

A bat on the brink? A range-wide survey of the Critically Endangered Livingstone's fruit bat *Pteropus livingstonii*

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Abstract The Livingstone's fruit bat *Pteropus livingstonii* is endemic to the small islands of Anjouan and Mohéli in the Comoros archipelago, Indian Ocean. The species is under threat from anthropogenic pressure on the little that remains of its forest habitat, now restricted to the islands' upper elevations and steepest slopes. We report the results of the most comprehensive survey of this species to date, and present recommendations for ongoing field conservation efforts and monitoring. Morning counts were conducted at roost sites in the wet and dry seasons during 2011–2013. Habitat structure around the roosting sites was characterized and roost numbers compared, to investigate the potential effect of habitat loss and degradation. We estimate the population to comprise c. 1,260 individuals distributed across 21 roosts on the two islands. All occupied roosting sites were restricted to a narrow altitudinal range, and roosting populations in agroforestry areas were smaller than those found in degraded and undisturbed forest. Only one of the 16 roosts on Anjouan was found in undisturbed, old-growth forest with no nearby signs of clearance for agriculture or landslides following tree-felling upslope. Following a suspected severe population decline as a result of widespread and long-term forest loss Livingstone's fruit bat has been recategorized as Critically Endangered on the IUCN Red List.

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Introduction

Fruit bats of the genus *Pteropus* are recognized as being important pollinators and seed dispersers (Cox et al., 1991; Fujita & Tuttle, 1991; Pierson & Rainey, 1992), especially on isolated island systems with a low abundance of pollinator fauna (Cox et al., 1991; Carroll & Feistner, 1996; Allen-Wardell et al., 1998; Mohd-Azlan et al., 2001), and in fragmented systems (Bollen & Van Elsacker, 2002; Nyhagen et al., 2005). The loss of fruit bat populations, particularly of endemic species, is of conservation concern as it is thought to lead to the loss of endemic plants and a decrease in plant biodiversity (Allen-Wardell et al., 1998; Mohd-Azlan et al., 2001; Bollen et al., 2004; Nyhagen et al., 2005; Jenkins et al., 2007).

Many *Pteropus* species are under threat, mainly from habitat loss and hunting, both for subsistence use and for sale (Jenkins et al., 2007; Epstein et al., 2008). Of the 62 *Pteropus* species on the IUCN Red List (IUCN, 2016), four have already gone extinct, five are Critically Endangered, five are Endangered and 20 are Vulnerable. Many *Pteropus* species are limited to islands in the Pacific and Indian Oceans, where typhoons and cyclones also pose a threat to the integrity of the remaining forest fragments (Pierson & Rainey, 1992; Carroll & Feistner, 1996; Mickleburgh et al., 1992; Powell & Wehnelt, 2003). As ecologically specialized island endemics with a preference for undisturbed old-growth forest (Brooke, 2001; Mildenstein et al., 2005; Nyhagen et al., 2005), many are particularly vulnerable to habitat loss. With a low reproductive rate of only one young per female per annum, *Pteropus* are limited in their ability to recover from population declines (Pierson & Rainey, 1992).

At the western limit of the genus' distribution, the western Indian Ocean is home to an assemblage of eight *Pteropus* species (Carroll & Feistner, 1996; Mickleburgh et al., 1992). The rarest of these is thought to be the Livingstone's fruit bat *Pteropus livingstonii*, which is found only on the islands of Anjouan and Mohéli in the Comoros archipelago (Anjouan, Mohéli and Grande Comore, which comprise

the Union of Comoros, plus the French Departement of Mayotte). The species was first described by the Victorian-era explorer David Livingstone, who shot an individual on Anjouan in 1861 (Cheke & Dahl, 1981). It is the only *Pteropus* species in the western Indian Ocean that is not threatened by hunting (Carroll & Feistner, 1996; Entwistle, 2001; Jenkins et al., 2007; Mickleburgh et al., 1992), but its population is suspected to have undergone severe declines as a result of widespread deforestation since the 1960s (Cheke & Dahl, 1981; Mickleburgh et al., 1992; Reason & Trehwella, 1994), which continues today. It was estimated that forest on the Comoro Islands was lost at a rate of 9.3% per year during 2000–2010, the highest rate of deforestation of any country (FAO, 2010). The main causes of natural forest loss are the cutting of large trees for construction wood and the extension of the agricultural frontier, driven by unproductive agricultural systems, a high population growth rate, poverty, a lack of economic alternatives and uncertain land tenure. Only c. 35 and 25 km² of undisturbed old-growth forest remains on Anjouan and Mohéli respectively, and this is largely restricted to higher elevations and steep slopes (Green, 2014a). The status of Livingstone's fruit bat was recently reassessed, and as a result of this habitat loss the species is now categorized as Critically Endangered on the IUCN Red List (Sewall et al., 2016).

