Range expansion of the globally Vulnerable Karamoja apalis *Apalis karamojae* in the Serengeti ecosystem

Philip Shaw[1]*, A.R.E. Sinclair[2,3], Kristine Metzger[2,3], Ally Nkwabi[3], Simon A.R. Mduma[3] and Neil Baker[4]

[1]School of Biology, Bute Building, University of St Andrews, Fife, KY16 9TS, U.K., [2]Centre for Biodiversity Research, 6270 University Boulevard, University of British Columbia, Vancouver, V6T 1Z4, Canada, [3]Serengeti Biodiversity Program, PO Box 661, Arusha, Tanzania and [4]Tanzania Bird Atlas, PO Box 1605, Iringa, Tanzania

Abstract

The underlying causes of change in geographic range size are less well understood in African birds than in north temperate species. Here, we examine factors associated with range expansion in the Karamoja apalis (*Apalis karamojae*), a globally Vulnerable warbler confined to north-east Uganda, north-central Tanzania and southern Kenya. In Tanzania, it was originally known only from the Wembere Steppe, but since 1993 (and possibly as early as 1983) has extended its range into the Serengeti ecosystem, *c.* 140 km to the north, reaching southern Kenya by 2004. Changes in the warbler's range within the Serengeti have broadly reflected a cyclical change in the density of its main habitat, *Acacia drepanolobium* woodland, which was low in the 1970s, high during the 1980s and 1990s, and declined in the early 2000s. Karamoja apalis records in the Serengeti showed a 5 year time lag behind *A. drepanolobium* density, which was in turn negatively correlated with the area of grassland burnt 10 years earlier. Previous studies in the Serengeti have also linked *Acacia* regeneration to changes in grazing pressure, as increasing wildebeest (*Connochaetes taurinus*) numbers have reduced the volume of combustible material present, and hence the frequency of damaging 'hot burns'. We conclude that this globally threatened warbler appears to have benefited from changes in ungulate populations in the Serengeti, which have influenced burning intensity and hence tree regeneration. The warbler's range now appears to be declining, however, following a recent reduction in the density and annual survival of *A. drepanolobium* in the northern Serengeti.

*Correspondence: E-mail: ps61@st-andrews.ac.uk

Résumé

Les causes sous-jacentes du changement de la taille d'une distribution géographique sont moins bien connues pour les oiseaux africains que pour les espèces du nord tempéré. Nous examinons ici des facteurs liés à l'expansion de l'aire de répartition de l'apalis de Karamoja *Apalis karamojae*, un sylviidé classé comme Vulnérable au niveau mondial, confiné au NE de l'Ouganda, au centre-nord de la Tanzanie et au sud du Kenya. En Tanzanie, on ne le connaissait à l'origine que dans la steppe de Wembere mais depuis 1993, et peut-être même dès 1983, il a étendu son aire de répartition dans l'écosystème du Serengeti, environ 140 km plus au nord, et atteint le sud du Kenya en 2004. Les changements de l'aire de répartition de ce sylviidé dans le Serengeti reflètent largement un changement cyclique de la densité de son habitat principal, la forêt d'*Acacia drepanolobium*, qui était faible dans les années 1970, forte pendant les années 1980 et 1990, et qui a diminué au début des années 2000. Les rapports sur l'apalis de Karamoja au Serengeti montrent un retard de cinq ans par rapport à l'évolution de la densité d'*A. drepanolobium*, elle-même étant négativement liée à la zone de prairie brûlée 10 ans plus tôt. Des études antérieures faites au Serengeti lient aussi la régénération des acacias aux changements de la pression du pâturage, étant donné que le nombre croissant de gnous, *Connochaetes taurinus*, a réduit le volume des matières combustibles restantes et donc la fréquence des feux trop chauds qui causent beaucoup de dégâts. Nous concluons que cet oiseau menacé au niveau

mondial semble avoir bénéficié des changements des populations d'ongulés au Serengeti, qui ont influencé l'intensité des feux et donc la régénération des arbres. L'aire de répartition de ce sylviidé semble pourtant en train de se réduire suite à une récente réduction de la densité et de la survie annuelle d'*A. drepanolobium* dans le nord du Serengeti.

