

Factors influencing the distribution and abundance of endemic pigeons on São Tomé Island (Gulf of Guinea)

MARIANA CARVALHO, JULIA E. FA, FRANCISCO C. REGO,
RICARDO F. DE LIMA, GABRIEL SANTOS and JORGE M. PALMEIRIM

Summary

Understanding the factors that determine habitat use and abundance of exploited species is essential to develop effective conservation strategies. We studied the four forest pigeons on São Tomé Island to assess the species' distribution and abundance patterns. We determined ecological factors likely to be associated with each species' use of habitats and numbers, as well as the influence of hunting pressure. In total, 35 km of line transects were surveyed in the rainy season and at the start of the dry season. Pigeons differed in their use of habitats; there were also strong seasonality effects. The most abundant species was the Lemon Dove *Columba simplex*, the only non-hunted species. The São Tomé Green Pigeon *Treron sanctithomae* and Maroon Pigeon *Columba thomensis* were less abundant and had more restricted ranges. Both species were strongly associated with old-growth forests. In contrast, the Bronze-naped Pigeon *Columba malherbii* was relatively abundant and widespread; this species favours human-altered habitats such as shade forests and non-forested areas. Fruit availability measured within the different habitats was linked with the distribution and abundance of the three hunted species. Potential human predation pressure on all species was determined from hunting signs found along the surveyed transects. There was a significant negative correlation between the abundance of two of the hunted species and hunting pressure. Our results indicate the importance of adequately protecting old-growth and secondary forests as core habitats for the survival of viable populations of all pigeon species in the island. However, control of hunting is also crucial.

Introduction

Pigeons and doves (Columbidae) are among the most successful and widespread bird families. They have colonised most of the world's oceanic islands, reaching eastern Polynesia and the Chatham Islands in the Pacific Ocean; Mauritius, the Seychelles and Réunion in the Indian Ocean, and the Azores in the Atlantic (Baptista *et al.* 1997, Gibbs *et al.* 2001, Walker 2007a). They are also highly vulnerable to extinction from hunting, introduced predators and habitat loss (Owens and Bennett 2000). Hence, nearly one third of the extant Columbidae now face some risk of extinction. Most threatened pigeons and doves are found in tropical and sub-tropical regions, are forest dependent, and a large number inhabit islands (Walker 2007a).

The island of São Tomé, in the Gulf of Guinea, West Africa, is an important centre of bird diversity and endemism, and is inhabited by four pigeon species (Christy 1991, Stattersfield *et al.* 1998). Three of the four São Tomé pigeons are single island endemics (Maroon Pigeon *Columba thomensis*, São Tomé Green Pigeon *Treron sanctithomae* and the Lemon Dove *Columba simplex*). Another Gulf of Guinea species, the Bronze-naped Pigeon *Columba malherbii*, is also found on the islands of Príncipe and Annobon.

Article updated on 12 August 2022.

All São Tomé pigeons, except the Lemon Dove, are extensively hunted (Atkinson *et al.* 1991, Jones and Tye 2005, Dallimer *et al.* 2009, Carvalho *et al.* 2014). Three species are globally threatened, according to the IUCN Red List (IUCN 2013): the Maroon Pigeon is 'Endangered', the São Tomé Green Pigeon 'Vulnerable', and the Bronze-naped Pigeon 'Near Threatened'. There is sufficient evidence available to show that populations of these birds have declined since the start of the 19th century (Bannerman 1931, Snow 1950, Peet and Atkinson 1994, Jones and Tye 2005, Olmos and Turshak 2007).

All São Tomé pigeons are found within the island's forested habitats (Atkinson *et al.* 1991, Dallimer *et al.* 2009, de Lima *et al.* 2012). The Maroon Pigeon is associated with old-growth and older secondary forests, its main population restricted to an area of around 320 km² of mid- to high-altitude old-growth forest (Peet and Atkinson 1994, Jones and Tye 2005). The São Tomé Green Pigeon is also common in old-growth and secondary forest, but similarly inhabits forest-edge habitats, shaded coffee and cocoa plantations (Jones and Tye 2005, Atkinson *et al.* 1991). It feeds high in the canopy that includes *Ficus* and *Musanga* fruits (Atkinson *et al.* 1991, Jones and Tye 2005). Bronze-naped Pigeons are found in forests and forest scrub within the island's northern savanna habitats. It forages in groups both on the ground and high up in trees (Atkinson *et al.* 1991, Jones and Tye 2005). Lemon Doves are described as common to abundant, found singly or in pairs, wherever there is dense cover on and near ground in old-growth forest, secondary, and shade plantations of coffee and cocoa, from sea-level to high elevations (Christy and Clarke 1998, Jones and Tye 2005).

In this paper, we present the first analyses of the abundance and distribution of all forest pigeons in São Tomé. We analyse: (a) the influence of environmental parameters on the distribution of pigeons; (b) whether fruiting patterns of trees affect their distribution; (c) the phenology of distribution patterns; and (d) whether hunting pressure influences abundance.

Methods

Study area

São Tomé (857 km²) is the larger of the two oceanic islands that constitute the República Democrática de São Tomé and Príncipe (Fig. 1). The island, located within the tropical belt, is about 250 km from the African coast. Annual rainfall ranges from less than 1,000 mm in the north-east to more than 6,000 mm in the south-west, and is marked by two main seasons: the rainy season between September and May and the dry season (or *gravana*) between June and August (Jones and Tye 2005). Mean annual temperatures vary between a minimum of 18° to 21°C to a maximum of 30° to 33°C, with little seasonal variation and high humidity all year (Carvalho *et al.* 2004). The island is characterised by rough relief, with numerous steep mountains and a maximum altitude of 2,024 m at the Pico de São Tomé.

With no human presence before the Portuguese arrived in 1470, the original vegetation on the island comprised tropical lowland and montane forests on the wetter side of the island, and mossy forest at the highest altitudes (Jones and Tye 2005). Native forest is distributed along a gradient from lower to higher altitudes (Fig. 1) with smaller trees (dbh < 2 m) predominating at the highest altitudes. A drier forest type, present in the north-east of the island, includes many deciduous trees, and is subject to frequent fires (Leventis and Olmos 2009). This area has been extensively cleared for farmland and estates and much of it has been turned into an anthropogenic savanna.

Although some forest areas have been heavily modified in the past for planting cocoa and coffee, there has been significant regeneration to secondary forest since the time of independence in 1975 (Oliveira 2002, Carvalho *et al.* 2004). One third of the island, comprising areas of remaining lowland and mountain forests, was declared a protected area (Parque Natural do Obô) though there is little or no enforcement (Albuquerque and Cesarini 2009). Hunting legislation has been drafted since 1995, but is still to be promulgated.