A number of surveys of Livingstone's fruit bat have been conducted since the early 1990s by counting at known daytime roosts, with more intensive survey effort on Anjouan than Mohéli. In 1995 a field expedition conducted the first survey of the species by counting bats at all known long-term roosts (Trehwella et al., 1998). The population was estimated to be as few as 400 individuals, found at 12 roost sites. Following the survey a long-term community-led monitoring programme was set up, in which local people, supported by technicians from the national NGO Action Comores, conducted monthly counts at known roosts, and searches for unknown roosting sites. By 2002, 22 active roosts were known to exist across Anjouan and Mohéli and were believed to support c. 1,200 bats (Sewall et al., 2007). However, the reliability of these counts conducted by community enumerators with varying levels of training and poor access to survey equipment has not yet been assessed.

Despite its threatened status Livingstone's fruit bat receives no legal protection at national level and there are currently no long-term forest conservation measures in place on either Anjouan or Mohéli. Forest conservation initiatives are being developed, including the planned designation of the first terrestrial protected area in the Comoros (UNDP, 2013), and the development of community-conserved areas by a local NGO, Dahari. The locations and sizes of current roosts, and proximate pressures on each roost site, need to be quantified and the data made available to conservation planners to ensure these conservation initiatives take into account the needs of Livingstone's fruit bat. We report the

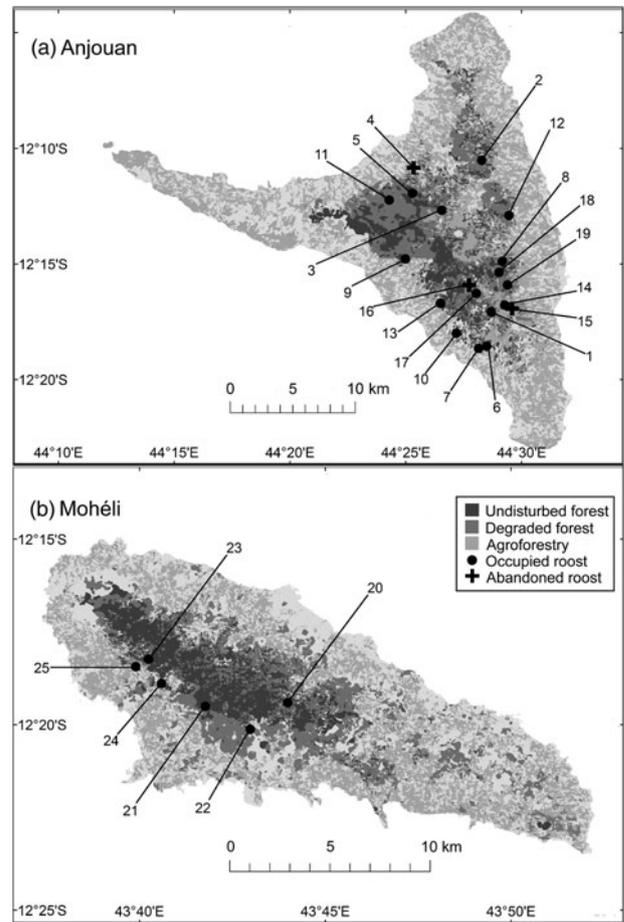


FIG. 1 Distribution of Livingstone's fruit bat *Pteropus livingstonii* roosts (numbers as in Table 1) on (a) Anjouan and (b) Mohéli islands in the Comoros archipelago, in the western Indian Ocean. Coverage of undisturbed and degraded forest is based on a land cover map by Green (2014a).

most comprehensive population estimate for the species, based on a 2011–2013 survey of all known roosts as well as previously unknown roosts. We characterize the condition of the forest around each roost and compare this to roost size to investigate the potential effects of habitat loss and degradation on the populations at roost sites. Based on our findings we make a series of recommendations for conservation efforts and population monitoring.