Introduction

Understanding the causes of change in a species' geographic range is of fundamental importance in conservation. Range size changes, particularly those resulting from climate change (Channell & Lomolino, 2000; Davis, 2003; Parmesan & Yohe, 2003; Schmitz, Post & Burns, 2003; Williams *et al.*, 2005) and agricultural practices (Li & Wilcove, 2005; Venter *et al.*, 2006; Watling & Donnelly, 2006; Butler, Vickery & Norris, 2007), are generally better understood at north temperate latitudes than in tropical regions, where the signature of climate change is present (Hulme *et al.*, 2001; Thuiller *et al.*, 2006) but less evident. In Africa, loss of native habitat through exploitation and land conversion is increasing rapidly (Brashares *et al.*, 2004; Newmark, 2008) and range reductions have been documented both for mammals and birds (Burgess *et al.*, 2004). In contrast, range expansion, for example in birds, is poorly documented, and the causes are usually unknown.

Recent examples of range expansions in Tanzania, East Africa, include savannah species such as the white-bellied turaco (*Corythaixoides leucogaster*), Taita fiscal (*Lanius dorsalis*), black-throated barbet (*Lybius melanocephalus flavibuccalis*) and Karamoja apalis (*Apalis karamojae*), these last two having recently spread north from the Wembere Steppe to the Serengeti (A. Sinclair and N. Baker, unpublished data; Shaw *et al.*, 2004). Here, we document the expansion of Karamoja apalis in the Serengeti ecosystem, and compare this with habitat change, itself the result of variation in burning and grazing pressure as ungulate populations have increased.

The Karamoja apalis is a restricted-range, threatened warbler which, in the 1960s, was known from two small areas, some 720 km apart: in north-east Uganda and north-central Tanzania (Collar & Stuart, 1985; Stattersfield *et al.*, 1998; Shaw & Mungaya, 2006). The Tanzania subspecies (*A. k. stronachi*) is phenotypically distinct, with a significantly longer wing and tail than has been recorded in the Ugandan, nominate race (Stuart & Collar, 1985; Shaw *et al.*, 2005). The species is classed as globally Vulnerable, partly on account of its small range, but also because its habitat has been severely fragmented by encroaching cultivation and livestock-farming, indicating a decline in its global population (Birdlife International, 2000, 2009).

In central Tanzania, Karamoja apalis were first recorded in 1961 in the Wembere Steppe (Fig. 1). Based on anecdotal reports from observers in the 1960s and 1970s, the species' *Acacia* habitat was thought to have extended throughout the length of the Steppe: a distance of *c.* 175 km (Collar & Stuart, 1985). However, a survey in 2003 showed that the warbler's range within the Wembere was by then less extensive than had previously been assumed; that it occurred at a relatively low density;
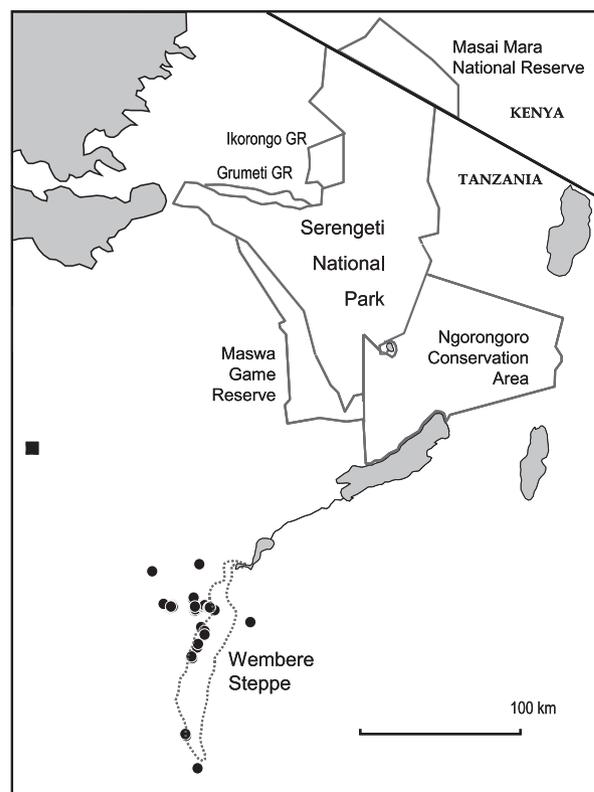

