Status of the relict population of the Critically Endangered Madagascar spider tortoise *Pyxis arachnoides*

Ryan C. J. Walker and Tsilavo H. Rafeliarisoa

Abstract The Madagascar spider tortoise *Pyxis arachnoides* is endemic to the coastal dry forests of south-west Madagascar. In recent years its range has been reduced by c. 71%, with the species now confined to eight fragmented populations occupying a total of 2,464 km^2. These remaining populations are facing a significant threat of extinction because of habitat destruction and other anthropogenic pressures. We developed methodology for a line transect distance sampling survey and applied it systematically across the species' range. The resulting distance model estimated a mean density of 226.9 tortoises km^{-2} (95% confidence interval, CI, 168.1–306.3) and a total population of 664,980 (95% CI 492,680–897,550). Fragmentation of the species' range suggests the current population could be $< 30\%$ of the historical population. Of the remaining population 73.5% falls within protected areas. However, nine of these 12 protected areas are designated as IUCN category III, V or VI parks, allowing some extractive activities to be undertaken. The most effective strategy for the conservation of *P. arachnoides* would be to reduce the threats to this species and its habitat, and to develop and expand the current community-based conservation and poverty alleviation programmes in the region.

Keywords Chelonia, distance sampling, Madagascar, population density, population size, *Pyxis arachnoides*

Introduction

Madagascar supports one of the highest rates of endemism (Brooks et al., 2006) and, like many other regions of high endemism, has complex patterns of micro-endemism (Goodman & Benstead, 2005; Wilmé et al., 2006). These patterns of micro-endemism apply to Madagascar's four species of endemic tortoises, all restricted in range and facing threats to their survival from loss of habitat and collection for illegal export to support the pet trade and, in some cases, local consumption (Walker et al., 2004; Leuteritz et al., 2005; Young et al., 2008; Walker, 2010). However, unlike the extensive research on the island's charismatic fauna there has been little research on the ecology and conservation status of Madagascar's tortoises, in particular the smallest genus, *Pyxis*. This genus comprises two species, the flat-tailed tortoise *P. planicauda* and the spider tortoise *P. arachnoides*, both categorized as Critically Endangered on the IUCN Red List (Leuteritz et al., 2008; Leuteritz & Walker, 2008).

The study reported here focuses on *P. arachnoides*, a species endemic to the dry coastal forests of south-west Madagascar, where the species occurs only within c. 10 km of the coast (Walker, 2010; Walker et al., in press). The species historically inhabited a continuous belt of dry forest habitat comprising 555 km of coastline (Pedrono, 2008), from the Mangoky River to Lac Anony (Bour, 1981; Pedrono, 2008). As a result of habitat destruction (Seddon et al., 2000), collection for international trade and domestic consumption (Walker et al., 2004; Pedrono, 2008; Walker, 2010) the species' range is now fragmented and is thought to have declined by 71% (Walker, 2010; Walker et al., in press).

Much of the conservation policy for Madagascar's rare, endemic tortoises has been based on limited biological and ecological data (Mittermeier et al., 2008) and the population size and density of *P. arachnoides* have never been rigorously estimated. The current study provides baseline data for the population size and density of the remaining wild population of *P. arachnoides*, using a distance sampling technique.

Study area

The biodiverse, dry coastal forests are unique to south-west Madagascar (Phillipson, 1996; Raxworthy & Nussbaum, 2000; Seddon et al., 2000). Spider tortoises are habitat specialists, typically favouring areas of $< 40\%$ canopy cover (Walker et al., 2007). Walker (2010) and Walker et al. (in press) used high-resolution satellite imagery to establish areas within the suspected historical extent of occurence (Bour, 1981) of the species where suitable habitat still exists and then undertook time-dependent searches along transects to establish the presence or absence of remaining tortoise populations. From these data the area of the

Ryan C.J. Walker* (Corresponding author) Nautilus Ecology, Oak House, Pond Lane, Greetham, Rutland, LE15 7NW, UK. E-mail ryan@nautilusecology.org

Tsilavo H. Rafeliarisoa[†] Département de Biologie Animale, Université d'Antananarivo, Antananarivo, Madagascar