Study area

The work was conducted on the islands of Anjouan and Mohéli in the Comoros archipelago, in the Western Indian Ocean (Fig. 1). Anjouan is both the larger (424 km²) and higher island, reaching an elevation of 1,575 m, and is characterized by steep ravines. Mohéli (210 km²) reaches only 860 m and consists of a single mountainous ridge. Both islands are dominated by agricultural and agroforestry areas but Mohéli retains a greater percentage of its original forest cover (Green, 2014a), partly because it has a smaller human population, of c. 35,000.

Anjouan has a population of c. 275,000, and its high population density of > 640 people km^{-2} has contributed to high levels of deforestation.

The annual climatic cycle in the Comoros consists of a cooler, drier season during May–October and a warm, humid season during November–April. To sample these two annual climatic extremes, and for the data to be directly comparable to previous surveys (Granek, 2002; Sewall et al., 2011), field work was carried out on Anjouan during the wet season in December 2011 and January 2012, and repeated in January 2013, and dry season counts were conducted across both Anjouan and Mohéli in June and July 2012. Limited project resources meant it was not possible to conduct a wet-season count on Mohéli.

Methods

A team of one scientist and four field technicians surveyed all known roost sites on each island in as short a time-frame as possible to minimize error caused by double counting as a result of inter-roost movements; the mean duration of the three main survey periods was 30 days. This included a total of 18 sites on Anjouan identified previously (Sewall et al., 2011) as having been used historically by Livingstone's fruit bats for roosting, and six on Mohéli (Table 1). Local reports of previously unidentified roosts were investigated by intensive searches of relevant areas of forest. Roost counts were carried out hourly during 07.00–10.00 from pre-identified vantage points, using binoculars. Vantage points were typically located c. 80–100 m from the roost, and slightly above or level with the crown of the trees used for roosting. Each surveyor conducted an independent count, and the results were compared after the count was finished. The final number was agreed following cross-checking of counts. The species of each tree used for roosting was recorded (during a survey of the roost site after the count was completed) along with the number of Seychelles fruit bats *Pteropus seychellensis comorensis* (which are readily distinguishable by their smaller size) to investigate the extent of mixing at the long-term roosts of Livingstone's fruit bats. Counts were not carried out during prolonged spells of rain or mist as this affected visibility.

Roost sites were defined as one or more trees at a discrete location (typically within 50 m of each other) that were used by at least one bat for roosting. To quantify the canopy structure and the composition of tree species at roost sites, the 10 nearest large trees (diameter at breast height > 45 cm) to the main roosting tree (the tree containing most bats) were identified and measured. If the number of roosting trees was greater than 10, all trees that contained roosting bats were sampled. The location of each tree was recorded with a global positioning system. To measure the dimensions of the trees, the total height and height of the first branch were estimated by eye by each team member and

the mean value taken. Canopy diameter was measured by two team members standing directly under opposite edges of the canopy and measuring the distance with a tape measure. Tree trunk diameter at breast height was measured using a tape measure. The Comorian names of tree species and any anthropogenic uses were identified by the Comorian field technicians and local guides.

The structure of the understorey vegetation was sampled at eight locations at 25 and 50 m north, south, east and west of the main roost tree. The location, list of plant species, and description of the ground substrate (rocky, loose soil or fertile soil) within a radius of 2 m of each sample point was also recorded. Canopy cover was measured at each point using a spherical densitometer (Lemmon, 1956). Observations of any trees felled for planks, clearance for agriculture, or damage caused by cyclones or floods were also recorded.

The land cover type (based on land cover maps produced by Green, 2014a) in which the roosts were located was identified using the geographical information system *ArcGIS v. 9.3.1* (ESRI, Redlands, USA). The land cover types were undisturbed forest (old-growth forest with closed canopy and little trace of human impact); degraded forest (mainly closed canopy consisting of native species but with abundant signs of human pressure, such as selective logging and/or clearing of understorey vegetation; some presence of non-native trees or crops); agroforestry (agroforestry species with natural or non-natural understorey); and plantation (few native and/or non-native trees present but dominated by crops). Percentage canopy cover at the roost site, diameter at breast height of the roost trees, elevation and land cover type were included as candidate variables in the analysis. All statistical analyses were conducted in *R v. 2.11.1* (R Development Core Team, 2010). An initial Poisson generalized linear model was run to investigate the relationship between the environmental variables and mean wet-season roost size in the 2 survey years. Wet-season roost counts were considered to be a superior estimate of population size to dry-season counts, as fruit bats are less dispersed throughout the landscape in the wetter part of the year (Mickleburgh et al., 1992; Jenkins et al., 2007). Goodness-of-fit tests revealed an overdispersion parameter of 9.79 for the Poisson generalized linear model, and therefore the standard errors were corrected using a quasi-Poisson generalized linear model in which the variance was the dispersion parameter multiplied by the mean of the dependent variable. Model selection was carried out using stepwise backward deletion of the least significant variable until all variables retained were significant at $\alpha = 0.05$.