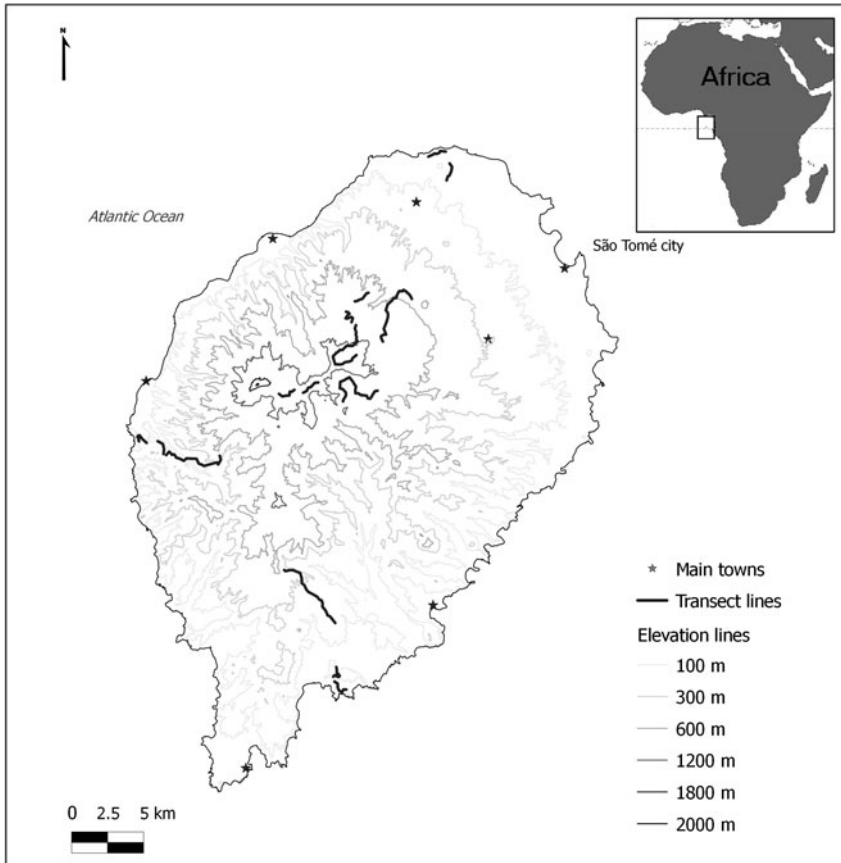


Figure 1. Map of São Tomé showing locations of the sampled transects. Elevation is shown as contour lines.

The human population of the island is estimated at around 187,000 people (c.212 inhabitants/km²; INESTP 2012) and growth rate is 2.0% (CIA 2012). About 60% of the inhabitants of the island live in the capital and adjacent districts. Poverty levels are high, with 34.5% of the population affected (Alkire *et al.* 2011). Infrastructure is generally poor.

Sampled habitats

We sampled pigeon populations within four broad habitat types, ranging from least disturbed formations (old-growth forest), through secondary forest to shade plantations and non-forested habitats (INTERFOREST 1990, Salgueiro and Carvalho 2007). Old-growth forests are areas of natural vegetation, often remaining in inaccessible parts of the island, which may contain some introduced and human-favoured species (e.g. *Bambusa vulgaris*, *Musanga cecropioides*, *Persea americana*, *Chinchona* sp.). Secondary forests, derived from the cutting of old-growth forests, contain a large proportion of introduced species, but no cultivated plant species (Carvalho *et al.* 2004). In contrast, shade plantation forests are characterised by the presence of coffee or cocoa, and a variable canopy cover of native and introduced species. Non-forested areas included in the sampling are mainly savannas but also include palm stands and open fields close to forests.

Bird surveys

We surveyed pigeons along 15 linear transects (total 35 km) in selected habitats (Fig. 1). Due to the difficult terrain, most transects followed existing trails. We walked five main (5-km long) transects; the maximum distance that could be sampled in one day in rough terrain without compromising census quality (Bibby *et al.* 2000). We also selected 10 shorter (1-km long) transects to increase sampling effort in habitats that were poorly represented within the main transects. All 15 transects were divided into 100-m sectors, within which we recorded habitat type (old-growth, secondary, shade or non-forested), altitude (measured with a GPS), and trail typology (forest trail, well marked footpath, old dirt road). In addition, the vegetation in each sector was characterised within two (10 m x 10 m) quadrats on each side of the initial point of each sector. In each quadrat we counted the number of trees (small: 30 cm to 2 m dbh, and large: > 2 m dbh), estimated canopy height and cover, as well as grass and shrub cover (Bibby *et al.* 2000, Buckland *et al.* 2008). All estimates were conducted by M. C. With the support of local assistants, tree species with fruits consumed by our study species were counted along a 20 m wide band along each transect. Fruiting status of all counted trees was documented from presence and ripeness of fruits present.

Bird censuses were undertaken by two trained observers (G. S. and Aristides Santana) during early mornings (between 05h00 and 11h00). Transects were walked at a slow pace (1 km/hour) and repeated twice, in January and June 2010 (rainy and dry season, respectively). Pigeons seen or heard were recorded, except for individuals observed flying over the transects. Coordinates for each transect, the main habitat sections and number of birds recorded in each season are shown in Appendix S1 in the online supplementary materials.

Human presence and hunting pressure

To analyse the effect of anthropogenic factors on pigeons, an index of potential hunting pressure within each 500 m transect sector was calculated as the average of site accessibility, human population, and signs of hunting activity. Site accessibility was estimated as the mean distance from the sector to the nearest road according to three distance classes (1: > 5 km, 2: 2.5–5 km, 3: < 2.5 km) and another parameter representing access type (1: lightly marked forest trail, 2: well-trodden path, 3: old road). The human population within a 5-km radius was obtained from the 2001 and 2012 population censuses (INESTP 2012) and expressed as 1: < 350 persons, 2: 351–700 persons, and 3: > 700 persons. Signs of hunting activity (hunters, cartridges, piles of feathers, traps, and temporary hunting camps) were recorded during habitat surveys and bird counts as 1 (up to one sign) to 3 (more than 3 signs).

Fruit availability index

To analyse the effect of fruit availability on pigeon distribution and abundance patterns, we derived a seasonal fruit availability index for the three canopy-living species: São Tomé Green Pigeon, Bronze-naped Pigeon and Maroon Pigeon. The index was not applicable to the Lemon Dove as this species usually feeds on the ground and its diet is poorly known.

