

Swayne's hartebeest in Ethiopia: population estimate, genetic variability and competition with livestock

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Abstract Swayne's hartebeest *Alcelaphus buselaphus swaynei* was once widely distributed in the Horn of Africa. By the early 20th century, however, it was extirpated across most of its range and is now limited to two relict populations in the Ethiopian Rift Valley and categorized as Endangered on the IUCN Red List. In this study, we estimated the size and genetic diversity of these two remaining populations, with a particular focus on competition with livestock. We used a total block count method for both Swayne's hartebeest and livestock population counts, and faecal samples for a population genetic analysis. We estimated the total population of Swayne's hartebeest to be 1,528, with 518 individuals in Senkele Swayne's Hartebeest Sanctuary and 1,010 individuals in Maze National Park. Livestock densities were 212 and 153 times those of Swayne's hartebeest in Senkele Swayne's Hartebeest Sanctuary and Maze National Park, respectively. Among 73 mitochondrial D-loop sequences (34 from Senkele Swayne's Hartebeest Sanctuary and 39 from Maze National Park), we found 22 haplotypes (Senkele 12, Maze 16, shared 6). Population genetic parameters suggest only weak sub-structuring between the two populations ($F_{ST} = 0.164$). Despite the positive population trends in both protected areas, the spatial overlap with livestock

may lead to future population decline as a result of resource competition and disease transmission. We therefore recommend further translocation to other protected areas within the species' former range.

Keywords *Alcelaphus buselaphus swaynei*, Endangered species, Ethiopia, livestock, population estimate, population genetics, Swayne's hartebeest, translocation

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Introduction

Swayne's hartebeest *Alcelaphus buselaphus swaynei* was once widely distributed throughout Ethiopia, Somalia and Djibouti (Swayne, 1892). The population was reduced by the rinderpest virus, transmitted from introduced European cattle in the early 20th century (Hunt, 1951), and has since been extirpated from Djibouti and Somalia (Hunt, 1951; Bolton, 1973; Berhanu, 1974). Habitat loss, competition with livestock for grazing and extensive hunting have further reduced the species' population and range (Lewis & Wilson, 1979; Flagstad et al., 2000; Datiko & Bekele, 2011). By 2019, Swayne's hartebeest was restricted to two isolated populations in Ethiopia (Tamrat et al., 2020). It was categorized as Endangered in 1986 and remains so as a result of habitat loss, competition with livestock and illegal hunting (IUCN SSC Antelope Specialist Group, 2017).

In sub-Saharan Africa, resource competition between livestock and wild ungulates is common as they often share the same grazing grounds (Hibert et al., 2010; Smart et al., 2010; Kumssa & Bekele, 2013). Large- and medium-sized grazing ungulates have been shown to have similar food preferences and nutritional requirements as livestock (Chaikina & Ruckstuhl, 2006; Georgiadis et al., 2007; Hibert et al., 2010). Since the 1970s, livestock grazing has increasingly encroached on the range of Swayne's hartebeest, resulting in competition and, occasionally, conflict (Messana & Netsereab, 1994; Kumssa & Bekele, 2013). For instance, in Senkele Swayne's Hartebeest Sanctuary the livestock density increased from 86.9 individuals per km² in 1994 (Messana & Netsereab, 1994) to 148.6 in 2013 (Kumssa & Bekele, 2013).

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Similarly, in Maze National Park, livestock density increased by 64.5% from 1997 to 2003 (Refera et al., 2003).

In Ethiopia, Swayne's hartebeest has been in decline since the 1970s (IUCN SSC Antelope Specialist Group, 2019). In the early 1970s, the total population of Swayne's hartebeest was estimated to be 700 individuals sparsely distributed across five isolated areas: (1) Awash River Valley, east of Awash River in south-west Afar, (2) the vicinity of Yabello, (3) Senkele Swayne's Hartebeest Sanctuary, (4) Maze National Park, and (5) Siraro Area (Bolton, 1973). The largest population was in Senkele Swayne's Hartebeest Sanctuary, where c. 400 individuals had been reported (Bolton, 1973). In 1974, 113 Swayne's hartebeest were translocated from the Sanctuary to Nechisar National Park and 90 to Awash National Park (Lewis & Wilson, 1977, 1979). Two years after the translocation only 12 individuals were found in the Awash National Park (Lewis & Wilson, 1977). In contrast, those translocated to Nechisar National Park appeared to thrive, increasing to 130 individuals within 2 years (Lewis & Wilson, 1977, 1979). However, their number had declined to 40 individuals by 1992 (Flagstad et al., 2000), 20 in 2004 (Refera et al., 2003), 12 by 2005 (Mamo et al., 2012), and to only one, a male, in 2016 (IUCN SSC Antelope Specialist Group, 2019). Although the reason for this decline is unclear, overgrazing in the Park by livestock is believed to be the primary cause (Refera et al., 2003; Datiko & Bekele, 2011). After the establishment of Maze National Park in 2005, poaching there appears to have ceased. Similarly, no hunting has been reported in Senkele Swayne's Hartebeest Sanctuary since 2000 (Lemessa, 2015). Livestock grazing, however, continued in both Maze National Park and Senkele Swayne's Hartebeest Sanctuary (Lemessa, 2015).