The Extent of Occurrence (EoO) and Area of Occupancy (AoO) of the species were calculated to provide two metrics of its geographical range, to guide reassessment for the IUCN Red List. The former was estimated by drawing a minimum convex polygon (MCP) around the outermost known active roosts on both islands. AoO was calculated

TABLE 1 Survey results from roost sites of Livingstone's fruit bats *Pteropus livingstonii* on the islands of Anjouan and Mohéli in the Comoros archipelago (Fig. 1), with the land cover type, altitude, presence of the Seychelles fruit bat *Pteropus seychellensis comorensis*, and land uses and impacts within a 100 m radius.

Roost name	Roost count (Number of trees used for roosting)			Land cover type	Altitude (m)	Seychelles fruit bat*	Land uses & impacts within 100 m
	Wet season 2011–2012	Dry season 2011–2012	Wet season 2012–2013				
Anjouan							
1. Adda (Chava)	28 (2)	18 (2)	41 (3)	Degraded forest	999		Extensive agriculture & felling for construction
2. Bazimini (Hamogne-Panga)	75 (7)	37 (5)	56 (6)	Degraded forest	771	> 10	Encroachment of agriculture
3. Dindri (Dremelani)	6 (2)	0 (0)	6 (2)	Agroforestry	762	> 200	Extensive felling for firewood, construction & agriculture since 2000; trees sparse; loose soil
4. Hombo (Mratsini/Massakini)	87 (3)	164 (3)	146 (3)	Undisturbed forest	812		Undisturbed forest; steep
5. Hombo (Mkirini)	0	0		Agriculture	369		Roost abandoned; agricultural fields
6. Kangani (Kove)	29 (2)	12 (2)	25 (2)	Degraded forest	616		Extensive agriculture & felling for construction
7. Kangani (Bwejou)	3 (2)	5 (3)	3 (2)	Agroforestry	645		Extensive agriculture, bare soil & few remaining large trees
8. Limbi (Trondroni)	69 (5)	46 (3)	53 (4)	Undisturbed forest	977		Mostly undisturbed forest; some banana planting
9. Lingoni (Yimere)	Present	Present		Undisturbed forest	741		Undisturbed forest; steep; major landslide in 2007
10. Moya (Makini)	77 (7)	73 (14)	75 (5)	Degraded forest	626		Encroachment of agriculture; landslides observed in May 2012
11. Mpage (Massakini)	53 (6)	37 (5)	128 (10)	Degraded forest	750		Clearance for agriculture started in May 2012
12. Mromaji (Bandra)	34 (3)	31 (3)	32 (4)	Agroforestry	452	> 200	Extensive agriculture
13. Outsa (Dindri-Jumpbe)	19 (2)	22 (2)	33 (2)	Agroforestry	615	> 90	Extensive agriculture; in 2011 a road was constructed within 200 m of roost
14. Outsa (Hadzoum)	0	0		Agriculture	698		Roost abandoned; agricultural field
15. Nindri-Kowet	67 (9)	18 (3)	81 (3)	Degraded forest	610		Extensive agriculture; roost trees felled in high winds in May 2012
16. Ouzini (Moihajou)	105 (13)	72 (14)	88 (13)	Degraded forest	953		Landslide in May 2012
17. Ouzini (Havoundre)	0	0		Agriculture	803		Roost abandoned; agricultural field
18. Salamani (Mroni-Papane)	97 (5)	40 (14)	59 (5)	Degraded forest	797	1	Extensive clearance for agriculture & felling for construction wood since 1995
19. Salamani (Maveyajou)		9 (2)	15 (2)	Degraded forest	1,078		First located in 2009; some clearance for agriculture & felling for construction wood
<i>Total</i>	749	584	841				

Table 1 (Cont.)