First, we identified 10 fruit-bearing tree species as important in the diets of the three canopy-living pigeons (Table 1), from observations in the field, suggestions from local informants, and available literature (Christy and Clarke 1998, Jones and Tye 2005). We then assessed the seasonal fruiting pattern of each tree species. In the transect areas, we selected 10 individuals of each tree species to monitor. Each individual was visited twice in each season (January–February, June–July), and its fruiting status classified in three levels: 0 - no fruits, 1 - few fruits and/or raw, 2 - many fruits and ripe. We derived a seasonal fruiting index for each tree species (rainy season/dry season) by averaging the values obtained for the 10 individual trees monitored.

We then calculated a *fruit availability index* in each sampling sector for each bird species, per season. To achieve this, we multiplied the number of trees of each identified species in each sampling sector and by the estimated seasonal index of fruiting for that sector in each season.

Table 1. Fruiting trees identified as relevant food sources for use in fruit availability indexes built for three species of pigeons: São Tomé Green Pigeon, Bronze-naped Pigeon and Maroon Pigeon. The observed fruiting refers to average number of fruits and their ripeness recorded in all identified trees located at sampled transects, and varies between 0 (no fruits or raw) and 2 (many ripe fruits).

Tree Species	São Tomé Green Pigeon fruit index	Bronze-naped Pigeon fruit index	Maroon Pigeon fruit index	Observed fruiting rainy season (Jan.)	Observed fruiting dry season (Jun.)
<i>Ficus chlamydocarpa</i>	+	-	+	1	2
<i>Ficus exasperata</i>	+	-	-	1	2
<i>Ficus kamerounensis</i>	+	+	-	2	1
<i>Cecropia peltata</i>	+	-	-	1.5	1.5
<i>Cestrum laevigatum</i>	-	+	-	0.5	2
<i>Trochidium didymostemon</i>	-	+	-	2	1
<i>Maesa lanceolata</i>	-	+	-	2	0.5
<i>Schefflera mannii</i>	-	-	+	1	2
<i>Margaritaria discoidea</i>	-	-	+	1.5	0.5
<i>Morinda lucida</i>	-	-	+	1.5	0.5

For each pigeon species and respective diet we estimated the fruit availability index by summing the values obtained for the four main species of trees of diet (Table 1) in every single sector.

Analysis

We used ordination techniques to develop an effective visual summary of site-specific changes in forest type structure, including all samples in the same ordination space (Borcard *et al.* 2011). We employed non-metric multidimensional scaling (NMDS) ordination based on Euclidean dissimilarities of standardised environmental variables. This procedure is considered robust for site-data analyses and is able to recover compositional dimensions associated with the underlying environmental gradients (Minchin 1987). To test the null hypothesis that habitat structure was similar in different forest types, a nonparametric analysis of similarity (ANOSIM) was conducted on the raw environmental data (Borcard *et al.* 2011). Envfit function was performed to test for the significance of sampled variables and its relation to the ordination axes (Borcard *et al.* 2011). These analyses were also used to select significant variables for the subsequent application of the statistical models.

An initial exploratory analysis was performed using the bird count data to determine if there were differences in abundance between habitats and seasons, for each species. General Linear Regression Models (GLM) were subsequently used to examine how canopy cover, number of large trees, habitat (old-growth, secondary, shade or non-forested), season (rainy or dry), indices of potential hunting pressure and fruit availability (for São Tomé Green Pigeon, Bronze-naped Pigeon and Maroon Pigeon) affected presence and abundance of each of the study species (Bolker *et al.* 2009, Zuur *et al.* 2009). To identify which variables best explained the abundance of each pigeon species, we used model selection based on Akaike's information criterion corrected for small samples sizes (AICc; Burnham and Anderson 2002, Barlow *et al.* 2010). We used the 'dredge' function from the 'MuMIn' package to test models defined by all possible variable combinations and rank them by their AICc-based model weight (Burnham and Anderson 2002). All statistical procedures were carried out in R v. 2.10.0 (R Development Core Team 2009).

Results

Habitat structure

Variation in environmental variables among the sampled sectors was summarised using a non-metric multidimensional scaling ordination (NMDS). This graphic summary (Figure 2) shows that the greatest environmental contrasts in the study area are the different forest types, which to a great extent reflect the degree of habitat disturbance by humans. In fact, the first ordination axis (Stress = 0.18, ANOSIM statistics $R = 0.54$, $P = 0.001$) represented a transition in habitat structure and disturbance levels from native forest (on the left of the plot, with dense canopy cover) to increasingly open woodland types (Figure 2). The second axis indicated a gradient from forest with large trees and high canopies (at the top of the plot, usually shade forest, often abandoned) to a lower forest type with denser undergrowth (usually younger and regenerating secondary forest).

The two variables which explained most of the variance along the two axes were canopy cover (NMDS1) and canopy height (NMDS2). The ANOSIM analysis of similarities indicated that the habitat types have statistically distinct environmental characteristics ($R = 0.54$, $P = 0.001$).

Species abundance and habitat use

The most common pigeon species counted on all transects was the Lemon Dove; a total of 759 birds observed (389 in the rainy season, 370 in the dry season) in 44.4% of the 350 sampling units. The species was widespread in all forested habitats (from old-growth to shade forests) and a considerably lower presence in non-forested sampled sectors (Figure 3). São Tomé Green Pigeons were recorded in fewer sectors (17.3%) and were found at lower numbers than the Lemon Dove (394 individuals,