In the latest census of Swayne's hartebeest, in 2008, the total population was estimated to be 840 individuals, in three protected areas: 465 in Senkele Swayne's Hartebeest Sanctuary, 364 in Maze National Park, and 12 in Nechisar National Park (Mamo et al., 2012). The decline and fragmentation of the population, as well as translocations, may have also affected the genetic diversity and genetic population structure of the species. Using mitochondrial D-loop sequences, Flagstad et al. (2000) reported a haplotype diversity for Swayne's hartebeest comparable to other *Alcelaphus* subspecies, although the diversity of the translocated population in Nechisar National Park was very low compared to the population in Senkele Swayne's Hartebeest Sanctuary.

Because of the increasing pressure of human settlements and livestock grazing, and the potential loss of genetic diversity across the species' range, continued monitoring is required. We surveyed Swayne's hartebeest in Senkele Swayne's Hartebeest Sanctuary and Maze National Park to provide an updated assessment of the species' conservation status. We also determined the mitochondrial genetic diversity among the remaining Swayne's hartebeest populations,

including that of Maze National Park, which had not previously been evaluated. In addition, we determined the level of grazing competition by estimating livestock abundance in both protected areas.

Study areas

Senkele Swayne's Hartebeest Sanctuary, established in 1976 to protect the largest remaining subpopulation (c. 400 individuals) of Swayne's hartebeest (Lewis & Wilson, 1979; Gebre & Yirga, 2004), lies in the southern Ethiopian Rift Valley at 2,000–2,100 m altitude. Total annual rainfall is c. 1,200 mm and the temperature range is 8–26 °C (Lemessa, 2015). The Sanctuary originally covered 200 km² but pressure from increasing human and livestock populations and civil unrest reduced it to the current area of c. 55 km² (Gebre & Yirga, 2004). There are no permanent open water sources in the Sanctuary and the nearest water is 28 km away, completely encircled by human settlements. Swayne's hartebeest in the Sanctuary may obtain their water from vegetation during the dry season (Lewis & Wilson, 1977). The Sanctuary is dominated by open grassland with scattered savannah woodland.

Maze National Park lies c. 150 km south-west of Senkele Swayne's Hartebeest Sanctuary in the southern Ethiopian Rift Valley, at 900–1,300 m altitude. The Park receives < 800 mm of rainfall annually and the temperature range is 18–36 °C (Refera et al., 2003). The Park was initially established as a controlled hunting area and designated as a National Park in 2005 (Mamo et al., 2012). The Park has an area of 175 km², includes several permanent rivers, and the vegetation is open grassland with scattered savannah woodland, bushland habitats and riverine forests (Tamrat et al., 2020).

Methods

Population estimate

We used a total census count to estimate the population size of Swayne's hartebeest and livestock in both study areas. We established permanent survey blocks that covered both protected areas: seven in Senkele Swayne's Hartebeest Sanctuary (demarcated using paved roads used for patrolling) and 10 in Maze National Park (demarcated using rivers, gorges, ridges and a road; Fig. 1, Table 1). Block size depended on habitat type, with a mean area of 7.9 and 17.4 km² in the Sanctuary and Park, respectively. We established survey transect lines, with the number per block dependent on size and habitat type. In open grassland, transects were c. 600 m wide, reduced to 400 m wide in other habitat types in Maze National Park. Teams of 2–4, comprising wardens, researchers, experienced wildlife