Fig 1 The Wembere Steppe and Serengeti ecosystem. Karamoja apalis were initially recorded in and around the Wembere Steppe, south of the Serengeti ecosystem. Dots represent one or more apalis sightings in the Wembere Steppe, 2003–2009 (from Shaw *et al.*, 2004, N.&E. Baker, unpublished). ■: New site discovered in 2009, near Shinyanga. GR: Game Reserve

and that it was associated almost exclusively with two tree species: whistling thorn (*Acacia drepanolobium* Harms ex B.Y. Sjöstedt) and, less frequently, white thorn (*A. seyal* Delile) (Shaw *et al.*, 2004). Half of all individuals encountered in the Wembere were found in the tallest, densest stands of whistling thorn, which occupied less than 6% of the area surveyed. Browsing by livestock, pruning for firewood and scrub clearance for pasture were widespread, being evident at over 80% of locations surveyed. Such pressures were thought likely to have intensified in 1988–2002, when the human population in areas surrounding the Wembere increased at an average of *c.* 4% per annum (Shaw *et al.*, 2004).

Since the early 1990s, Karamoja apalis have been recorded intermittently from the Serengeti ecosystem (Fig. 1) (Baker & Baker, 2002). By the early 2000s, the number and geographical spread of sightings suggested that Serengeti National Park and adjoining protected areas might support a significant population of the apalis. Based on records from the 1990s onwards, and on vegetation and grass fire surveys, this paper compares the changing status of Karamoja apalis in the Serengeti with that of its main habitat, *A. drepanolobium,* and suggests a possible explanation for the warbler's expansion.

Materials and methods

Bird numbers and distribution

Records of Karamoja apalis in the Serengeti ecosystem were compiled from three sources. Firstly, sightings up to July 2009 were collated from published sources and from information provided by researchers and tour guides, much of it held in the Tanzania Bird Atlas database (Baker & Baker, 2009). For most of these observations, the length of time that a habitat was under observation is unknown. However, since 1967 one of us (ARES) has noted the amount of time spent recording in each habitat, including observation time during which no apalises were detected.

Secondly, a number of permanent sites within different *Acacia* habitats have been repeatedly censused over the period 1997–2008. At each site, birds were recorded either by sight or by call for 10 min. These records provide both a measure of effort and an index of the frequency of apalis detections.

Finally, an intensive survey was conducted in August–September 2005 and July 2006. Areas of the Serengeti ecosystem within Serengeti National Park and Ngorongoro

Conservation Area known to hold extensive stands of *Acacia drepanolobium* or *A. seyal* were visited at least once. Each stand was scanned for 10 min. Fifty-four 10 min point counts were made in *A. drepanolobium* or *A. seyal* in areas throughout the Serengeti ecosystem, excluding the open plains.

Tree density

Karamoja apalis in the Wembere Steppe showed a strong preference for the tallest, densest stands of *A. drepanolobium* (Shaw and Mungaya, 2006). To determine whether the structure of *A. drepanolobium* in the Serengeti ecosystem was similar to that of the Wembere Steppe, stem heights and densities were measured at 188 survey points, *A. drepanolobium* or *A. seyal* being the dominant species at 145 of these. At each site, a line transect was followed on a fixed bearing for up to 2 km through an extensive stand dominated by *A. drepanolobium* or *A. seyal*. Tree density was assessed at intervals of 100 m, using a global positioning system to determine the distance and bearing to each survey point. The nearest ten stems (of at least 0.5 m high) to each survey point were measured. Density was estimated using the formula $\Pi^* dmax^2$, where *dmax* is the distance between the first and tenth nearest stem. The same measurements were made of ten stems nearest to, and including, the stem on which each Karamoja apalis individual or pair was first encountered.