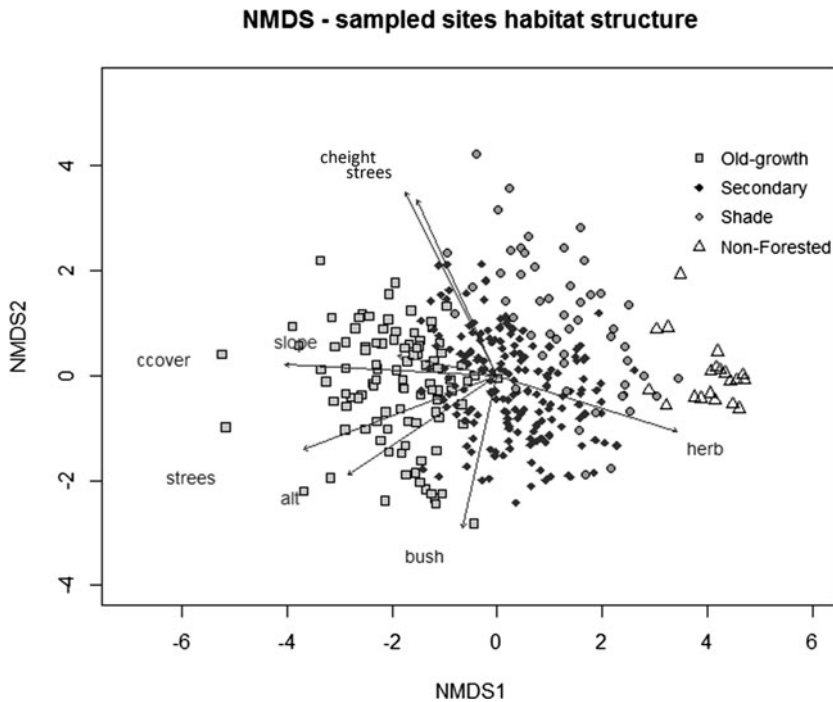


Figure 2. Two dimensional non-metric multidimensional-scaling ordination of transect sectors (as points; $n = 347$) based on nine environmental variables: habitat type, altitude (alt), % canopy cover (ccover), canopy height (cheight), slope (slope), number of large trees (ltrees), number of small trees (strees), % shrub cover (bush), % grass cover (herb) (Stress = 0.18). The diagram symbolises the sectors' compositional dimensions associated with assessed environmental gradients and general habitat typology. Each habitat type is represented by a distinct symbol. Fitted environmental variables are represented as arrows, and correspond to their input for the ordination axes, both in direction and length of the arrow.

144 in the rainy season and 250 in the dry season). São Tomé Green Pigeons were observed mainly in mature forested habitats (old-growth and older secondary); non-forested areas were not important for this species (Fig. 3). In contrast, the Bronze-naped Pigeon was abundant in human-altered habitats, including shade forests and non-forested areas (such as savanna). This species was observed in 37.8% of sectors; 830 individuals (643 in the rainy season, 187 in the dry season). The species was observed significantly less during the dry season (Mann-Whitney U-test, $V = 17,570$, $P < 0.001$) (Fig. 3). The Maroon Pigeon was the rarest species, being observed mainly in old-growth forests and some isolated individuals in secondary growth and non-forested areas. This species was observed in just 0.5 % of sectors, totalling 37 individuals (Fig 3). The abundance of all species varied significantly among the four sampled habitat types (Kruskal-Wallis test, $P < 0.05$). Habitat use during the wet and dry seasons for each pigeon species is shown in separate ordination diagrams in Figure 4.

Lemon Dove numbers were similar during both seasons, but frequencies per habitat varied during the dry season; Lemon Doves tended to concentrate in old-growth, shade and particularly in young or regenerating secondary forests (characterised by a lower tree canopy and denser undergrowth and shrub cover).

São Tomé Green Pigeons underutilised degraded habitats and young or regenerating forests, and were more common overall in more mature forests with higher canopies and greater canopy

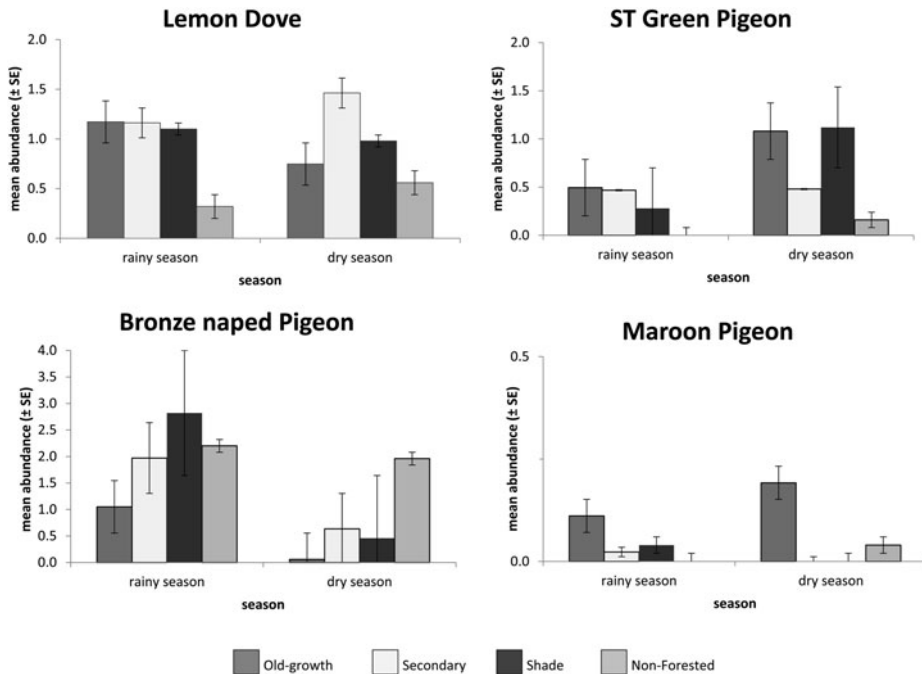


Figure 3. Mean abundance per sector of all four pigeon species in sampled habitats per sampling season: old-growth ($n = 99$), secondary ($n = 171$) and shade ($n = 56$) forests, and non-forested areas ($n = 24$).

cover, during both seasons. They were seasonally present in shade forests, concentrating at this habitat during early dry season.

The Bronze-naped Pigeon was more abundant in lower altitude forests with denser shrub cover than in forest with high trees. It was not present in high-altitude forests. During the rainy season it was more common in lower, old-growth forests. Its distribution in shade forests is seasonal, as it uses this habitat type more extensively during the rainy season. It was observed in non-forested habitats in both seasons, but more in the rainy season.

The Maroon Pigeon data suggest a greater concentration in highland forests during the early dry season, with groups of up to 10 individuals being noted during this period. However, the species was also observed in low altitude old-growth forest, secondary forest and in a non-forested sector, mostly during the wet season, in pairs or as isolated individuals.

Factors associated with species abundance and distribution

Results of associations between environmental variables and pigeon abundance and distribution for the four São Tomé pigeon species are given in Table 2. Presence and abundance of the Lemon Dove were associated with habitat, especially secondary forest during the dry season (coef = 0.69, $P = 0.03$). Potential hunting pressure was also negatively correlated with species presence and abundance, significant during the rainy season (coef = -2.06, $P = 0.05$). Presence and abundance of the São Tomé Green Pigeon were significantly correlated with hunting pressure during both seasons (coef = -0.72, $P < 0.001$). Fruit availability was positively related to abundance of this species (coef = 0.05, $P = 0.02$). For the Bronze-naped Pigeon, season was linked to the distribution and abundance of the species (coef = -1.33, $P < 0.001$). There was a negative relation with altitude (coef = -0.001, $P < 0.001$) and canopy cover (coef = -0.01, $P = 0.04$), but a positive regression with canopy