*Also at: Department of Environment, Earth and Ecosystems, The Open University, Milton Keynes, UK

†Also at: Madagascar Biodiversity Partnership, Omaha's Henry Doorly Zoo, Grewcock's Center for Conservation and Research, Omaha, Nebraska, USA

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TABLE 1 Current known range of the three subspecies of the spider tortoise *Pyxis arachnoides* in Madagascar and the intergrades between them (Fig. 1), with the subpopulations indicated by the letters A–E, which correspond to the locations labelled in Fig. 1, and known total range of each subspecies or intergrade population, the source of these data, and the number of transects used to survey each subspecies and intergrade population and the years in which the surveys took place.

Subspecies	No. of subpopulations	Range (km^2)	Source	No. of transects	Year of survey
P. a. brygooi (A)	3	499.6	Walker (2010), Walker et al. (in press), Rhodin et al. (2011)	13	2009
P. a. brygooi/P. a. arachnoides intergrades (B)	1	99.7	Walker et al. (in press)	4	2009
P. a. arachnoides (C)	1	1,029.1	Walker et al. (in press)	22	2010
P. a. arachnoides/ P. a. oblonga (D)	1	267.0	Walker et al. (in press)	6	2010
P. a. oblonga (E)	2	568.5	Walker et al. (in press)	19	2010/2011
Total	8	2,468.8		64	

fragments of remaining habitat supporting tortoises was calculated using a geographical information system (Walker, 2012), to give an accurate depiction of the remaining area of occupancy of the species.

P. arachnoides is extant in eight areas of forest comprising a total area of 2,463.8 km^2 (Walker, 2010; Walker et al., in press; Table 1, Fig. 1). There are three subspecies (Chiari et al., 2005; Pedrono, 2008) and two zones of intergradation between these subspecies (Walker, 2010; Rhodin et al., 2011; Walker et al., in press). *P. a. brygooi* occupies the north of the species' range, comprising three fragmented populations north of the Manombo River, *P. a. arachnoides* occupies the range south of the Onilahy River to c. 30 km north of the Linta River (Fig. 1), and *P. a. oblonga* occupies the southernmost extent of the range around Cap Sainte Marie, with a further population stretching 70 km east of the Manambovo River through the coastal dunes to c. 70 km east of the Manambovo River (Walker, 2010; Walker et al., in press; Fig. 2). The two small intergrade populations are found within the transitional zones between *P. a. brygooi* and *P. a. arachnoides* (Walker, 2010) and between the ranges of *P. a. arachnoides* and *P. a. oblonga* (Walker et al., in press; Fig. 1).

Methods

Distance sampling

Line transect distance sampling is a widely used method for estimating the density and/or abundance of biological populations (Thomas et al., 2010) and has been widely applied to an array of taxa (Newey et al., 2003; Rivera-Milan et al., 2004; Jathanna et al., 2008), including southern Madagascar's two other dry forest tortoise species *P. planicauda* and *Astrochelys radiata* (O'Brien et al., 2003; Leuteritz et al., 2005; Young et al., 2008). Census techniques must be tailored to the study species (Krebs, 1999; Southwood & Henderson, 2000) and we took into account the ecological characteristics of *P. arachnoides*, surveying when the species was most active.

The statistical routine used for analysing line transect data obtained by distance sampling is based on Fourier analysis (Burnham et al., 1980; Akin, 1998), the accuracy of which depends on four assumptions: (1) surveyed objects directly on the line (at zero distance) will not be missed (i.e. $g(0) = 1$), (2) objects are fixed at the initial sighting position (i.e. they do not move rapidly upon detection and are not counted more than once), (3) distances are measured exactly, and (4) all sightings are independent (Burnham et al., 1980). Tortoises lend themselves to this method of estimation by not violating these key assumptions (Burnham et al., 1980; Akin, 1998; Leuteritz et al., 2005). However, *P. arachnoides* aestivates seasonally, during the dry season from May to November (Walker et al., 2007), and also daily during the warmest part of the day, between December and April when the species is otherwise at its most active (Walker et al., 2007; Walker, 2012). Therefore, if surveys are undertaken at inappropriate times of the day and/or year, the first and/or fourth assumption will be violated.