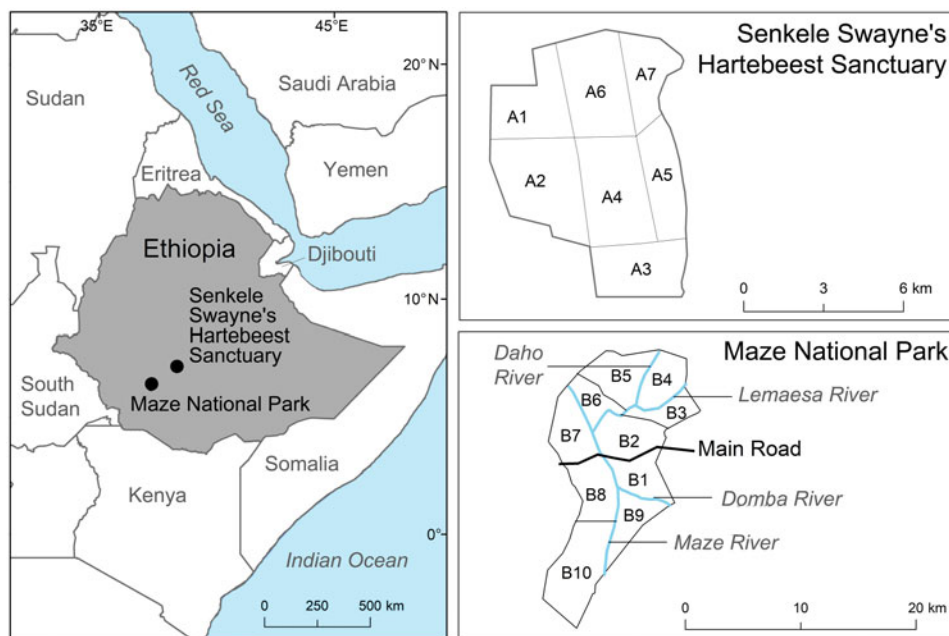


FIG. 1 Location of Senkele Swayne's Hartebeest Sanctuary and Maze National Park in Ethiopia, with the locations of the survey blocks (Table 1).

experts, and game scouts, conducted the counts simultaneously in each block (i.e. all blocks in a protected area were surveyed simultaneously) in each protected area.

The counts were made during February–August 2017, three times each in the dry (February, March, May) and wet season (June, July, August), during 6.00–10.00 and 4.00–6.00, the times when Swayne's hartebeest are most active (Mamo et al., 2012; Fryxell et al., 2014). When individuals were observed we recorded sex, age class and group size. Age classes were categorized (after Mamo et al., 2012) as calf (< 9 months old), juvenile (9–18 months), subadult (18–30), adult male or female (> 30 months), and unknown. Sex was determined by visible reproductive organs and horn size (males have larger horns). We used trees and hilltops where possible, for good visibility, and surveyed all blocks simultaneously to avoid double counting. We calculated means and ranges of population counts for each study area (Plumptre, 2000; Caro, 2016).

Livestock abundance

Hartebeests and livestock are grazers with a high potential for exploitative competition (Vavra, 2005; Bonnington et al., 2007). We assume that the negative effect of competition is more severe for Swayne's hartebeests when livestock are using the same area. We estimated livestock density directly in Senkele Swayne's Hartebeest Sanctuary, where visibility is good, and indirectly by counting faecal droppings of both livestock and Swayne's hartebeests in Maze National Park, where visibility is more restricted. Faecal counts were made in 1,002 randomly positioned 4 × 5 m sample plots (20 m²). Potential overlap of the pellets of livestock

and Swayne's hartebeest was examined using a logistic regression model in which the presence or absence of pellet samples was the response variable, origin (livestock or Swayne's hartebeest) a fixed effect, and plots a random factor, with $R_{3.5.1}$ (R Core Team, 2018).

Population genetics

To estimate genetic diversity, we collected 34 and 39 fresh faecal samples from Senkele Swayne's Hartebeest Sanctuary and Maze National Park, respectively (c. 7% of an estimated population of 518, and 4% of 1,010, respectively; see Results), with a minimum distance of 500 m between samples, to increase the probability of sampling different individuals. Samples were air-dried, and preserved in plastic tubes on silica beads. We extracted DNA from each sample using the First DNA All Tissue Kit (Gen-Ial, Göttingen, Germany) following the manufacturer's protocols. To compare our results with those of Flagstad et al. (2000), we used the same genetic marker; the hypervariable region I of the mitochondrial D-loop (478 bp). For amplification, we used the primers of Flagstad et al. (2000): (L15333) 5'-ACACCAGT CTTGTAAACCG-3' and (H15947) 5'-TATGGCCCTGAA GTAAGAACCGA-3'. Polymerase chain reactions were carried out in a total volume of 30 µl containing 1 U Biotherm DNA Taq polymerase, 1 reaction buffer, 0.16 mM of each dNTP, 0.33 µM of each primer and c. 100 ng genomic DNA. Conditions consisted of a pre-denaturation step at 95 °C for 10 minutes, followed by 40–50 cycles, each with denaturation at 95 °C for 30 s, annealing at 50 °C for 30 s and extension at 72 °C for 30 s, with a final extension step at 72 °C for 7 minutes. Sequencing was carried out at

