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In the land of giants: habitat use and selection of the Aldabra giant tortoise on Aldabra Atoll

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Abstract

With habitat loss and fragmentation among the greatest threats to biodiversity, a better understanding of the habitat use of keystone species is critical in any conservation management strategy. Aldabra Atoll, in the Seychelles archipelago, has the largest population worldwide of giant tortoises. This endemic species (*Aldabrachelys gigantea*) could be vulnerable to habitat fragmentation and loss induced by climate change related reduction in rainfall. Here, we assess habitat use and selection by *A. gigantea* in its natural environment on Aldabra. We quantified the habitat areas of *A. gigantea* based on the first high-resolution terrestrial habitat map of Aldabra, produced for this purpose using satellite imagery. The resulting map was combined with 4 years of movement data to assess *A. gigantea* habitat use and selection at landscape and home range scales. Grassland or 'tortoise turf' habitat was most preferred by *A. gigantea* on Aldabra, at the landscape scale across seasons, followed by open mixed scrub. These two habitats cover only 30 km^2 (19.2%) of the surface of the atoll (total area: 155.5 km^2). At the home range scale, there was no significant preference shown and habitat was used randomly. Our results suggest that Aldabra's grassland habitat, despite its small area, is of great importance to *A. gigantea*. Conservation management actions for *A. gigantea* on Aldabra and elsewhere should therefore focus on the protection and maintenance of this habitat.

Keywords Habitat mapping · Home range · Megaherbivore · Remote sensing · Seychelles · Western Indian Ocean

Introduction

Habitat type and quality can influence an animal's physiological capacities and subsequently its demography and ecology (Beyer et al. 2010). Habitat selection, which occurs if habitat types are used disproportionately to their availability (Johnson 1980), may be

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governed by a variety of environmental features, such as seasonal weather patterns, food availability, habitat structure, and mobility of the animal (Bailey et al. 1996; Krausman 1999; Franks et al. 2011; Rozylowicz and Popescu 2012). This is especially accentuated in environments where fluctuations in water availability and high temperatures are physiologically stressful to the animal (Franks et al. 2011). Species of conservation concern can be particularly vulnerable to these effects, and informed decisions on their conservation management must be based on sound knowledge of key ecological aspects such as habitat selection, structure and availability (Zylstra and Steidl 2009), particularly in light of likely climate change impacts on habitats.

For ectotherms such as tortoises, survival in (semi-)arid environments depends heavily on the availability and selection of suitable shade refuges (Moulherat et al. 2014). Several tortoise species have been observed to move in relation to habitat configuration and composition, such as *Testudo hermanni* in Italy (Rugiero and Luiselli 2006) and *T. graeca* in Spain (Anadon et al. 2006). In our study we focus on Aldabra Atoll in Seychelles, home to the largest population of giant tortoises in the world, numbering approximately 100,000 individuals (Bourn et al. 1999). Previous studies have suggested the importance of certain habitats, such as grassland, to the Aldabra giant tortoise (*Aldabrachelys gigantea*; Gaymer 1968; Merton et al. 1976; Gibson and Hamilton 1983).

Despite several studies of the vegetation of Aldabra (Fosberg 1971; Hnatiuk et al. 1976; Hnatiuk and Merton 1979; Gibson and Phillipson 1983a, b), the only existing vegetation map until recently was developed by Gibson and Phillipson (1983a, b). The methodology for this map however, was based on aerial imagery from the 1960s. Recent advances in remote sensing techniques and methods offer increased accuracy to discriminate between vegetation types (Kerr and Ostrovsky 2003). Combining GPS technology with remote sensing data allows fine-scale associations between animals and habitat features or vegetation types to be identified (Rutter 2007; Cagnacci et al. 2010). Here we use this combined approach to provide a much-improved level of detail related to the species' current habitat use.

Aldabrachelys gigantea is one of two extant species of giant tortoise, the other being the Galapagos tortoise (*Chelonoidis nigra*). Both species are considered threatened and as high-profile iconic species they have been major flagship species for conservation efforts. Many islands worldwide used to harbour large or giant tortoises until recently (Hansen et al. 2010) and they were often among the largest, if not the largest, vertebrates in these ecosystems. They thus likely play or played similar functional roles as continental mega-faunal herbivores (Hansen and Galetti 2009) and can be considered as island ecosystem engineers. Recent studies of Galapagos tortoises support this view, as the tortoises have been found to physically modify their habitats through seed dispersal, trampling, nutrient cycling, and by altering vegetation composition through selective herbivory (Gibbs et al. 2010; Froyd et al. 2014; Bastille-Rousseau et al. 2017). Additionally, the introduction of non-native extant giant tortoises to restore missing ecological functions has been proposed and implemented to mitigate the ecological consequences of giant tortoise extinction on islands in the Galapagos, the Mascarenes, Madagascar and in some granitic Seychelles islands (Griffiths et al. 2010; Hansen et al. 2010; Froyd et al. 2014). Understanding the habitat requirements of *A. gigantea* in its original habitat is therefore valuable for the successful introduction and management of extant giant tortoises as ecological engineers in such rewilding projects (Griffiths et al. 2010; Hansen et al. 2010).