Changes in Acacia drepanolobium *densities over time*

Vegetation coverage of the Serengeti National Park has been mapped by Herlocker (1974) from aerial photographs with extensive ground-truthing. Both *A. drepanolobium* and *A. seyal* are widespread in the Serengeti, where they occur on impeded drainage soils that become inundated during the rainy season. This type of silty soil has not changed in area over the past decades, although the density of trees on it has changed, as described below. The combined area of the two vegetation types, based on Geographic Information System analysis, comprises 13% of the savannah woodland, covering *c.* 1000 km^2. Within the Serengeti ecosystem the density of *A. drepanolobium* has been measured since the 1960s in two ways. Firstly, present density (2006) was measured at permanent bird survey sites across the Serengeti ecosystem using Point Centre Quarter methods (Krebs, 2001). Similar methods were used for other sites in stands of *A. drepanolobium* in 1999

(K. Metzger, unpublished data) and 2005 (P. Shaw, unpublished data). Density values for 1986 are given by Stronach (1988). Secondly, a number of locations have been monitored using oblique photographs repeated at intervals from 1965 up to the present time (Sinclair *et al.*, 2007). On these photographs the same area was demarcated and the number of trees counted, and a relative density was calculated, with the present time set at unity. These relative densities were transformed to actual densities from the measurements taken in 2006.

Extent and frequency of grass fires

Grass fires occur annually in the dry season. The locations and extent of the fires have been recorded at intervals since the early 1960s. These records came from aerial surveys starting in 1963, in which the location was recorded on maps. For logistical reasons only the northern half of the ecosystem was monitored in the 1970s and 1980s, and few records were available for the 1990s. From 1999 to 2005, satellite imagery was used to record burns (Dempewolf *et al.*, 2007).

Results

Distribution of Karamoja apalis

The changing distribution of Karamoja apalis sightings in the Serengeti ecosystem is shown in Fig. 2, at a resolution of 10×10 km. While an unconfirmed sighting of Karamoja apalis in 1983 appears to be the earliest record of the species in the Serengeti (van Someren *in litt.* in Collar and Stuart, 1985), the first confirmed sightings were made in 1993, in south-western Serengeti and Maswa Game Reserve (Moyer, 1995). Twenty-four sightings were recorded from western and central Serengeti during 1994–2003, and by 2004 the apalis had spread north of the Masai Mara National Reserve in southern Kenya (Fig. 2; P. Shaw, unpublished data). This was the first recorded sighting in Kenya.

The number of Karamoja apalis sightings recorded in the Serengeti peaked in 2005 (Fig. 3a), coinciding with an intensive survey of the species. Since the frequency of sightings is likely to have been biased by variation in search effort (for example, appropriate habitats may not have been searched in earlier years), we show in Fig. 3b only records for sites in *A. drepanolobium* and *A. seyal* that were systematically surveyed for known time periods. The
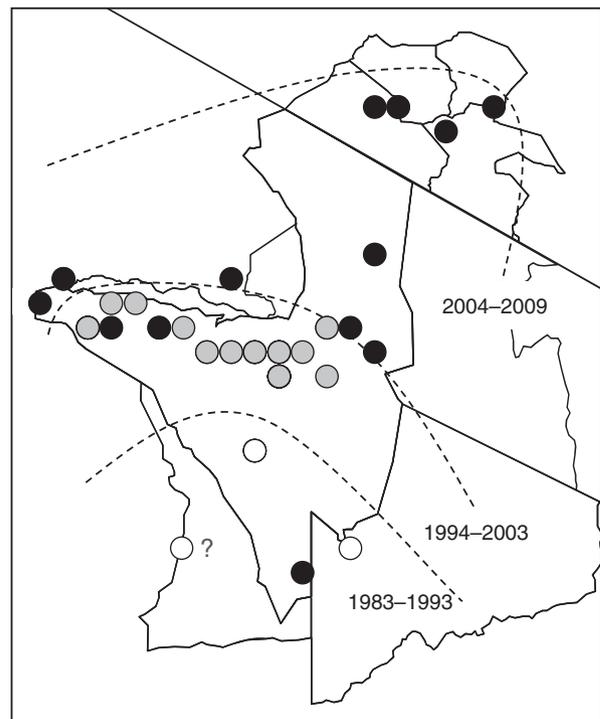