Roost name	Roost count (Number of trees used for roosting)			Land cover type	Altitude (m)	Seychelles fruit bat*	Land uses & impacts within 100 m
	Wet season 2011–2012	Dry season 2011–2012	Wet season 2012–2013				
Mohéli							
1. Fomboni (Mlédjélé)		20 (> 3)		Undisturbed forest	582		Undisturbed forest; bats moved from the original roost site nearby, which shows evidence of recent agriculture
2. Ndrondroni (Hanakulemba)		37 (> 4)		Degraded forest	466		Extensive agriculture
3. Nioumachoi (Banda)		150 (> 6)		Degraded forest	354		Encroachment of agriculture
4. Ouallah (Hassera-Ndrenge)		25 (> 12)		Undisturbed forest	360		Undisturbed forest
5. Ouallah (Kidogo-Basse)		45 (5)		Undisturbed forest	223		Encroachment of agriculture
6. Ouallah (Mkirini)		3 (> 1)		Undisturbed forest	339		Possibly only a feeding site; encroachment of agriculture
Total			280				

*Minimum number recorded at roost site

as the surface area of undisturbed and degraded forest and agroforestry within the MCP located between the altitudes of the lowest and highest currently active roosts (452–1,078 m on Anjouan; 223–582 m on Mohéli).

Results

On Anjouan 15 of the 18 historical roost sites identified in the surveys of 1998–2003 (Sewall et al., 2011) were found to be still active. Ouzini-Havoundre appeared to be abandoned following extensive recent tree-felling (Fig. 1) and no individuals were found at Hombo and Outs-Hadzoum; the sites are now agricultural fields. No bats were found at the Dindri roost during the dry season but six individuals were counted during both wet-season surveys. The Lingoni roost, previously reported as being one of the largest (Sewall et al., 2011), was visited but accurate counts were not possible as no clear vantage point could be accessed safely. Following reports by local farmers, a small, previously unknown roost site was located at Salamani Maveyajou. We therefore consider that there are currently 16 active roosts on Anjouan.

In the wet season of 2012, 749 individuals were recorded at Anjouan roosts (not including the Lingoni roost; Table 1). During the following dry season 584 individuals were recorded, including nine at the newly discovered roost in Salamani. In the wet season of 2013, 841 individuals were recorded across the Anjouan roosts (not including the Lingoni roost), including 15 at the newly discovered roost, confirming that the newly identified site is used in both seasons (Table 1). The altitudinal range of occupied roosts on Anjouan was 452–1,078 m (Table 1), and the four abandoned roosts were all located at 369–803 m.

All five roost sites on Mohéli identified during 1998–2003 were found to be occupied in 2012 (Fig. 1); however, the roost at Fomboni was a few hundred metres from the historically recorded location. Following local reports, three individuals were found at a sixth site in Ouallah (Mkirini), but further monitoring is required to confirm that this is a roost rather than a feeding site. A seventh roost was reported locally but confirmation of its existence was not possible. All Mohéli roosts were found at altitudes of 223–582 m. A total of 280 individuals were recorded in the dry season; no wet-season counts were conducted. Summing the Anjouan 2013 wet-season counts and the Mohéli dry season counts (Table 1) we calculate the minimum global Livingstone's fruit bat population to be 1,121 individuals. The mean size of roosting populations in the dry season was $46.7 \pm SE 9.1$ on Mohéli and $30.7 \pm SE 21.5$ on Anjouan (Table 1).

We estimated the EoO of Livingstone's fruit bat to be 866.7 km² (an MCP around all occupied roosts). Within the EoO the surface area of potentially occupied habitat, and therefore the AoO, was estimated to be 113.6 km² in total (80.6 km² on Anjouan, 33.0 km² on Mohéli).

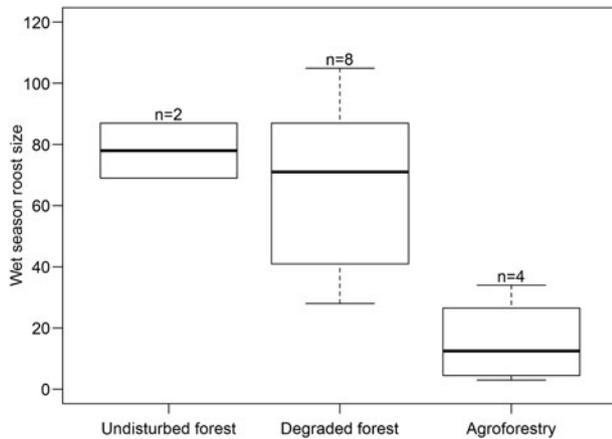


FIG. 2 Boxplot of Livingstone's fruit bat's wet-season roost size in undisturbed forest, degraded forest and agroforestry areas. Mean roost size is significantly lower in agroforestry areas than in undisturbed ($P = 0.005$) and degraded forest ($P = 0.008$), with no significant difference between the latter two ($P = 0.364$).