Tortoises are known to move seasonally in response to behavioural and ecological factors, such as food availability and quantity, the suitability of habitat for nesting, and reproductive status (Rozylowicz and Popescu 2012; Blake et al. 2013). On the tropical, arid

atoll of Aldabra the tortoises' daily survival is reliant on thermal refuges created by trees, shrubs, caves, pools and mud wallows (Merton et al. 1976; Bourn and Coe 1978). The tortoises are found in the largest densities on 'tortoise turf' grassland, a mixture of grasses and herbs, which comprises a large proportion of their diet (Hnatiuk et al. 1976; Merton et al. 1976; Gibson and Hamilton 1983). Indeed, the overall availability of food, shade and water has been suggested as the main limiting factor on the growth and survival of the *A. gigantea* population on Aldabra (Merton et al. 1976). Reflecting this, seasonal movements of *A. gigantea* have been documented in response to changing food availability, with the use of grassland habitat by tortoises declining as the dry season progressed (Grubb 1971; Bourn and Coe 1978; Gibson and Hamilton 1983). However, these studies did not quantify the habitat selection of *A. gigantea* continuously over time, collecting data only at one point in time. Furthermore, they did not examine habitat selection at an individual level or across levels.

As long-lived reptiles, with limited dispersal capabilities, tortoises are vulnerable to habitat loss or fragmentation (Rozylowicz and Popescu 2012). While generally flat and seemingly well connected as a whole, Aldabra as a tortoise habitat is broken up into several regions, both by deep channels between the main islands, and by habitat barriers within islands (Gibson and Hamilton 1983). Although the population of *A. gigantea* on Aldabra is currently considered to be stable, the difference in subpopulation densities is thought to be due to differences in prevailing main habitat type between some of the regions, resulting in varying ecological selective pressures on the subpopulations (Turnbull et al. 2015). Future effects of climate change, such as decreased rainfall, increased droughts and subsequent reduced productivity of vegetation, could have a pronounced effect on the habitats of Aldabra that the tortoises depend on (Haverkamp et al. 2017).

Here, our aim is to map the terrestrial habitat types of Aldabra and their use and selection by *A. gigantea* to provide a basis for informed conservation management decisions on Aldabra and in rewilding projects on other islands. We combine a high-resolution terrestrial habitat map of Aldabra produced using remote sensing imagery, and GPS telemetry data from 34 tortoises and assess; (1) the used, selected and avoided habitats of giant tortoises on Aldabra with respect to available habitat: and (2) whether the climatic seasons affect habitat selection.

Methods

Study site

The UNESCO World Heritage site of Aldabra Atoll (9°24′S, 46°20′E), in the Seychelles archipelago, Western Indian Ocean, is one of the largest raised coral atolls in the world with a land area (to high water mark) of 155.5 km^2. Aldabra is comprised of four main islands (Picard, Polymnie, Malabar and Grande Terre) that are separated by tidal channels. The atoll is composed of exposed coral limestone, defined as 'champignon', a highly pitted and eroded rock, and 'platin' which is smooth and flat. The terrestrial vegetation is dominated by a dense scrub of varying height and extensive mangrove forest. This is interspersed with open platin areas that are covered with a mixture of grasses and sedges or 'tortoise turf', and mixed scrub (Merton et al. 1976). The platin areas are important for giant tortoises as they host temporary rainwater pools during the wet season (Gaymer

1968). On Aldabra, *A. gigantea* occurs on Picard, Malabar and Grande Terre, with Grande Terre containing the majority of the population (Bourn and Coe 1978).