Fig 2 Contour lines showing the northern expansion of Karamoja apalis in the Serengeti ecosystem. Karamoja apalis observations are shown at a resolution of 10×10 km, and grouped in three time intervals, indicated by symbols in white (1983–1993), grey (1994–2003) or black (2004–2009). Each symbol shows the period in which a 10×10 km square was first occupied. The location of one record during 1993 (indicated with a '?') is unclear

two figures show similar trends, namely the appearance of Karamoja apalis in the early 1990s, an increase to a peak in 2004–2005, followed by a decline.

Changes in the habitat of Karamoja apalis

In the Serengeti, the mean density of stems recorded in stands dominated by *A. drepanolobium* and *A. seyal* (354.3 stems ha^{-1}; ±51.89 SE; n = 145) was lower than that recorded in the Wembere Steppe (455.7 stems ha^{-1}; ±52.07 SE; n = 149). At both sites, however, mean stem density fell substantially below that recorded in the vicinity of Karamoja apalis sightings (pooled between the two sites): 1938.4 stems ha^{-1} (±344.3 SE; n = 44). Half of all Karamoja apalis detected during the surveys of 2003 and 2005–2006 were found in stands with a density of at least 1000 stems ha^{-1}. Such densities occurred at only 7.6% of survey points in the Serengeti and at 13.4% of survey points in the Wembere (χ^2_1 = 2.654; difference n.s.).
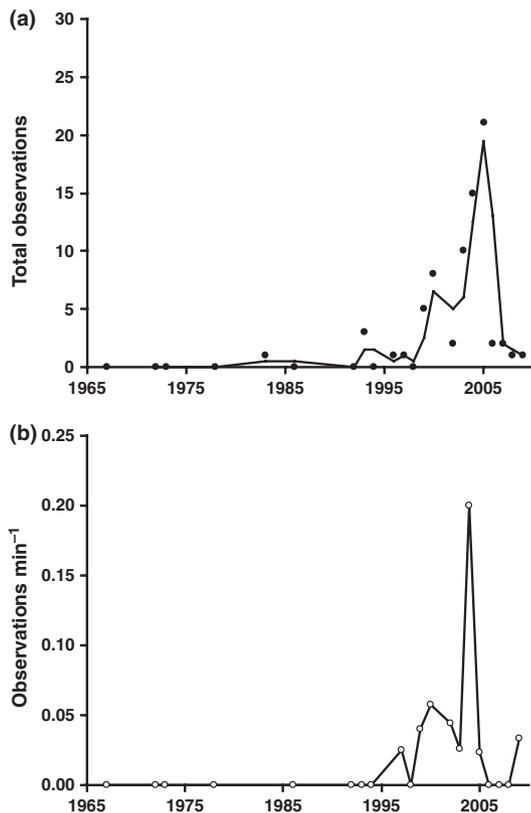
Fig 3 (a) Total observations of Karamoja apalis in the Serengeti ecosystem from both systematic sites and incidental observations. The solid line is a two-point running average. (b) Observations of Karamoja apalis per minute of recording time in systematically monitored sites. Both figures show the arrival of the apalis in the 1990s, peak numbers in 2004–2005, and a subsequent decline