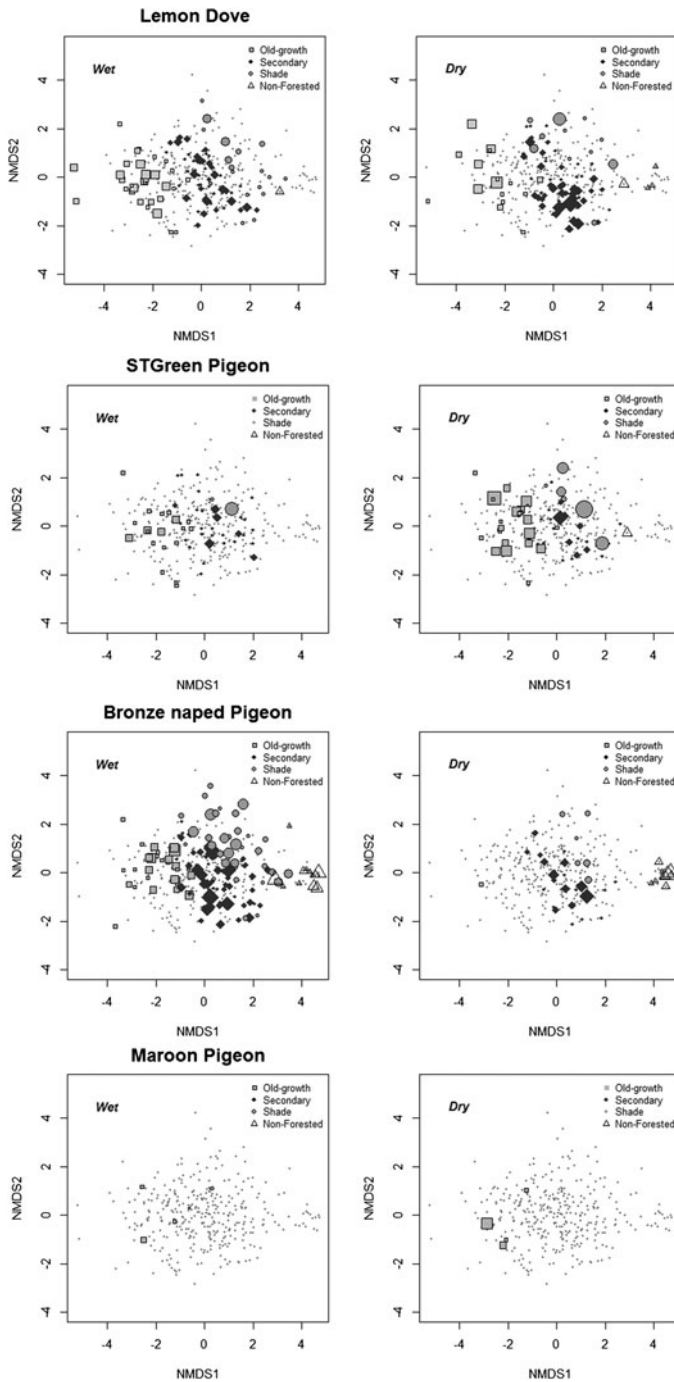


Figure 4. Use of ecological space by the four species of pigeons in rainy and dry seasons, using as a reference the transect sectors' ordination, as in Fig. 2. Small dots are sampled sectors and symbols indicate the sectors where each pigeon species was observed. The size of the symbols reflects pigeon abundance, and its shape and colour the different habitats (as in Fig. 2).

Table 2. Results of the GLM models with significant variables selected by the best model and model averaging of top performing models (using dredge, delta < 2; RI – relative importance of the variable for best regression models). Significant values are in bold.

Species	Variables	GLM- full model		Model averaging		GLM - rainy season		Model averaging		GLM - dry season		Model averaging	
		Coef	P	P	RI	Coef	P	P	RI	Coef	P	P	RI
Lemon Dove	Habitat - Secondary	0.437	0.03	0.04	1	0.174	0.490	0.73	0.61	0.685	0.03	0.02	1
	Human pressure	-0.116	0.1105	0.08	0.79	-0.206	0.114	0.05	0.83	-0.09	0.54	0.45	0.17
São Tomé Green Pigeon	Fruit availability	0.052	0.02	0.01	1	0.056	0.089	0.07	0.72	0.058	0.05	0.04	0.83
	Human pressure	-0.72	<0.001	<0.001	1	-0.481	0.087	0.01	1	-1.003	0.001	<0.001	1
Bronze-naped Pigeon	Intercept	1.947	<0.001	<0.001	1	1.244	0.004	0.58	0.4	2.540	<0.001	<0.001	1
	Habitat - Secondary	0.537	0.02	0.01	1	-0.130	0.582	<0.001	1	-1.9E-04	0.72	0.51	0.15
Maroon Pigeon	Altitude	-0.001	<0.001	<0.001	1	-0.001	<0.001	0.04	0.85	5.2E-05	0.99	0.73	0.12
	Canopy cover	-0.007	0.04	0.04	0.85	-0.01	0.007	0.03	1	-2.3E-03	0.93	na	Na
	Canopy height	0.023	0.06	0.04	1	0.024	0.052	0.01	1	3.7E-03	0.91	na	Na
	Fruit availability	0.028	0.06	0.75	0.84	0.040	0.013	0.01	1	na	na	na	na
	Season	-1.331	<0.001	<0.001	1	1.089	0.008	0.03	1	0.008	0.04	0.06	0.76
Maroon Pigeon	Large trees	1.026	<0.001	0.002	1	0.092	0.493	0.56	0.17	0.33	<0.001	<0.001	1
	Fruit availability	0.206	<0.001	0.01	1	-2.843	0.045	0.07	1	na	na	<0.001	1
	Human pressure	-0.292	0.02	0.02	1	0.10	0.56	0.07	1	na	na	<0.001	1
Season	-1.258	0.09	0.10	0.56									

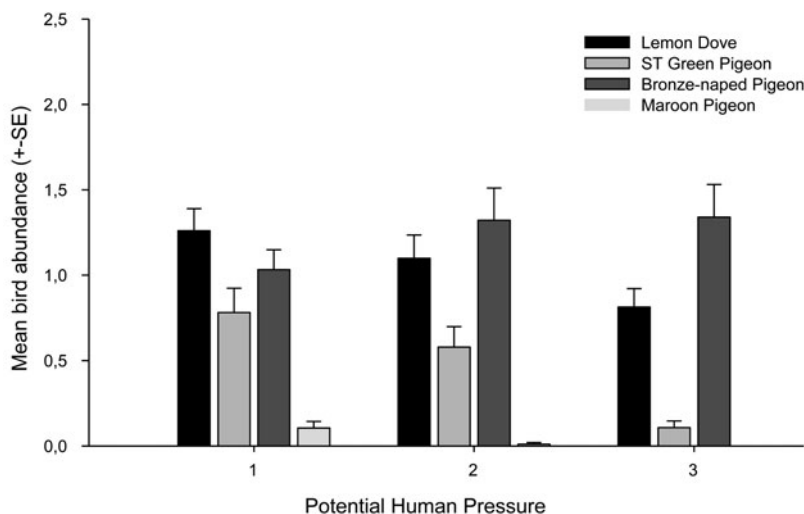


Figure 5. Average relative abundance of all four pigeon species in sites with light, medium or high potential human pressure.

height (coef = 0.02, $P = 0.05$), associated with its seasonal use of shade forests. Species abundance was positively correlated with secondary forest (coef = 0.54, $P = 0.02$); this effect was stronger during the dry season (coef = 2.54, $P < 0.001$). Bronze-naped Pigeon abundance was not correlated with fruit availability although close to significance (coef = 0.028, $P = 0.06$), as this species tends to congregate in the available fruiting trees in closed forests. This effect is significant for the rainy season (coef = 0.040, $P = 0.013$).