There are two main tropical climatic seasons on Aldabra; the wetter northwest monsoon (November–April) and the drier southeast monsoon (May–October) (Gibson and Hamilton 1983). The mean monthly temperature ranges between 24 and 28 °C throughout the year (1968–2008, excluding 1992–1999) (Shekeine et al. 2015), but the midday temperature can reach more than 36 °C (Duhec et al. 2010). Mean annual rainfall is ca. 975 mm with the majority falling between December and April. Shekeine et al. (2015) identified a decline in rainfall at Aldabra during 2004–2012 of 6.6 mm per year.

Data collection

Satellite imagery for terrestrial habitat map

Four satellite images of Aldabra were acquired by the GeoEye-1 satellite (Digital Globe 2011) on 19th November 2011. The multispectral images (blue: 450–510 nm, green: 510–580 nm, red: 655–690 nm, near-IR: 780–920 nm) have a spatial resolution of 2×2 m. To remove atmospheric signal contributions and derive surface reflectance (Horning et al. 2010), the images were pre-processed using the cos(t) atmospheric correction algorithm implemented in IDRISI (Cos(t) model, ATMOSC module, IDRISI Selva v17.0 Geographic Information Systems and image processing software package (www.clarklabs.org/produ cts); spectral band characteristics, satellite configuration and solar angle parameters according to metadata of imagery; band-wise maximum dark object subtraction value parameter retrieved from darkest ocean pixels). Once corrected, a mosaic was created (MOSAIC module, IDRISI), with the projected coordinate system WGS 1984 UTM Zone 38 South.

Aldabrachelys gigantea movement data

Thirty-four adult *A. gigantea* were fitted with custom-built GPS tags (www.e-obs.de) and tracked between February 2012 and May 2016, to study their movement and habitat use. These included 17 tags deployed on Grande Terre tortoises, eight on Picard, and six on Malabar. The final three tags were re-used on new individuals (two on Grande Terre, one on Malabar) when the original deployment detached (two tortoises) or the tortoise died (one tortoise was found dead from unknown causes). The tags recorded geographical position data every hour between 06:00 and 20:00 (local time). Data were downloaded from the tags every 3–6 months, using radio telemetry equipment to locate the tortoises.

Data analysis

Terrestrial habitat mapping

Based on classes used in a previous map by Gibson and Phillipson (1983a, b) and extensive field knowledge, we identified eight main habitat classes on Aldabra Atoll (Table 1). To map the distribution of those habitats, we used a supervised classification approach, namely the Maximum Likelihood Classification (MLC) (Environment for Visualising Images (ENVI) 5.1 [www.exelisvis.com]). Originally, 538 data points were collected in 2009 from 11 transects across the atoll. A subset of these data points (10–20

Table 1 Description and area (and % cover) of habitat categories of the final atoll-wide terrestrial habitat map of Aldabra Atoll

Habitat Category	Description	Across Aldabra		Area km^2 (% cover) per island			
		Area km^2	% Cover	Picard	Malabar	Grande Terre	Polymnie
Mangrove	Homogeneous areas covered by mangrove tree species	17.2	11.1	1.76 (19.5)	3.38 (13.1)	9.53 (8.82)	0.18 (9.3)
Open mixed scrub	Woody plants at low density. Ground layer vegetation has high percentage cover of tortoise turf. Dicotyledonous herbs and long grasses are rare	25.4	16.3	0.87 (9.61)	1.61 (6.24)	22.47 (20.8)	0.14 (7.34)
Standard mixed scrub	Similar to open mixed scrub but woody plants at higher density	42.3	27.2	2.63 (29.1)	7.62 (29.6)	30.42 (28.2)	0.9 (47.04)
Pemphis scrub	Homogeneous habitat dominated by *Pemphis acidula*	35.8	23.0	3.14 (34.8)	12.54 (29.6)	19.14 (28.2)	0.51 (26.82)
Grassland	Homogeneous areas of tortoise turf grass. Composed of 21 species of sedges, grasses and herbs	4.5	2.89	0.13 (1.43)	0.09 (0.36)	4.18 (3.86)	0.01 (0.31)
Exposed surface	Limited vegetation cover, absent in some areas and where present dominated by tortoise turf. Bare substrate composed of champignon, sand or platin	20.1	12.9	0.03 (3.51)	0.33 (1.27)	17.32 (16.0)	0.12 (6.15)
Champignon	Dominated by areas of champignon rock, with minimal vegetation	4.8	3.07	0.17 (1.87)	0.17 (0.68)	4.3 (3.99)	0.02 (2.96)
Sand	Dominated by sand substrate, small amount of ground level vegetation in some areas. Also includes dried out seasonal pools on Grande Terre	2.8	1.83	0.02 (0.20)	0.00 (0.02)	0.7 (0.64)	0.00 (0.08)
Unclassified	Masked areas due to cloud cover and cloud shadows on satellite imagery	2.6	1.71	n/a	n/a	n/a	n/a

data points per habitat category) was selected to train the classifier based on an even spatial distribution across the atoll, and on homogeneity for the given habitat type (Tso and Mather 2009). Before running the classifier, we calculated the mathematical separability of the training points using the transformed divergence (TD) values. A cloud and sea mask was applied to enhance the performance of the classification algorithms.

