana species from other release sites, but lianas contribute importantly to total plant biomass and fruit production on Ipassa Island, Gabon (Hladik, 1974), and lianas were among the top dietary items for released chimpanzees in the Conkouati Reserve, Congo (Table 8.8, Farmer, 2002b).

Seasonal fluctuations in fruit availability and corresponding periods of habitat-wide fruit scarcity occur at most endemic chimpanzee study sites (e.g. Yamakoshi, 1998; Basabose, 2002), and were also observed at all three release sites (see Table 4). The availability and quality of fallback foods that can be utilized during periods of resource scarcity can influence chimpanzee carrying capacity (Tutin et al., 2001) and levels of intraspecific feeding competition (Marshall et al., 2009). The fruit of the liana *S. comorensis* is a high-quality fallback food for Rubondo chimpanzees, based on its stable presence across seasons and increases in consumption coinciding with the dry-season period of reduced tree fruit availability (Moscovice et al., 2007). The liana ordination indicated that *S. comorensis* and other liana species are widely-distributed across all monitored regions. As a result, Rubondo chimpanzees encounter high-quality fallback foods throughout their ranging areas. In contrast, at several endemic study sites fallback foods are either of lower quality (e.g. Wrangham et al., 1991) or more restricted in distribution (e.g. Furuichi et al., 2001). The Rubondo pattern is again similar to data from the Ngogo forest within Kibale National Park, Uganda, which supports a higher population density of chimpanzees than the nearby Kanyawara forest, and also has a greater abundance of species fruiting outside of peak habitat-wide fruiting periods (Potts, 2008). At the Conkouati Reserve as well, released chimpanzees utilized high-quality fruit fallback foods during periods of habitat-wide food scarcity (Tutin et al., 2001). In contrast, chimpanzees on Ipassa Island utilized low-quality fallback foods, including stems from the *Marantaceae* plant family (Hladik, 1977), a common fallback food at some endemic sites (e.g. Wrangham et al., 1991). The presence of high-quality fallback foods on Rubondo Island and at the Conkouati Reserve release site may have been important factors in establishing self-sustaining chimpanzee populations.

4.2.2. Ecological population density

An estimated 81% of Rubondo Island, or roughly 194 km^2, consists of primary forest and based on estimates of home range size, chimpanzees regularly utilize between 22–42% of the available forested habitat. The large size of the island prohibited regular monitoring outside of the areas of heavy utilization identified during our pilot study. During the 2003 tracking period there was one chimpanzee sighting far outside of the main tracking regions, reported by a park ranger stationed at a Southern ranger post. This sighting occurred during a short period without any chimpanzee sightings within the main study areas, suggesting that chimpanzees made a brief excursion into habitat to the south of the monitored areas. When including this sighting in a 100% MCP estimate, the maximum ranging area increases to 119 km^2. However, current direct and indirect evidence suggests only limited utilization of habitat outside of the monitored areas, and such excursions may not be representative of home range.

Even our conservative home range estimates far exceed the total size of most other release sites (reviewed in Hannah and McGrew, 1991), and are also greater than typical home ranges for endemic populations at forested study sites (MCP estimates of 5.37–27.7 km^2, Chapman and Wrangham, 1993; Herbinger et al., 2001; Williams et al., 2002; Newton-Fisher, 2003; Amsler, 2009). At most endemic study sites forested ranging area is limited, either due to geographical barriers and habitat disturbance (Sugiyama, 1991; Basabose, 2005) or to aggressive territorial defense of overlapping home ranges by conspecifics (Herbinger et al., 2001). In comparison, the Rubondo chimpanzee home range estimates may be based almost entirely on habitat preferences for foraging and nesting.