The number of large trees (coef = 1.03, $P < 0.001$), and fruit availability, particularly during the dry season (coef = 0.33, $P < 0.001$), were positively correlated with distribution and abundance of the maroon pigeon, while with human pressure the correlation is negative (coef = -2.92, $P = 0.017$).

Potential hunting pressure is negatively correlated with the abundance of three of the four species of pigeons (Fig. 5). The abundance of the Lemon Dove, São Tomé Green Pigeon and the Maroon Pigeon declined with increasing potential hunting pressure. This effect was not observed for the Bronze-naped Pigeon.

Discussion

Distribution and abundance

The observed patterns of distribution and abundance of the four species of pigeons on São Tomé reflect habitat structure, food availability and hunting pressure, with a marked seasonal effect in most cases. Secondary forests were significantly associated with the distribution of at least three of the studied pigeon species. This was important for the Lemon Dove and Bronze-naped Pigeon, but we also found a significant association for the São Tomé Green Pigeon. Secondary forest is presently the most abundant forest type in São Tomé, but also the one most threatened by deforestation (selectively or intensively) and land-use intensification.

Old-growth forests found at higher altitudes seem to support a higher abundance of Maroon Pigeon and São Tomé Green Pigeon. However, these species' association with these habitats may be the result of loss of populations of these species from lowland forests. In fact, both species were once noted as common and widespread, even within the coastal areas and Rolas Islet (Jones and Tye 2005). Remote old-growth forests now probably constitute the core habitat for these pigeons because of their inaccessibility to bird hunters.

At lower altitudes, shade forests with high canopies as well as non-forested open habitats (mainly savanna) are linked to relatively large populations of the Bronze-naped Pigeon. However, its commonness in these human-altered areas makes the species more susceptible to hunting, so the regulation of this activity is vitally important.

Importance of fruit availability

Fruit availability in sampling sectors was identified as a significant correlate of the distribution and abundance of the Maroon Pigeon, São Tomé Green Pigeon and Bronze-naped Pigeon. As in other studies, forest pigeons were observed to respond to spatial differences in fruit abundance within fragments and habitats (Lambert 1989, Levey 1988, Strong and Johnson 2001, Oliveira *et al.* 2006). Although fruit availability was shown to affect bird distribution and abundance patterns, relating seasonal bird movements and fruit availability will require more research to clarify this point. Our study may have been limited by the fact that we did not monitor all species of fruiting tree species, but the four species recorded in our study represented significant food items for pigeons. This is so because São Tomé pigeons, like other frugivorous Columbidae, are opportunistic feeders that consume a large variety of fruits when available (e.g. Bancroft *et al.* 2000, Oliveira *et al.* 2006, Walker 2007b).

As shown in previous studies, the highest tree fruit diversity and abundance was typical of secondary and shade forests (e.g. Levey 1988, DeWalt *et al.* 2003, Hart *et al.* 2013). In these habitats, a number of pioneer and transitional forest trees such as *Musanga cecropioides* and several *Ficus* species, as well as the introduced South American *Cecropia peltata*, are found. Fruits from all these tree species are important for canopy-living pigeons (Levey 1988, Carvalho *et al.* 2004). Figs, even though low in lipids and proteins, are very abundant seasonally and represent a large part of the diets of many tropical pigeons, up to 50% for *Treron* species in continental Africa (Lambert 1989, Walker 2007b, Devi and Saikia 2012).

Old-growth forests generally have lower fruit availability than secondary forests, though this may be relatively constant throughout the year (Levey 1988). Asynchronous fruiting patterns of the various tree species found in the different habitats ensure year-round food resources for the pigeons. Although we are certain that the São Tomé pigeons forage in a variety of habitats, information on this is limited. Further research is required to clarify these birds' dietary patterns and their role as dispersers. Moreover, detailed studies of fruiting tree phenology and distribution will assist conservation managers on the island to ensure the long-term survival of its forests and biodiversity.

Impact of hunting

We show that hunting pressure is negatively correlated with the distribution and abundance of three pigeon species; Lemon Dove, Maroon Pigeon and São Tomé Green Pigeon. Although the Lemon Dove is not considered a game species on the island, we found that its presence and abundance were negatively correlated with potential hunting pressure. Children and rural inhabitants opportunistically take the species and even this infrequent human pressure may explain the correlation, although this needs further study. In contrast, there is evidence to support that hunting of the Bronze-naped Pigeon, São Tomé Green Pigeon and Maroon Pigeon is heavy (and may be increasing) given the considerable commercial value these species have in bars and restaurants in the main cities (Carvalho *et al.* 2014). The relatively low abundance and restricted range of the Maroon Pigeon and São Tomé Green Pigeon may be a function of hunting intensity, since both species have been intensively hunted for decades or even centuries (e.g. Bannerman 1931, Snow 1950, Jones and Tye 2005). However, differences in each species' reproductive rate and niche width may also explain the disparities observed in their ecological densities on the island. The Bronze-naped Pigeon, for example, despite heavy hunting pressure is more abundant, presumably because it has adapted to utilising human-altered habitats and a wider range of resources than the other species. In general, commercial hunting is a real threat to pigeons and other bird species on the

island; they are relatively tame and easy to shoot at close range, which has enabled hunters to take large numbers of individuals in a short space of time (Carvalho *et al.* 2014).

Conservation measures

Previous studies on São Tomé have highlighted that human-modified habitats such as secondary forests and shade plantations are important as reservoirs for a significant numbers of the island's endemics (e.g. de Lima *et al.* 2012, Rocha 2008). In our study we also confirm this to be the case for most of the island's endemic pigeons, at least seasonally. Although there is still much forest left on São Tomé, the fast growing human population and consequent urbanisation may change this; plans for infrastructure development and an intensifying agricultural pressure are ongoing (Dallimer *et al.* 2009, Klueh *et al.* 2007, UNDP 2006). Combined with factors such as invasive species associated with human settlement, as well as increased illegal logging and exploitation of other natural resources, most endemic birds and particularly hunted pigeons are likely to be at increasing risk of extinction.