We used a confusion matrix to assess the accuracy of the classification, where the category of each training data point was compared with the class assigned by the MLC to the same pixel (EXILIS 2016). Due to mixing of classes and low confusion matrix scores in early iterations of the classifier, we removed the training points for sand, grassland, and (open) champignon habitat classes and selected image-based training points for these classes. The final iteration of the classification used a total of eight habitat classes (Table 1) and resulted in a confusion matrix score of 83.7%.

Validation and accuracy assessment of classification images is a critical step in the mapping process (Horning et al. 2010). To further assess the accuracy of the final habitat classification, we used a set of independent points from the training data set, which had not been used as training samples, as validation against the classification image. This method is an accepted approach for the validation of classification images (Jones and Vaughan 2010). The overall accuracy score of the confusion matrix was 90.9%. We produced the final terrestrial habitat map of Aldabra at a resolution of 2×2 m to maintain a high level of spatial detail and information, and the projection was set as WGS-84 UTM 38 South. No spatial filters were applied to the classification image as the original level of pixel resolution was required for the further data analysis undertaken in this study.

Aldabrachelys gigantea habitat use

To analyse *A. gigantea* habitat use and selection we first processed all of the GPS locations in the R 3.1.2 software program (R Core Team 2013) using the R package adehabitatLT (Calenge 2009). We then removed any remaining clear outliers (e.g. those far out at sea) by eye in ArcMap v10.2.2 with the data locations overlaid on the habitat map. All remaining locations (352,953 locations) were used irrespective of the temporal variations in the data collection period between individuals.

To extract habitat use, we estimated individual home ranges by applying the adaptive local convex hull (aLoCoH) method to the GPS location data (Wall 2014; Getz et al. 2007) (ArcMET tool, extension version 10.2.2v3 in ArcMap). We selected the aLoCoH method as it gives a more conservative estimate of home range than the minimum convex polygon method (Walter et al. 2011). For each animal we selected 100th percentile values and the '*a*' parameter value was set to 0.0. This allowed the algorithm to use the maximum displacement value between any two points in the data, which is considered to be the optimum value (Wall 2014). We then extracted the habitat available in each individual aLoCoH home range polygon from the terrestrial habitat map.

For the within home range use, we extracted the habitat at the single GPS location points. We first applied a 3-m radius buffer to reduce the influence of the GPS tag location uncertainty. Using a distance root mean squared (DRMS) method, which is the square root of the average of the square errors (σ^2) of longitude (x) and latitude (y), Baxter (2015) established an average tag location uncertainty of 7.9 m. Using the buffered points we extracted the tortoise's habitat use from the terrestrial habitat map.

Compositional analysis of habitat selection

We performed all statistical analysis in the R 3.1.2 software program (R Core Team 2013). We used Johnson's model of habitat selection (Johnson 1980), which has been applied in several studies of tortoise habitat use (Kazmaier et al. 2001; Anadon et al. 2006; Rozylowicz and Popescu 2012). We adopted a hierarchical approach of habitat selection at the local scale using a compositional analysis (Aebischer et al. 1993; Ade-HabitatHS package v.0.3.10 Calenge 2006). Compositional analysis uses a multivariate analysis of variance (MANOVA) approach to analyze two sets of data in which variables are represented as proportions (Aebischer et al. 1993). It determines the statistical significance of differences among habitats to be determined and orders habitats in their relative preference (John and Kostkan 2009). Compositional analysis is also considered an appropriate statistical test for data collected by GPS tracking devices, which are characterised by non-independence and autocorrelation (Pendleton et al. 1998).

We analysed data following Johnson's (1980) model and using a compositional statistical analysis for 34 *A. gigantea* and seven habitat classes at two scales. We omitted the eighth habitat class 'sand' from all analyses following Aebischer et al. (1993) as there were zero or proportionally very low (< 1.0%) values in 70% of the home ranges, indicating that this habitat is infrequently used by *A. gigantea*. We applied parametric tests in all analyses and replaced any other zero values that occurred in the used habitat proportions with 0.01 (Aebischer et al. 1993).