In the analysis of environmental correlates of roost size, only land cover type was retained in the final model ($F_{(2,13)} = 8.30$, $P = 0.006$), with evidence of a significantly lower wet-season roost size in agroforestry areas (mean = $17.0 \pm \text{SE } 7.4$, $n = 4$) than in undisturbed (mean = $88.8 \pm \text{SE } 27.8$, $n = 2$; $P = 0.005$) and degraded forest (mean = $72.5 \pm \text{SE } 8.5$, $n = 7$; $P = 0.008$; Fig. 2). Although the mean roost size in undisturbed forest was greater than in degraded forest, there was no evidence of a significant difference ($P = 0.364$).

All but one occupied roost site on Anjouan, Hombomrantsini, had signs of vegetation clearance or significant erosion (Table 1). Severe weather caused landslides or brought down roost trees at three roost sites during the survey period alone and signs of recent felling of trees for agriculture and/or construction wood were evident at 13 of the 16 occupied sites (Plate 1).

Only four tree species were used for roosting on Mohéli, compared with 12 on Anjouan (Table 2). *Ficus exasperata* was the only species used as a roost tree on both islands; it was the most frequently used species for roosting and was found at the greatest number of sites. Larger numbers of *F. exasperata* roost trees were found mainly at elevations < 500 m. Of all tree species used for roosting, 80% were native or endemic to the Comoros, with the hard wood *Gyrostipula comoriensis* being the most frequently used for roosting on Anjouan ($n = 15$ trees). *Albizia glaberrima* was the only introduced species used for roosting on Anjouan. Two introduced species were used on Mohéli: *Albizia lebbek* was the most frequently used ($n = 9$) at three sites, and *Terminalia catappa* was used only at one site (Table 2).

Discussion

We report the most comprehensive survey to date of Livingstone's fruit bat, in which we recorded 749–841

individuals at 15 long-term roosts and one previously unknown roost on Anjouan, and 280 individuals at five roosts on Mohéli during the dry season. The largest roosts on Anjouan were found at sites within a narrow altitudinal range of 600–960 m, with three roosts located at lower altitudes found to be abandoned. Given the extent and intensity of the survey, alongside a contemporaneous major biodiversity assessment of Anjouan's forest (Green, 2014b), we consider it unlikely that we missed any Livingstone's fruit bat roosts supporting more than a few individuals on this island.

However, resource and logistical constraints meant the survey had a number of limitations. It was not possible to conduct simultaneous counts at all the roosts on each island, and therefore we cannot rule out the possibility that bats were moving between roosts within the survey period and were double-counted or missed entirely, although these sources of bias are likely to balance each other out. On Anjouan a landslide rendered the Lingoni roost inaccessible and no counts were possible. Bat numbers at this roost were previously reported to have been high (Sewall et al., 2007), with 96 counted in 1998 (Granek, 2002) and 125 in 2002 (Sewall et al., 2011). Assuming the Lingoni roost population has not changed markedly since then we are likely to have underestimated the Anjouan population by c. 100 individuals.

Counts on Mohéli were only possible during the dry season, when roost populations on Anjouan were on average 30% lower than in the wet season. This is in line with previous observations of this species (Granek, 2002) and seasonal changes in colony size of other *Pteropus* species (Mickleburgh et al., 1992; Jenkins et al., 2007), and is attributed to the lower availability of fruit during the dry season resulting in bats roosting more frequently at temporary sites nearer to food resources. If we adjust the Anjouan population estimate to take into account the missing Lingoni count and increase the Mohéli count by 30% to allow for seasonal differences, we estimate the global population of Livingstone's fruit bat to be c. 1,260 individuals.