In our study we confirm that habitats and hunting pressure explain pigeon abundance and must be used to drive conservation actions for these species. The São Tomé Green Pigeon and the Maroon Pigeon are likely to be less threatened because of their association with the more inaccessible old-growth forests, though improved roads and continuous opening of agricultural fields are of major concern. Most pigeon hunting is conducted by commercial urban hunters coming from main towns to forest fringes (Carvalho *et al.* 2014), and increased accessibility of well-preserved forests will surely intensify hunting pressure over both pigeons. For these species, adequate habitat protection and the strong application of hunting restrictions within the national park are necessary, since the main habitats for these species are here.

The protection of the Bronze-naped Pigeon may be more problematic given that it is most often found in human-altered habitats, particularly in the dry season. This pigeon is known to use agricultural land where it feeds on the abundant fruits of the shrub *Cestrum laevigatum* along hedgerows. More research is needed on the drivers of seasonal movements of this species and its use of native and altered habitats.

All three exploited species are known to have declined in numbers during the last few decades and the main reason seems to be excessive hunting (Carvalho *et al.* 2014). Thus, enforcement of strong hunting regulations perhaps through the definition of restricted areas and periods for hunting, specific quotas for the more abundant species and the total ban of species such as the Maroon Pigeon would alleviate the current situation. A combination of hunting control and habitat preservation has resulted in the recovery of other forest pigeon species (e.g. Pierce *et al.* 1993, Oliveira *et al.* 2006).

Supporting the conservation authorities on the island to implement the existing hunting legislation and enforce protection should also be accompanied by more targeted environmental education and awareness-raising among all islanders. São Tomé hunters and game consumers are not aware of the difference between endemic, native or exotic species, or the conservation problems resulting from overhunting. A main element of this strategy must be to reduce demand by consumers in town and city restaurants. Hunters, and particularly bird hunters, should also be involved in conservation efforts, both by capturing their knowledge on the species and as a critical point for the definition of livelihood alternatives which can ensure pigeon conservation.

Supplementary Material

The supplementary materials for this article can be found at journals.cambridge.org/bci

Acknowledgements

We particularly express gratitude to Eng. Arlindo Carvalho, the General Director for the Environment, and to Dr Vitor Bonfim and Eng. Salvador Pontes from the Direction for

Conservation, for local support and integration in São Tomé. The Associação Monte Pico, particularly Luis Mário Almeida, provided technical support and advice. We warmly thank all the São Tomé citizens who facilitated field work, either by providing initial guidance, helping with overnight stays, meals and/or valuable company. This study was conducted within the scope of the project PTDC/BIA-BIC/115223/2009, a PhD grant SFRH / BD / 30171 / 2006 and a Post-doc grant SFRH/ BPD/ 91494/ 2012, all funded by the Portuguese Government (Foundation for Science and Technology - FCT/MCTES). M. C. was also supported by a Rufford Small Grant for Conservation of Nature.

References

- Albuquerque, C. and Cesarini, D. (2009) *Plano de Manejo do Parque Nacional Obô de São Tomé*. São Tomé: ECOFAC.
- Alkire, S., Roche, J. M., Santos, M. E. and Seth, S. (2011) *São Tomé and Príncipe country briefing*. Oxford, UK: Oxford Poverty & Human Development Initiative (OPHI) Multidimensional Poverty Index Country Briefing Series. Available at www.ophi.org.uk/policy/multidimensional-poverty-index/mpi-country-briefings/.
- Atkinson, P., Peet, N. and Alexander, J. (1991) The status and conservation of the endemic bird species of São Tomé and Príncipe, West Africa. *Bird Conserv. Internatn.* 1: 255–282.
- Bancroft, G. T., Bowman, R. and Sawicki, R. J. (2000) Rainfall, fruiting phenology and the nesting season of White-Crowned Pigeons in the Upper Florida Keys. *Auk* 117: 416–426.
- Bannerman, D. A. (1931) The maroon pigeon of São Thomé. *Ibis* 73: 652–654.
- Baptista, L. F., Trail, P. W. and Horblit, H. M., (1997) Family Columbidae (pigeons and doves). Pp. 60–243 in J. del Hoyo, A. Elliot and J. Sargatal, eds. *Handbook of the birds of the world, Vol. 4: Sandgrouse to cuckoos*. Barcelona, Spain: Lynx Edicions.
- Barlow, J., Louzada, J., Parry, L., Hernández, M. I. M., Hawes, J., Peres, C. A., Vaz-de-Mello, F. Z. and Gardner, T. A. (2010) Improving the design and management of forest strips in human-dominated tropical landscapes: a field test on Amazonian dung beetles. *J. Appl. Ecol.* 47: 779–788.
- Bibby, C., Marsden, S. and Fielding, A. (2000) Bird-habitat studies. Pp. 98–113 in *Bird surveys - expedition field techniques*. Cambridge, UK: BirdLife International.
- Bolker, B. M., Brooks, M. E., Clark, C. J., Geange, S. W., Poulsen, J. R., Stevens, M. H. H. and White, J. S. S. (2009) Generalized linear mixed models: a practical guide for ecology and evolution. *Trends Ecol. Evol.* 24: 127–35.
- Borcard, D., Gillet, F. and Legendre, P. (2011) *Numerical ecology with R*. New York: Springer.
- Buckland, S. T., Marsden, S. J. and Green, R. E. (2008) Estimating bird abundance: making methods work. *Bird Conserv. Internatn.* 18: 91–108.
- Burnham, K. P. and Anderson, D. R. (2002) *Model selection and multi-model inference: a practical information-theoretic approach*. New York: Springer.
- Carvalho, M., Palmeirim, J. M., Rego, F. C., Sole, N., Santana, A. and Fa, J. E. (2014) What motivates hunters to target exotic or endemic species on the island of São Tomé, Gulf of Guinea? *Oryx* doi:10.1017/S0030605313000550.
- Carvalho, S., de Oliveira, F. and Vaz, H. (2004) *Situation des ressources génétiques forestières de la République Démocratique de Sao Tomé-et-Príncipe*. Rome, Italy: Division des Ressources Forestières, FAO. (Working document FGR/63F).
- Christy, P. (1991) São Tomé and Príncipe. Pp. 727–732 in L. Fishpool and M. Evans, eds. *Important Bird Areas in Africa and associated islands*. Cambridge, UK: BirdLife International. (Birdlife Conservation Series No. 11).
- Christy, P. and Clarke, W. V. (1998) *Guide des oiseaux de São Tomé et Príncipe*. Gabon: ECOFAC.
- Dallimer, M., King, T. and Atkinson, R. J. (2009) Pervasive threats within a protected