We intended to perform the first-order selection analysis, where the home range habitat used was tested against the physical or geographical range of a species, but this was not possible as the only natural population of *A. gigantea* is at Aldabra. All populations on other islands in Seychelles, and elsewhere, are reintroduced/rewilded populations and GPS location data is not available yet. In the second-order selection, the collective home range habitat use of the 34 tortoises was tested against the habitat available across Aldabra. We also analysed second-order selection at the island scale, where the home range habitat use of the tortoises tagged on that island (Picard: $n = 8$; Malabar: $n = 7$; Grande Terre: $n = 19$) was tested against the available habitat on that island. In the third-order selection, the collective habitat use of the 34 tortoises (from GPS location data) was tested against the habitat available in their collective home ranges. Third-order selection analyses were also conducted at the island scale, where again the collective habitat use of *A. gigantea* on each island was tested against the habitat available on that island.

To determine the seasonal habitat use of *A. gigantea* we selected GPS location points in core periods of the wet (December–January) and dry (September–October) seasons, which represented the wettest and driest 2-month periods of the year, respectively (mean rainfall during 4 years of study period in December–January: 125.6 mm ± 23.7 SE; September–October: 10.1 mm ± 2.4; SIF, unpublished data). The available movement data allowed for four dry and wet season periods each (dry season: 01/09–31/10/2012, 01/09–31/10/2013, 01/09–31/10/2014, 01/09–31/10/2015; wet season: 01/12/2012–31/01/2013, 01/12/2013–31/01/2014, 01/12/2014–31/01/2015, 01/12/2015–31/01/2016). We used a compositional analysis approach as described previously. We applied a third-order selection approach, in which the habitat available in all *A. gigantea* home ranges was compared to the habitat used by *A. gigantea* in each season.

Results

Terrestrial habitat map

Of Aldabra's 155.5 km^2 area, standard mixed scrub was the dominant habitat type (42.3 km^2), followed by pemphis scrub (35.8 km^2), open mixed scrub (25.4 km^2) and other habitat types (Table 1; Fig. 1). There was distinct variation between islands in the proportional area of each habitat type (Table 1).

Tortoise habitat use and selection

Habitat use within the home ranges by *A. gigantea* varied between islands (Fig. 2), with open mixed scrub and standard mixed scrub having the greatest utilization. The overall home range size for all tracked *A. gigantea* was 1.2–151.1 ha (mean ± SE: 23.4 ± 5.2 ha, $n = 34$). Home range size for Picard was 24.1 ± 7.8 ha ($n = 8$), for Malabar 4.9 ± 0.9 ha ($n = 7$) and for Grande Terre 30.0 ± 8.4 ha ($n = 19$).

Tracked *A. gigantea* did not select their home range habitat randomly either across the atoll (second-order selection analysis of habitat composition of all *A. gigantea* home ranges compared to the entire atoll: $\Lambda = 0.01$ and $P < 0.05$), or on each island (second-order selection of habitat use by island, comparing habitat available in home ranges to that of each island: Picard: $\Lambda = 0.005$, $P = <0.05$; Malabar: $\Lambda = 0.022$, $P = <0.05$; Grande Terre: $\Lambda = 0.063$, $P = <0.05$). The ranking matrix of the comparison of all *A. gigantea* home ranges compared to the entire atoll resulted in the simplified rank order of grassland > open mixed scrub > exposed surface > standard mixed scrub > champignon > mangrove > pemphis scrub (Table 2). In the comparison of habitat available in home ranges to that of each island, grassland was the most preferred habitat and pemphis scrub least preferred, with no inter-island differences shown in the rank preference order despite variation in availability of habitats between islands. Habitat use by *A. gigantea* within their home ranges was random (third order selection analysis of habitat used compared to that available within home ranges for all tortoises across atoll: $\Lambda = 0.081$, $P = 0.33$); however, when delineated by island habitat was not selected randomly on Malabar or Grande Terre (third-order selection analysis by island, of habitat used compared to that available in their home ranges: Malabar: $\Lambda = 0.002$, $P = <0.05$; Grande Terre: $\Lambda = 0.381$, $P = <0.05$), but was random on Picard (Picard: $\Lambda = 0.295$, $P = 0.14$). On Malabar the most preferred habitats were standard mixed scrub and open mixed scrub and least preferred was exposed surface. Whereas on Grande Terre pemphis and grassland were most preferred and champignon least preferred.