Field techniques

Sixty-four transects were surveyed across the species' range (Walker, 2010; Walker et al., in press; Table 1; Fig. 1); 63 were 1,000 m in length and one was 600 m. Field work was during January and February in either 2009, 2010 or 2011, during the annual period of highest tortoise activity (Walker et al., 2007; Pedrono, 2008). The species is crepuscular (Walker et al., 2007; Walker, 2012) and therefore surveying was limited to the cooler parts of the day: 6.30–10.30 and 15.30–18.30 (Walker et al., 2007).

Two observers traversed each transect, walking side by side on an easterly bearing using the tracking function of a

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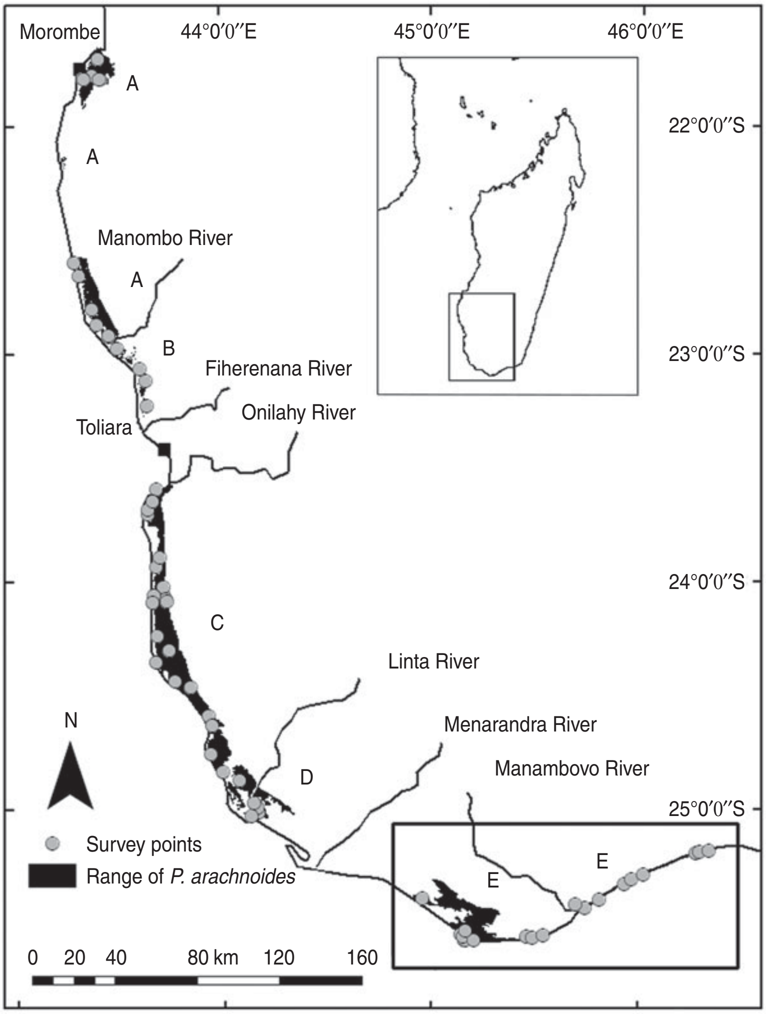

FIG. 1 The current known area of occurence of the three subspecies of the spider tortoise *Pyxis arachnoides* in eight areas of forest (Table 1; Walker, 2010; Walker et al., in press) and the locations of the 64 survey transects. A, three subpopulations of *P. a. brygooi*; B, one subpopulation of *P. a. brygooi/P. a. arachnoides* intergrades; C, one subpopulation of *P. a. arachnoides*; D, one subpopulation of *P. a. arachnoides/P. a. oblonga* intergrades; E, two subpopulations of *P. a. oblonga*. The rectangle on the inset indicates the location of the main figure in south-west Madagascar.

global positioning system to measure the distance covered. The surveyors searched carefully for tortoises on their respective side of the transect line and directly in front them. The mean time to traverse the 1,000 m transects was 34.7 ± SD 5.1 minutes (not including the time spent stationary when tortoises were detected), with time dependent upon terrain and density of the vegetation. Upon encountering a tortoise the perpendicular distance from the centre of the transect line (where the observer was standing) was measured in cm to the middle of the carapace of the point of first detection for each tortoise, using a 15-m retractable steel tape measure. Each tortoise was marked using a small dot of nail polish on the top of the carapace, to avoid duplicate counting.