- area: conserving the endemic birds of São Tomé, West Africa. *Anim. Conserv.* 12: 209–219.
- De Lima, R. F., Dallimer, M., Atkinson, P. W. and Barlow, J. (2012) Biodiversity and land-use change: understanding the complex responses of an endemic-rich bird assemblage. *Divers. Distrib.* 19: 411–422.
- Devi, O. S. and Saikia, P. K. (2012) Diet composition and habitat preferences of fruit eating pigeons in a tropical forest of eastern Assam, India. *NeBio* 3: 51–57.
- DeWalt, S. J., Maliakal, S. K. and Denslow, J. S. (2003) Changes in vegetation structure and composition along a tropical forest chronosequence: implications for wildlife. *For. Ecol. Manage.* 182: 139–151.
- Gibbs, D., Barnes, E. and Cox, J. (2001) *Pigeons and doves*. Robertsbridge, UK: Pica Press.
- Hart, L. A., Grieve, G. R. H. and Downs, C. T. (2013) Fruiting phenology and implications of fruit availability in the fragmented Ngele Forest Complex, KwaZulu-Natal, South Africa. *South African J. Bot.* 88: 296–305.
- INESTP (2012) *São Tomé e Príncipe em números*. São Tomé: Instituto Nacional de Estatística de São Tomé e Príncipe. Available at: <http://www.ine.st/>.
- INTERFOREST (1990) *Results of national forest inventory – Democratic Republic of São Tomé and Príncipe*. São Tomé: INTERFOREST AB.
- IUCN (2013) *The IUCN Red List of threatened species*. Version 2013.1. <www.iucnredlist.org>
- Jones, P. and Tye, A. (2005) *The birds of Príncipe, São Tomé and Annobón - an annotated checklist*. Oxford, UK: British Ornithologists' Union.
- Klueh, U., Pastor, G., Segura, A. and Zarate, W. (2007) *Inter-sectoral linkages and local content in extractive industries and beyond—the case of São Tomé and Príncipe*. Washington DC: International Monetary Fund Working Paper: WP/07/213.
- Lambert, F. R. (1989) Pigeons as seed predators and dispersers of figs in a Malaysian lowland forest. *Ibis* 131: 521–527.
- Leventis, A. P. and Olmos, F. (2009) *The birds of Sao Tome e Principe \ As aves de Sao Tome e Principe: A photo guide \ Um guia fotografico*. São Paulo, Brazil: Aves & Fotos Editora.
- Levey, D. J. (1988) Spatial and temporal variation in Costa Rican fruit and fruit-eating bird abundance. *Ecol. Monogr.* 58: 251–269.
- Minchin, P. R. (1987) An evaluation of the relative robustness of techniques for ecological ordination. *Vegetation* 69: 89–107.
- Oliveira, F. (2002) *Relatório sobre a Floresta. Estratégia Nacional de Conservação da Biodiversidade*. São Tomé: Ministério do Ambiente e Recursos Naturais.
- Oliveira, P., Menezes, D., Jones, M. and Nogales, M. (2006) The influence of fruit abundance on the use of forest and cultivated field habitats by the endemic Madeira laurel pigeon *Columba trocaz*: Implications for conservation. *Biol. Conserv.* 130: 538–548.
- Olmos, F. and Turshak, L. G. (2007) Observations on birds at São Tomé and Príncipe. African Bird Club report.
- Owens, I. P. and Bennett, P. M. (2000) Ecological basis of extinction risk in birds: habitat loss versus human persecution and introduced predators. *Proc. Natl. Acad. Sci. U.S.A.* 97: 12144–12148.
- Peet, N. B. and Atkinson, P. W. (1994) The biodiversity and conservation of the birds of São Tomé and Príncipe. *Biodivers. Conserv.* 3: 851–867.
- Pierce, R. J., Atkinson, R. and Smith, E. (1993). Changes in bird numbers in six Northland forests 1979–1993. *Notornis* 40: 285–293.
- R Development Core Team (2009) *R: A language and environment for statistical computing*. Available at: <www.r-project.org/>
- Rocha, R. T. (2008) *Birds in humanized landscapes: São Tomé endemic birds' response to agricultural intensification*. MSc Thesis. Imperial College London, UK.
- Salgueiro, A. and Carvalho, S. (2007) *Proposta de Plano Nacional de Desenvolvimento Florestal 2003–2005*. São Tomé: ECOFAC.
- Snow, D. W. (1950) The birds of São Tomé and Príncipe in the Gulf of Guinea. *Ibis* 92: 579–595.
- Stattersfield, A. J., Crosby, M. J., Long, A. J. and Wege, D. C. (1998) *Endemic bird areas*

- of the world: Priorities for biodiversity conservation*. Cambridge, UK: ICBP.
- Strong, A. M. and Johnson, M. D. (2001) Exploitation of a seasonal resource by non-breeding plain and white-crowned pigeons: implications for conservation of tropical dry forests. *Wilson Bull.* 113: 73–77.
- UNDP (2006) *Draft country programme document for São Tomé and Príncipe*, Geneva: UNDP.
- Walker, J. S. (2007a) Geographical patterns of threat among pigeons and doves (Columbidae). *Oryx* 41: 289–299.
- Walker, J. S. (2007b) Dietary specialization and fruit availability among frugivorous birds on Sulawesi. *Ibis* 149: 345–356.
- Zuur, A. F., Ieno, E. N., Walker, N., Saveliev, A. A. and Smith, G. M. (2009) *Mixed effects models and extensions in ecology with R*. New York: Springer.

MARIANA CARVALHO, FRANCISCO C. REGO

Centro de Ecologia Aplicada 'Prof. Baeta Neves', Instituto Superior de Agronomia, Tapada da Ajuda, 1349-017 Lisboa, Portugal.

JORGE M. PALMEIRIM, RICARDO F. DE LIMA

Dept. Biologia Animal e Centro de Biologia Ambiental, Faculdade de Ciências, Universidade de Lisboa, Lisboa, Portugal.

GABRIEL SANTOS

Associação Monte Pico, Monte Café, São Tomé, Democratic Republic of São Tomé and Príncipe.

JULIA E. FA*

ICCS, Imperial College London, Division of Biology, Silwood Park Campus, Ascot, UK.

*Author for correspondence; e-mail: jfa949@gmail.com

Received 3 March 2014; revision accepted 17 July 2014;

Published online 30 December 2014