Seasonal habitat use and selection

Habitat selection within the home ranges was random in all seasons (third-order selection analysis: Year 1: $\Lambda = 0.760$, $P = 0.22$ *dry*; $\Lambda = 0.682$, $P = 0.07$ *wet*; year two: $\Lambda = 0.829$, $P = 0.44$ *dry*; $\Lambda = 0.858$, $P = 0.58$ *wet*; year three: $\Lambda = 0.756$, $P = 0.32$ *dry*; $\Lambda = 0.673$, $P = 0.17$ *wet*).
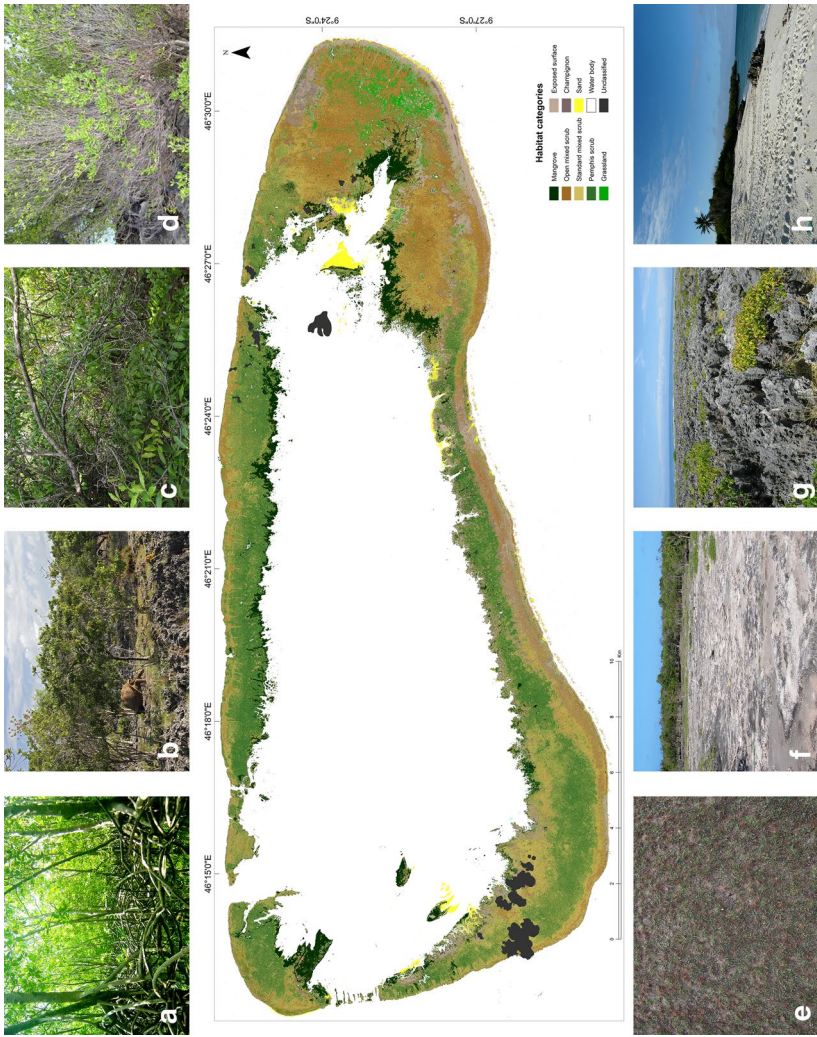
Fig. 1 Terrestrial habitat map of Aldabra Atoll (reference year 2011). Photos show examples of habitat categories: **a** mangroves; **b** open mixed scrub; **c** standard mixed scrub; **d** pemphis scrub; **e** grassland; **f** exposed surface; **g** champignon; and **h** sand (*Source* Baxter, Hansen, Quanz and van de Crommenacker)
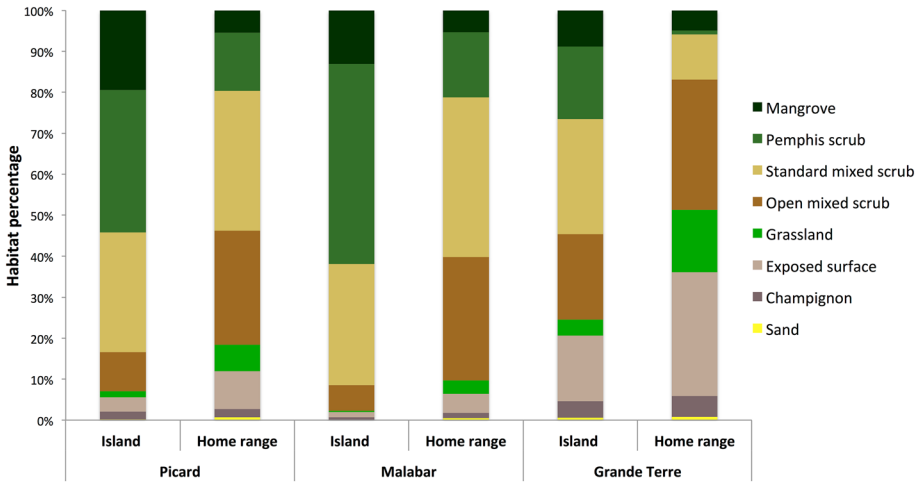
Fig. 2 Percentage of habitat type available by island and home ranges for the tagged giant tortoises on Aldabra