Data analysis

Using *Distance v. 5.0* (Thomas et al., 2010) a conventional distance sampling model was developed using the line transect data, comprising 109 tortoise records, of all size classes, across the transects. The probability of detection was modelled as a function of observed distance from the transect line using robust, semi-parametric methods. The perpendicular distance data for the 109 tortoises were examined in a histogram of 16 intervals of equal width (Laake, 1978), to investigate any responsive movement to the observer and clumping of observations (Fig. 3). No strong evidence of evasive movement was detected but there was clumping at 151–300 cm from the centre line and at zero distance (< 50 cm; Fig. 3). A quantile–quantile plot analysis indicated heaping in areas of the detection function, possibly as a result of inconsistent detection further from the centre line because of the small size of the species (adult mean straight carapace length 169 ± SD 23.3 mm; Walker et al., 2007), its cryptic behaviour and variations in habitat complexity (Best, 1981; Verner, 1985). It was therefore necessary to truncate at 700 cm from the centre line and transform the data into automatically adjusted intervals using the data filter function to gain a shoulder at zero distance (Fig. 4) and improve model robustness (Thomas et al., 2010). The following models, considered to be general and robust (Leuteritz et al., 2005; Young et al., 2008; Thomas et al., 2010), were considered:

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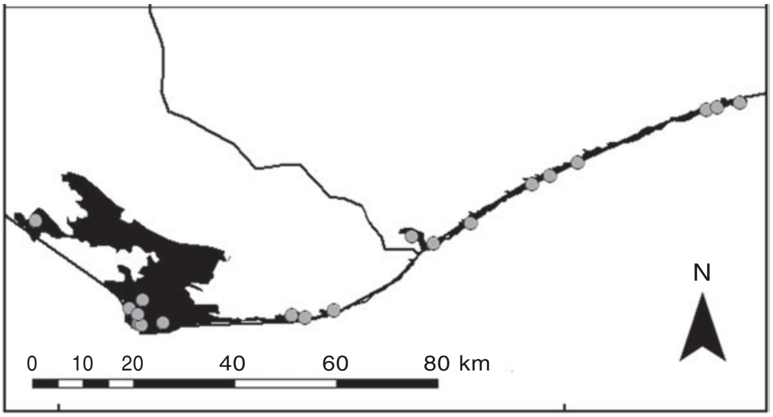

FIG. 2 Range of *P. a. oblonga* (the rectangle in Fig. 1), showing the narrow area occupied in the eastern part of its range as a result of habitat loss, which has forced the tortoises to occupy coastal sand dunes.

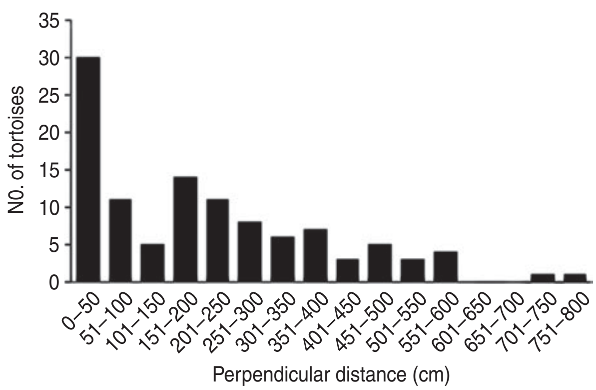

FIG. 3 A graphical representation of the raw distance sampling data showing the number of tortoises recorded in each 50 cm interval from the centre of the transect line. Heaping of the data can be seen at 151–300 cm and a spike at zero distance, results of the small size of the species and the influence of variations in habitat complexity on detection probability.