This is substantially lower than numbers of any other Indian Ocean fruit bat for which robust population data exist, and possibly the lowest of any fruit bat globally. The Critically Endangered Rodrigues fruit bat *Pteropus rodricensis* has the next lowest known population size of c. 10,000 individuals (V. Tatayah, pers. comm.). The Vulnerable Aldabra fruit bat *Pteropus aldabrensis* is thought to be low in number but has not been subject to rigorous surveys and therefore its population size is uncertain. It is difficult to relate the current population estimate to those published previously (Reason & Trehwella, 1994; Trehwella et al., 1998; Granek, 2002; Sewall et al., 2007), to quantify population trends in this species. In particular, the survey intensity and number of roost sites visited has varied between studies. Prior to this study the most recent published estimate of 1,200 individuals (Sewall et al., 2007), based on surveys conducted in 2002, was obtained using a team of local



PLATE 1 Livingstone's fruit bat *Pteropus livingstonii* roost sites on the islands of Anjouan and Mohéli in the Comoros archipelago (Fig. 1). (a) View of the Moya roost from the survey point; (b) undisturbed forest at the Fomboni roost; (c) landslide at the Ouzini-Moihajou roost; (d) unstable soil resulting from recent land clearance for agriculture at the Mpage roost.

community members with variable levels of training and access to survey equipment, and the reliability of these counts has never been assessed. The current study used a small number of well-trained and experienced observers, who conducted simultaneous counts at sites, and therefore the estimate reported here is likely to be the most reliable to date.

However, given the ongoing habitat loss and degradation over the previous decade, our estimate of 1,260 bats probably does not indicate that the population has remained unchanged across this time period. Deforestation rates in the Comoros were the highest of any country during 2000–2010 (FAO, 2010). Three roosts on Anjouan have been lost since the early 2000s, following tree felling and clearance for agriculture. We found evidence of agricultural encroachment, under-planting of crops, tree-cutting or major landslides following clearance of vegetation within 50 m of all but one of the 16 occupied roosts on Anjouan. During the study heavy rains resulted in flooding and landslides, which swept away at least two trees used for roosting and opened the canopy at three roost sites. Only the Hombo-Mratsini roost appears to be under no immediate threat from vegetation clearance or landslides as it is situated on a well-forested slope that is too steep for agriculture. Fragmented forests are more vulnerable to damage caused

by severe weather, as edge effects such as increased air temperature, reduced canopy cover and elevated tree mortality increase with proximity to the forest boundaries (Laurance et al., 2002). On Anjouan the remaining natural forest is fragmented and found only on steep slopes at high elevations, and therefore we expect further damage to roosting sites in the coming years. Furthermore, all 15 tree species used for roosting are currently exploited by local people for firewood, animal forage, medicinal uses and producing planks. Eleven of these are hard woods, of which eight are known to be felled for planks used in building construction, and the emerging use of chain-saws and a commercial market on Anjouan appear to be driving widespread tree cutting (H. Doulton, pers. comm.).

The only environmental variable associated with size of roost populations was land cover, with roosts located in agroforestry areas being on average 3–5 times smaller than in degraded and undisturbed forests. A previous study (Granek, 2002) found that the size of bat roosts was positively associated with increasing canopy cover, presence of a watercourse, steepness of slopes and a south-east aspect, suggesting they prefer to roost at sites with higher humidity and sheltered from the midday sun and stronger winds. The newly discovered Anjouan roost was found at an altitude of

TABLE 2 Tree species used for roosting by Livingstone's fruit bats on the islands of Anjouan and Mohéli in the Comoros archipelago (Fig. 1), with no. of roost trees, no. of roost sites, geographical status, human uses, and whether the species is known to be used by the bats for feeding.

Tree species	No. of roost trees	No. of roost sites	Island	Geographical status	Human uses	Used for feeding
<i>Ficus exasperata</i>	23	12	Anjouan & Mohéli	Native	Animal forage, firewood	Yes
<i>Gyrostipula comoriensis</i>	15	6	Anjouan	Native	Planks, firewood	
<i>Gambeya</i> spp.	10	6	Anjouan	Native	Planks (high demand)	
<i>Ficus lutea</i>	10	6	Anjouan	Native	Animal forage, firewood	Yes
<i>Nuxia pseudodontata</i>	10	8	Anjouan	Endemic	Planks, firewood	
<i>Albizia lebeck</i>	9	3	Mohéli	Introduced	Animal forage, firewood	
<i>Ocotea comoriensis</i>	6	3	Anjouan	Endemic	Planks (high demand), firewood	Yes
<i>Weinmannia comoriensis</i>	5	4	Anjouan	Endemic	Planks (high demand), firewood	Yes
<i>Brachylaena ramiflora</i>	5	5	Anjouan	Native	Firewood	
<i>Ficus pirifolia</i>	3	3	Anjouan	Native	Animal forage, medicinal	Yes
<i>Terminalia catappa</i>	3	1	Mohéli	Introduced	Animal forage, firewood	Yes
<i>Antidesma hildebrandtii</i>	2	1	Anjouan	Native	Planks	
<i>Albizia glaberrima</i>	2	2	Anjouan	Introduced	Animal forage, firewood	
<i>Khaya comorensis</i>	2	2	Mohéli	Endemic	Planks, medicinal	Yes
<i>Cryptocarya</i> spp.	1	1	Anjouan	Native	Planks	