Discussion

The terrestrial habitat map produced using remote sensing techniques is the first validated map based on supervised automated classification for Aldabra and will be invaluable in management and research of the atoll. Through the delineation of habitat classes alongside data on use and selection, the habitat map will allow researchers and conservation managers to generate more accurate and precise population estimates of *A. gigantea* in the future through the use of parameters, such as occupancy or density. The map also has implications beyond the management of the *A. gigantea* population and will serve as an important baseline in the monitoring of long-term changes in habitat area that might affect the biodiversity of Aldabra.

We show that grassland is the most preferred habitat of *A. gigantea*, followed by open mixed scrub. Grassland is an important habitat for several tortoise species worldwide (e.g. spur-thighed tortoise *Testudo graeca* in southern Spain, Anadon et al. 2006; eastern Hermann's tortoise *Testudo hermanni boettgeri* in Romania, Rozylowicz and Popescu 2012). Aldabra's tortoise turf grassland is a relatively rich, diverse habitat (Merton et al. 1976) and its importance for *A. gigantea* as a preferred food resource is supported by both this research and other studies (Merton et al. 1976; Gibson and Hamilton 1983). Merton et al. (1976) suggested that there has been a strong evolutionary pressure on tortoise turf plant species by *A. gigantea*, to the extent that some of the plants have evolved specific traits (e.g. dwarf and prostrate growth forms), and that the habitat is both created and maintained as a result of intense grazing pressure by the tortoises. Grassland constitutes a small proportion (2.9%; Fig. 1) of Aldabra's land area, but as the preferred habitat for *A. gigantea* across the atoll, it is thus a habitat of high conservation importance.

Studies of other tortoise species have confirmed the importance of habitat structure in thermoregulation (Anadon et al. 2006; Falcón et al. 2018). As a poikilothermic species, *A. gigantea* must seek shade for most of the day, and it is common to find many tortoises sheltering densely together under trees and shrubs (Bourn and Coe 1978). Habitat accessibility also plays a role in its use and preference; the preferred habitats of *A. gigantea*,

Table 2 Ranking matrix for Aldabra giant tortoise habitat preference at second-order selection level based on comparing proportions of habitat within 34 individual home ranges and that available on the atoll

	Mangrove	Open mixed scrub	Standard mixed scrub	Pemphis scrub	Grassland	Exposed surface	Champignon	Rank
Mangrove	0	– – –	– – –	+++	– – –	– – –	– – –	1
Open mixed scrub	+++	0	+++	+++	–	+++	+++	5
Standard mixed scrub	+++	– – –	0	+++	– – –	– – –	+	3
Pemphis scrub	– – –	– – –	– – –	0	– – –	– – –	– – –	0
Grassland	+++	+	+++	+++	0	+++	+++	6
Exposed surface	+++	– – –	+++	+++	– – –	0	+++	4
Champignon	+++	– – –	–	+++	– – –	– – –	0	2