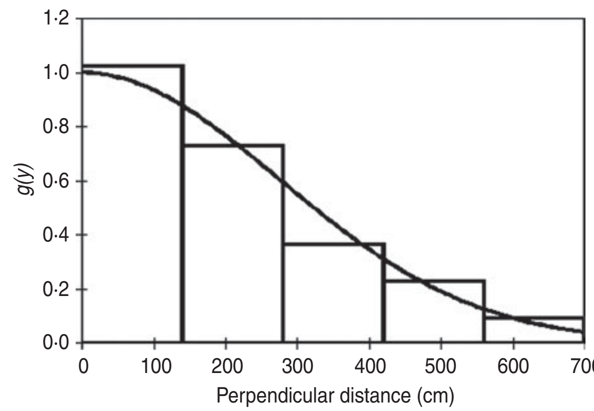

FIG. 4 Detection probability $g(y)$ for *P. arachnoides* after truncation of the data (Fig. 3) at 700 cm from the centre line and transformation into automatically adjusted intervals, using *Distance*.

uniform/cosine (Burnham et al., 1980), uniform/simple polynomial (Anderson & Pospahala, 1970), half-normal/hermite polynomial and hazard-rate/simple polynomial (Buckland, 1985). Model fit was assessed using Akaike's information criterion (AIC), trading off the bias of simple models against the higher variance of more complex models (Burnham & Anderson, 2002), and fit was tested using a χ^2 goodness-of-fit test.

Results

The half-normal + hermite polynomial adjustment model proved a good fit to the data ($\chi^2 = 1.10$, df $= 3.00$, P $= 0.78$) within the conventional distance sampling model. This adjustment model supported the lowest ΔAIC values (Table 2). The model's 15.2% coefficient of variation fell within the targeted level of precision ($< 20\%$) suggested by Thomas et al. (2010). The mean tortoise density across its range was estimated to be 226.9 km^{-2} (95% confidence interval, CI, 168.1–306.3; Table 2). Using this density and the area of the known total range the total population size was estimated to be 664,980 tortoises (95% CI 492,680–897,550; Table 2). Detection of tortoises fell dramatically with increasing distance from the centre of the transect line, as indicated by the effective strip half width of 340.7 cm (Fig. 4); i.e. it was difficult to detect tortoises > 3 m away from the centre line of the transect.

Discussion

Distance sampling is widely regarded as the most effective method for estimating the density and population of tortoises in dry forest environments (Hailey & Willemsen, 2000; Anderson et al., 2001; Young et al., 2008). Leuteritz et al. (2005) compared distance sampling with the Lincoln–Petersen mark recapture technique (Greenwood, 1996) and concluded that the latter method was prone to overestimation when applied to the *A. radiata* population in south-west Madagascar. The half-normal model that we used is known to perform well with data that show a rapid fall in detection (Newey et al., 2003; Thomas et al., 2010), as shown in Fig. 3. This model works well for data collected on cryptic animals that inhabit areas of thick and patchy

Table 2 Each of the four *Distance* models used to estimate the total population of spider tortoises, with corresponding ΔAIC and % coefficient of variation (% CV), and estimated mean density per km^2 and population size (both with 95% CI).

Model	Δ AIC	% CV	Density, km^{-2} (95% CI)	Population size (95% CI)
Uniform + cosine	1.23	13.82	209.4 (159.3–275.2)	613,570 (466,740–806,590)
Uniform + simple polynomial	2.87	10.44	247.4 (178.1–343.8)	725,100 (512,830–1,000,750)
Half-normal + hermite polynomial	0.00	15.23	226.9 (168.1–306.3)	664,980 (492,680–897,550)
Hazard rate + simple polynomial	1.39	12.15	231.6 (163.2–328.7)	678,600 (478,110–963,160)

vegetation cover (Rivera-Milan et al., 2004), such as *P. arachnoides*.