Fig 4 (a) The density of *A. drepanolobium*, as trees ha^{-1} in the Serengeti ecosystem. Density was high in the 1960s, declined to low levels in the 1970s and then regenerated in the 1980s. (b) The extent of burning in the northern half of Serengeti National Park by year. Burning declined through the 1960s and was low in the 1970s. It has increased to moderate levels since the 1980s, due to early-burn management. The smoothed curve is a three-term polynomial

All records of Karamoja apalis in the Serengeti were also in stands of *A. drepanolobium* or *A. seyal*. The locations of these species, determined by soil type, have remained the same over time, but their densities within these locations have altered, following a cycle of increase and decline. The density of *A. drepanolobium* in the 1960s was high (Fig. 4a), but declined throughout the 1970s, when several known sites reverted to open grassland. Beginning in about 1980, *A. drepanolobium* began to regenerate in their previous locations and reached a maximum density in the late 1980s and 1990s. During the 2000s there has been a decline, however, many sites now having few plants remaining. The observed ch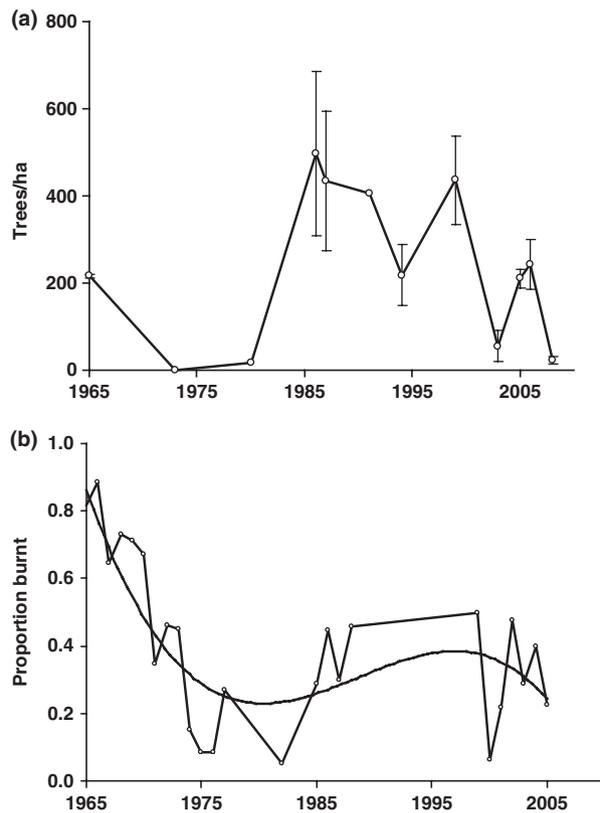anges in *A. drepanolobium* over time appear to have influenced Karamoja apalis abundance, the number of apalis records (y) from Serengeti being positively correlated with the density of *A. drepanolobium* (x) 5 years earlier ($y = 0.00001 x^{2.87}$; $r^2 = 0.74$; $P < 0.01$).

Changes in the frequency and extent of grass fires

The proportion of the northern half of the Serengeti burnt each dry season is shown in Fig. 4b. The extent of burning declined during 1965–1975, and was at a minimum during 1974–1985. This was followed by a moderate increase, due to the introduction of early-burn management by National Parks staff. These changes in burning intensity

appear to have influenced subsequent woodland cover, the density of *A. drepanolobium* (trees ha^{-1}) (y) showing a strong, negative correlation with the extent of burns (x) 10 years earlier ($y = 515–682x$; $r^2 = 0.66$; $P < 0.01$).

Discussion

The known range of Karamoja apalis within the Serengeti ecosystem has expanded greatly since the early 1990s. As in the Wembere Steppe, Karamoja apalis were recorded mainly in stands of *A. drepanolobium*, a widespread tree species whose geographic range greatly exceeds that of the apalis, particularly in Kenya, where the warbler has only recently been discovered. The warbler's distribution was positively correlated with the denser, mature stands of *A. drepanolobium* in the Wembere Steppe (Shaw & Mungaya, 2006) and with the distribution of *A. drepanolobium* and *A. seyal* in the Serengeti.