TABLE 1 Population counts and density (individuals per km²) of Swayne's hartebeest *Alcelaphus buselaphus swaynei* in Senkele Swayne's Hartebeest Sanctuary and Maze National Park (Fig. 1) during the dry (February, March and May) and wet (June, July and August) seasons.

Block	Area (km ²)	Habitat type	Feb.		Mar.		May		June		July		Aug.	
			Count	Density	Count	Density	Count	Density	Count	Density	Count	Density	Count	Density
Senkele Swayne's Hartebeest Sanctuary¹														
A1	7.2	Grassland	121	16.8	125	17.4	134	18.6	69	5.6	73	10.1	81	11.3
A2	10.6	Grassland	0	0.0	0	0.0	0	0.0	81	7.6	75	7.1	81	7.6
A3	7.0	Grassland	0	0.0	4	0.6	2	0.3	19	2.7	17	2.4	27	3.9
A4	9.8	Grassland	51	5.2	55	5.6	59	6.0	101	10.3	95	9.7	110	11.2
A5	5.1	Grassland	23	4.5	21	4.1	28	5.5	39	7.6	48	9.4	48	9.4
A6	9.1	Grassland	297	32.6	309	34.0	318	34.9	149	16.4	154	16.9	150	16.5
A7	6.3	Grassland	9	1.4	7	1.1	2	0.3	39	6.2	43	6.8	44	7.0
<i>Total/mean</i>	55.1		501	9.1	521	9.5	543	9.9	497	9.0	505	9.2	541	9.8
Maze National Park²														
B1	15.4	Grassland	398	25.8	386	25.1	395	25.6	419	27.2	427	27.7	441	26.7
B2	16.8	Grassland	317	18.9	314	18.7	305	18.2	7	0.4	11	0.7	12	0.7
B3	12.0	Rugged bushland	88	7.3	101	8.4	102	8.5	9	0.8	6	0.5	6	0.5
B4	15.1	Rugged bushland	34	2.3	46	3.0	38	2.5	11	0.7	5	0.3	5	0.3
B5	16.8	Rugged bushland	85	5.1	77	4.6	84	5.0	6	0.4	9	0.5	5	0.3
B6	12.0	Rugged bushland	9	0.8	11	0.9	19	1.6	13	1.1	11	0.9	9	0.8
B7	18.8	Grassland	49	2.6	61	3.2	58	3.1	317	16.9	322	17.1	324	17.2
B8	21.6	Sloped bushland	33	1.5	31	1.4	32	1.5	4	0.2	3	0.1	8	0.4
B9	14.2	Grassland	75	5.3	66	4.6	72	5.1	121	9.9	126	8.9	137	9.6
B10	31.2	Plain bushland	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0
<i>Total/mean</i>	173.9		1,088	6.3	1,093	6.3	1,105	6.4	907	5.2	920	5.3	947	5.4

¹Mean population count 518 ± SD 20.3.

²Mean population count 1,010 ± SD 86.3; habitat classification from Tamrat et al. (2020).

Eurofins, Germany. Sequences were manually checked and corrected in *AliView 1.18* (Larsson, 2014).

We estimated population genetic parameters with *DnaSP 5* (Librado & Rozas, 2009). The number of sites was 475 and sites with alignment gaps were considered a fifth state. To infer relationships among haplotypes found in both protected areas, we constructed a median-joining network (Bandelt et al., 1999). To determine phylogenetic relationships among *Alcelaphus buselaphus* D-loop haplotypes on an Africa-wide scale, we reconstructed maximum likelihood and Bayesian trees, adding additional *A. buselaphus* sequences (subspecies *buselaphus*, *caama*, *cokii*, *lelwel*, *lichtensteini*, *major*, *swaynei*, *tora*) from across Africa, which we retrieved from GenBank (National Center for Biotechnology Information, Bethesda, USA; Supplementary Table 1).