All previous studies detailing the density of this species lacked spatial resolution and were confined to geographically small areas. Jesu & Schimmenti (1995) and Walker et al. (2007) reported densities for *P. a. arachnoides* of > 3.0 and $4.6 \pm$ SD 1.6 ha^{-1}, respectively, in the Anakao region during the same time of year as our surveys, using sweep searches or simple belt transects. Pedrono (2008) observed densities of > 16 ha^{-1} using sweep searches in areas of good habitat. Our results, however, suggest that the mean density across the species' remaining range is lower, at 2.3 ha^{-1} (Table 2).

Pedrono (2008) speculated there were 2–3 million *P. arachnoides* and Randriamahazo et al. (2007) estimated 282,000, neither using a distance model. Randriamahazo et al.'s (2007) estimate was based on data from one isolated area (Cap Sainte Marie Special Reserve), using incidental sightings of *P. a. oblonga* recorded by Luteritiz et al. (2005) during their study of *A. radiata*. Our figure of 664,980 falls between these two estimates. Comparison with other small tortoise species of arid environments is difficult as the appropriate data are not available. Young et al. (2008), however, reported a total population of c. 28,000 *P. planicauda*, sparsely distributed (0.4 ha^{-1}) across its narrow extent of occurence.

The range of *P. arachnoides* once spanned at least 555 km of coastline (Pedrono, 2008). The dry coastal forests of south-west Madagascar are, however, one of the country's most threatened terrestrial habitats, with habitat loss of 1.2% per year (Harper et al., 2007). This loss has resulted in severe fragmentation of the remaining area of occupancy of *P. arachnoides* (Walker, 2010; Walker et al., in press). As a result the population size is possibly $< 30\%$ of historical figures and could be less if the density of existing populations has been reduced by collection pressure and habitat degradation. Habitat degradation is a wide-ranging conservation threat for the remaining populations of *P. arachnoides*. Aponte et al. (2003) demonstrated that habitat degradation in South America can result in altered age structure, population density and growth rates of *Chelonoidis carbonaria*. The effects of habitat degradation and subsequent fragmentation of the spider tortoise's range may increase in the near future as a result of the proposal to extract mineral sand from south-west Madagascar (Sarrasin, 2006). This mining operation could affect 18% of the remaining range of the spider tortoise (Walker et al., in press).

The Système des'Aires Protégées de Madagascar has recently increased Madagascar's protected area threefold (Rabearivony et al., 2010). Several new protected areas have been established within the coastal dry forest, previously the least represented ecoregion within the country's protected area network (Fenn, 2003). Currently 73.5% of the remaining area of occupancy of *P. arachnoides* falls within existing or proposed protected areas (Walker et al., in press). However, with the exception of the Mikea Forest National Park and the extension to Tsimanampesotsa National Park, all new protected areas are IUCN category III, V and VI multiple-use protected areas (but see the critique of Gardner, 2011), co-managed by local community associations (WWF, unpubl. data). *P. arachnoides* may not receive complete protection from habitat destruction and poaching under such a management regime.

Currently, habitat loss resulting from subsistence agriculture and fuelwood harvesting is probably the greatest driver of the decline of the spider tortoise (Pedrono, 2008). It is important therefore to address the socio-economic and cultural issues causing local communities to harvest timber from the coastal dry forests. Such matters can only be addressed through targeted poverty alleviation and conservation programmes. Several NGOs in the region are engaged in livelihood generation projects, habitat restoration and community-based tortoise conservation projects (Rafeliarisoa et al., 2010; WWF, 2010). A project is underway within the range of *P. a. brygooi* to provide local communities within the Velondriake locally-managed marine area in south-west Madagascar with reproductive health and family planning (Harris et al., 2012), and this could alleviate local human population pressure on tortoise habitat. However, these projects are limited in their geographical scope and most areas within the region lack initiatives to diminish the heavy reliance of communities on natural resources.

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Biographical sketches

Ryan C.J. Walker is a freelance wildlife biologist currently contracted by several NGOs and environmental consultancies. He is also continuing his research on the biogeography and conservation management of *P. arachnoides*. Tsilavo H. Rafeliarisoa is a herpetologist and geneticist. He is currently researching the biogeography and population genetics of the Critically Endangered radiated tortoise *Astrochelys radiata*.