The only known source population for Karamoja apalis in the Serengeti is the Wembere Steppe where, in 2003, the species was found to be patchily distributed within an area spanning 102 km N-S by 53 km E-W (Shaw & Mungaya, 2006). Much of the land between the Wembere Steppe, Serengeti and Lake Victoria (Sukumaland) has seen a rapid rise in the demand for farmland and pasture which, coupled with the effects of a tsetse control programme in the 1920s–1930s, has resulted in the formation of a largely treeless 'cultivation steppe' (Meertens *et al.*, 1995). While Sukumaland is thought to have retained little suitable habitat for the apalis, its recent discovery in an extensive stand of *A. drepanolobium* near Shinyanga (N. Baker personal observation 2009; Fig. 1), confirms that at least one occupied site persists in Sukumaland, and suggests that the Serengeti could have been colonized from this area rather than from the Wembere Steppe.

Acacia drepanolobium has undergone marked changes in density in the Serengeti, with two periods of high density (1960s, 1980s–1990s) and an intervening period of low density (1970s) (Fig. 4a). Similar changes have been observed anecdotally for *A. seyal*. During the 2000s the density of *A. drepanolobium* has declined, coinciding with a drop in the survival of individually marked trees. Tree survival during 1997–2002 was almost 100%, compared with 23% (±9.5% SE) subsequently (Hilborn *et al.*, 2006). An increase in the density of *A. drepanolobium* during the mid- to late-1980s was followed 5 years later by an increase in the number of apalis records from Serengeti, by

which time the tree had presumably grown to a height or density appropriate for the warbler. By 2009, sightings in the Serengeti had covered a wider area than that occupied in the Wembere Steppe, spanning 200 km N-S by 180 km E-W in the Serengeti-Mara, and 130 km N-S by 130 km E-W in Tanzania alone. However, the observed decline in both acacia species, and in the number of apalis sightings since 2005, suggest that the warbler's population in the Serengeti has now declined substantially.

The trends in apalis habitat described here reflect changes in burning frequency and grazing pressure that have affected all major tree species in the Serengeti (Sinclair *et al.*, 2007, 2008). Following the elimination of rinderpest in the early 1960s the wildebeest (*Connochaetes taurinus*) population of the Serengeti-Mara increased six-fold (Sinclair & Norton-Griffiths, 1979), leading to a reduction in the volume of grass remaining during the dry season, and hence in the amount of combustible material present. As a result, there was a decline in the extent of burning during 1963–1973, and both the frequency and extent of damaging 'hot burns' was reduced (Sinclair & Norton-Griffiths, 1979). Tree seedling survival subsequently improved, with the result that more seedlings reached heights at which they were resistant to burning (Sinclair & Norton-Griffiths 1979; Dublin, 1995). The dominant tree species, *A. robusta* Burch and *A. tortilis* Hayne, both responded positively to these changes across the whole ecosystem, and it appears that *A. drepanolobium* did likewise, the highest densities being recorded in areas where burns were at a minimum 10 years previously.

While factors leading to the colonization or expansion of Karamoja apalis in the Serengeti ecosystem remain speculative, it seems plausible that its recent spread into the Serengeti's protected area network may have resulted from an expansion of its highly specific habitat due, indirectly, to an increase in the wildebeest population during the 1970s, and a reduction in burning during 1975–1985. If this interpretation is correct, the Karamoja apalis population would seem likely to benefit from continued high wildebeest numbers and controlled burning, limiting the frequency of damaging 'hot burns'. *Acacia drepanolobium* and *A. seyal* appear to have a life-cycle of about 30 years, however, and both their densities and the number of Karamoja apalis recorded in the northern Serengeti have declined since 2004–2005. Continued monitoring of Karamoja apalis in both the Wembere Steppe and Serengeti ecosystem is required to track its changing status, and for its effective conservation.

Acknowledgements

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