The symbols represent whether the habitat in the home range (row) was used more (+) or less (−) than expected compared to the habitat available on the atoll (column). A triple sign indicates preference (+++) or avoidance (−−−) significant at $P < 0.05$. A single sign indicates a non-significant difference. The importance or rank of the habitats was determined by the relative number of + signs in each row. The rank is ordered from least important (0), to most important (6) habitat type

grassland and open mixed scrub, have an open structure with low vegetation density under the canopy that allows *A. gigantea* to move around easily (Kazmaier et al. 2001), which could also explain the preference. Although grassland was preferred to open mixed scrub these habitats are not always homogenous; in some patches both habitats are intermixed, meeting both the food and shelter requirements of the tortoises in the same area. In contrast, large homogenous areas of pemphis scrub form dense thickets that can be a barrier to tortoise movement (Grubb 1971), which is supported by *A. gigantea*'s lack of preference for this habitat. The proposal that *A. gigantea* can engineer tortoise turf grassland (Merton et al. 1976), begs the question why they have not modified more pemphis habitat to make it more accessible. The dense structure of pemphis would require a considerable expenditure of energy by *A. gigantea* to either move through or modify its structure to become more accessible. It is also not a preferred food resource of *A. gigantea* (Gibson and Hamilton 1983). The habitat that was least preferred by *A. gigantea* was champignon, presumably due to the absence of shade. The open champignon habitat class only accounts for 3.1% of Aldabra's land area, so even if inaccessible, it should not deplete the habitat available to the tortoises.

No evidence of seasonal habitat selection was found. Previous research has shown *A. gigantea* to be idiosyncratic in their movements, with some animals appearing to move very little, and others moving more than 2 km in under 2 months (Bourn and Coe 1978). Baxter (2015) found that *A. gigantea* on Aldabra can be classified as 'migrators' or 'residents' according to their movements: residents remain close to the point of origin and do not travel large distances at any time of the year whereas the migrators move significant distances between core areas of the overall home range. It is also possible that the tortoises are not using distinct homogenous areas of habitat in different seasons. Aldabra has many heterogeneous areas that are a mosaic of several habitat types across quite small areas (Gibson and Phillipson 1983a), and these areas could provide food, shade and water. *Aldabrachelys gigantea* was found to utilize some of these habitats for only a short period of time in a season, sometimes for only a few days. Rather than a mass seasonal migration as seen in the Galapagos tortoise (Blake et al. 2013), *A. gigantea* may be moving at staggered intervals and at different times. Further finer scale analysis of *A. gigantea* daily habitat use and movement should provide a clearer distinction of seasonal habitat preference.

In this study we defined 'season' by the amount of rainfall; however, other biotic factors, such as plant productivity and fruit availability, are likely to more directly affect *A. gigantea* movements, as seen in other grazing herbivores (Bailey et al. 1996). Plant growth following rainfall drives movements of other tortoise species in arid environments as food resources fluctuate (e.g. leopard tortoise *Stigmochelys pardalis* and hingeback tortoise *Kinixys belliana* in the Serengeti, Bertram 1979a, b). Previous research on *A. gigantea* has shown a seasonal dietary shift, with grassland preferred during the wet season and leaf litter during the dry (Gibson and Phillipson 1983a).

Our results are based on movement data of adult tortoises and their preferred habitat. It is likely that smaller tortoises prefer different habitats, such as pemphis scrub, as they can move through smaller spaces. They may also prefer a denser habitat with more cover to avoid predators such as coconut crabs, pied crows and herons (Gaymer 1968). Movement data from juvenile *A. gigantea* are not yet available, so investigating movement and habitat use in this age class is recommended to fully understand the habitat requirements of the species in different age groups, which will ultimately help to maintain a stable population.

This study has yielded useful insights into the habitat use and selection of *A. gigantea* that will be valuable for not only the management of *A. gigantea* on Aldabra, but more importantly for the conservation and restoration of native biota in rewilding projects using

A. gigantea. The tortoises' need for grassland and open, shaded habitat should be considered in future reintroductions to ensure the success of the project and the survival and well-being of the tortoises.

The IUCN Red List classifies *A. gigantea* as Vulnerable due to its restricted distribution, but the population is currently considered to be stable (Turnbull et al. 2015). The shrinkage of either of its preferred habitats, however, would threaten the species' population stability on Aldabra by reducing the availability of food and shade. Recent research shows a marked increase in drought frequency on Aldabra over the last few decades, with associated strong declines of productivity in the most preferred habitats identified in the current study (Haverkamp et al. 2017). Increasing droughts are therefore likely to be reducing preferred food resources and shade areas for *A. gigantea*. The avoidance by *A. gigantea* of champignon habitat, which has little vegetation, strongly suggests that decreasing vegetation cover will affect their behavior and survival. Further research should be conducted on the seasonal habitat use of *A. gigantea* and its correlation with vegetation productivity and rainfall. It will be important to anticipate the potential responses of *A. gigantea* to climatic changes, such as increasing temperature, and extended droughts, and to nutritional deprivation. Effective biosecurity and active management of invasive plants (and animals) may be needed to ensure that areas of native grassland are maintained.

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