The IUCN estimates that island release sites of less than 50,000 ha may have insufficient resources to support a self-sustaining population (Beck et al., 2007). However, Rubondo Island is half that size and has supported an unprovisioned chimpanzee population for over four decades. Estimates of ecological population density, referring to the density of conspecifics within their ranging area (e.g. Chapman et al., 1995; Ganzhorn, 1999), may provide a more relevant indicator of habitat suitability than the absolute size of chimpanzee release sites. The estimated ecological population density on Rubondo Island, from 0.33–0.81 individuals/km^2, is lower than estimates from forested endemic sites, which range from 0.91 individuals/km^2 at Tai Forest (based on Herbinger et al. (2001)), to 5.96 individuals/km^2 at Gombe, Tanzania (based on Williams et al. (2002)). The estimated ecological population density within the Conkouati Reserve release site is also relatively low (Goossens et al., 2005). In contrast, the ecological population density on Ipassa Island was extremely high, which may have contributed to the need for long-term provisioning of chimpanzees at that site (see Table 4).

4.2.3. Plant species diversity and overlap with endemic sites

A plant survey within the Conkouati Reserve release site identified over 100 known chimpanzee foods, including at least 12 species used as fallback foods at other study sites (Tutin et al., 2001). Vegetation diversity on Ipassa Island is also high in comparison with many endemic study sites (Hladik and Halle, 1973; Hladik, 1977). In contrast, Rubondo Island has fewer total inventoried plant species and a small number of species accounted for 50% of the surveyed tree population (see Table 4). At release sites with less forested habitat, a high diversity of plant species may provide a sufficient range of dietary items for chimpanzees. At release sites containing a relatively large forested area, chimpanzees may maintain a sufficiently diverse diet, even in a more homogeneous habitat, through wide-ranging patterns to access plant species with localized fruiting patterns.

Rubondo chimpanzees quickly adjusted to a natural diet at a release site that contained only a moderate amount of overlap in food species with nearby native chimpanzee study sites. There appears to be even less overlap of Rubondo plant foods at study sites within the released chimpanzees' areas of origin in West Africa. Considering this, it is likely that the founders had little prior exposure to the plant species that became important dietary staples following their release. Interestingly, between 22–68% of the confirmed Rubondo

chimpanzee plant foods that are also found at nearby East African study sites are not consumed by chimpanzees at those sites. Much like the site-specific dietary preferences of neighboring endemic chimpanzee populations in East Africa (Nishida et al., 1983), descendents of introduced chimpanzees on Rubondo Island also appear to exhibit population-specific dietary preferences.

At the Conkouati and Ipassa Island release sites as well, released chimpanzees adapted to a diet containing only a moderate degree of overlap in plant food species with nearby endemic sites, and released chimpanzees also utilized foods that were present, but not consumed, at nearby endemic sites (Appendix E, Farmer, 2002b). Based on this comparison, the abundance and diversity of fleshy-fruit-producing species may have more relevance than the extent of plant species overlap with nearby endemic sites in assessing release site habitat suitability. However, at both Rubondo Island and the Conkouati Reserve, a relatively high percentage of plant food genera at the release site are also present at endemic sites in the same region (Appendix E, Farmer, 2002b; see Table 2), suggesting that a high level (e.g. >60%) of genera overlap of woody plants between potential chimpanzee release sites and endemic sites in the same region may be a useful indicator of release site habitat suitability.

5. Conclusions

In summary, the relatively high density of fleshy-fruit producing trees and lianas, the presence of a high-quality and widely-distributed fallback food and the relatively low ecological population density on Rubondo Island are among the important ecological factors that likely facilitated the long-term success of Rubondo chimpanzees in adapting to a novel habitat, despite their lack of rehabilitation and minimal provisioning post-release. Available ecological data from the Triangle release site in Conkouati Reserve are consistent with these patterns, providing further support for a role of these specific factors in helping to establish a self-sustaining released chimpanzee population.

Developing more precise ecological criteria for evaluating release site habitat suitability will improve the outcomes of conservation and welfare-motivated chimpanzee releases, by increasing the likelihood that chimpanzees will become self-sufficient post-release. Comparative ecological data are needed from release sites where chimpanzees require supplemental provisioning and also from the exceptional sites like Rubondo Island, where chimpanzees have become nutritionally self-sufficient after a release.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.biocon.2010.07.018.

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