1,078 m but all others are located below 1,000 m despite the majority of remaining undisturbed forest lying above this elevation; this suggests there is an altitudinal limit to roosting, although the mechanism for this is not clear.

Given the suspected severe population decline as a result of widespread and long-term forest loss, with these threats continuing even around long-term roosting sites, Livingstone's fruit bat has now been recategorized as Critically Endangered on the IUCN Red List (Sewall et al., 2016). The species is in urgent need of conservation measures. In the western Indian Ocean and beyond there have been some notable conservation successes in the recovery of fruit bats; for example, the Pemba fruit bat *Pteropus voeltzkowi* population in Tanzania was reduced to only a few hundred individuals by the early 1990s, following severe habitat fragmentation and hunting for food (Mickleburgh et al., 1992). Since the establishment of a community-based conservation programme enforcing habitat protection and a reduction in hunting in the mid 1990s (Entwistle, 2001), the population had increased to c. 19,000 by the end of 2006 (Juma, 2007). The Rodrigues fruit bat has recovered from just a few hundred individuals in the 1970s to perhaps > 10,000 today thanks to long-term forest restoration work and a moratorium on hunting (Powell & Wehnelt, 2003). Recovery of Livingstone's fruit bat in a similar way will be challenging considering that hunting bans have played an important role in these successful recoveries of other *Pteropus* species (Mickleburgh et al., 1992; Robinson et al., 2010) and that hunting is not a threat in the Comoros.

Efforts are now underway by the NGO Dahari to conserve the southern Moya forests of Anjouan to protect and restore water catchments and biodiversity. The project intervention zone covers seven roosts of 250–400 bats. Alongside this initiative are government-led plans to establish the first terrestrial protected area on Anjouan, around the Nringui forest block, and to extend the reach of the Mohéli Marine Park to forest habitat (UNDP, 2013). However, given the vulnerability of the remaining roost sites to erosion, the apparent fidelity of the bat to these long-term roosts, and the lack of remaining suitable habitat for roosts, local-scale action to protect these sites is urgent. This is in line with previous recommendations by Sewall et al. (2011) for local-scale forest reserves. The challenge, however, will be to design a locally acceptable and sustainable mechanism that will both protect and restore roost sites as well as offset the opportunity costs to local impoverished farmers.

A payment for ecosystem services scheme to protect bat roosts may form part of the solution and is being trialled by local NGO Dahari. They are currently signing agreements with landholders around three pilot roost sites, with the aim of protecting the roost trees from felling and gradually reforesting the surrounding area with native trees to provide food and shade. In return the landholders will be supported by Dahari to improve agricultural revenues from their other plots through provision of improved varieties of banana and taro to plant under the native forest cover. In the longer term the aim is for the initiative to be financed through

ecotourism and contributions from partner zoos holding the species for in situ conservation.

However, identifying specific conservation recommendations beyond protection of important roost sites is hampered by a lack of knowledge of the distribution of other key ecological resources, such as the main foraging sites. Future study of the population dynamics of Livingstone's fruit bats is necessary to understand the degree of movement between roosts and islands. Most importantly the feeding ecology of the species needs to be investigated further than initial studies (Trehwella et al., 2001; Sewall, 2002) to understand the availability of food resources and to identify important feeding sites requiring protection. This work would also help to elucidate the bat's role in the ecosystem as a pollinator and seed disperser, and therefore its potentially high-value role in forest dynamics.

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Author contributions

BD led the data collection, data analysis and drafting of the article. KG conducted data collection and analysis and made comments on the article. HD helped draft and edit the article. DS and IS advised on survey design and collected field data. MH and JD supported data analysis and provided comments on the article. RY oversaw the design and delivery of the study and drafted and edited the article.

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Biographical sketches

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