The final dataset contained 69 sequences, including one sequence of *Damascus lunatus* that served as an out-group. The alignment was generated with *Muscle 3.8.31* (Edgar, 2010) in *AliView* and corrected by eye. We conducted tree reconstructions with maximum likelihood using *IQ-TREE 1.5.2* (Nguyen et al., 2015) and Bayesian algorithms using *MrBayes 3.2.6* (Ronquist et al., 2012). For both analyses, we used the optimal substitution models (TPM3u+I+G4) as selected by *ModelFinder* (Chernomor et al., 2016; Kalyaanamoorthy et al., 2017) in *IQ-TREE* under the Bayesian information criterion. We reconstructed Bayesian trees via four independent Markov chain Monte Carlo runs. We ran all repetitions for 1 million generations, with tree and parameter sampling occurring every 100 generations, and applied a burn-in of 25%. To check convergence of all parameters and the adequacy of the burn-in, we assessed the uncorrected potential scale reduction factor (Gelman & Rubin, 1992) as calculated by *MrBayes* (Bayesian inference of phylogeny). We calculated posterior probabilities and a phylogram with mean branch lengths from the posterior density of trees using *MrBayes*. We performed the maximum likelihood analyses with 1,000 ultrafast bootstrap replications (Minh et al., 2013). Phylogenetic trees were visualized in *FigTree 1.4.2* (Rambaut, 2017). The degree of genetic differentiation of the two Swayne hartebeest populations was analysed using *DnaSP 6* (Rozas et al., 2017).

Results

Population estimate The mean total census count of Swayne's hartebeest across the six surveys was 1,528 (range 1,404–1,648) individuals; 518 (range 497–543) in Senkele Swayne's Hartebeest Sanctuary, and 1,010 (range 907–1,105) in Maze National Park (Table 1). In both dry and wet seasons, the per cent of calves was higher in Maze National Park (14.0 and 9.8 in the dry and wet seasons, respectively) than in Senkele Swayne's Hartebeest Sanctuary (6.0 and 4.2 in the dry and wet seasons, respectively). The sex ratio of adult

females to males was 1.43 and 1.37 in the Sanctuary and National Park, respectively (Supplementary Fig. 1).

Livestock abundance In the Sanctuary the mean count of the three surveys was 11,424 livestock (207.7 individuals per km²) in the dry season and 18,892 livestock (343.5 individuals per km²) in the wet season (Supplementary Table 2). The corresponding numbers in the National Park were 15,785 livestock (90.2 individuals per km²) in the dry season and 11,976 livestock (97.0 individuals per km²) in the wet season (Supplementary Table 2), far greater than the density of Swayne's hartebeest in both protected areas. In the dry season the ratio of livestock per one hartebeest was on average 180.0 ± SD 275.7 and 48.1 ± SD 52.6 during the wet season (Supplementary Fig. 2, Table 2). The corresponding values in Maze National Park were 12.4 ± SD 11.0 during the dry and 6.7 ± SD 5.0 during the wet season (Supplementary Fig. 3, Table 2). Of the 1,002 plots in Maze National Park, 335 contained pellets of both livestock and hartebeests. We counted significantly more pellets of livestock than of hartebeests ($z = 4.84$, $P < 0.001$).

Genetic variability From the 73 faecal samples we found 12 haplotypes in Senkele Swayne's Hartebeest Sanctuary and 16 haplotypes in Maze National Park, with six haplotypes common to both populations. Network analysis did not reveal a clear haplotype segregation between the two populations (Fig. 2). There were five private haplotypes in the Sanctuary and nine in the National Park (Table 3). The F_{ST} was 0.1643, which suggests only weak population sub-structuring, and we did not find any genetic structure in the median-joining network analysis (Fig. 2). Overall nucleotide diversity was 0.044, with a higher nucleotide diversity (0.041) in the National Park than in the Sanctuary (0.035). Regardless of the presence of shared haplotypes, the genetic population differentiation is significant ($\chi^2 = 45.05$, $P < 0.001$, $df = 13$).

Phylogenetic relationships The African-wide phylogenetic analysis suggested a clear split between southern (*A. buselaphus lichtensteini* and *A. buselaphus caama*), and northern subspecies (*A. buselaphus buselaphus*), but no sub-structuring of the subspecies that extend from east to west (*A. buselaphus tora*, *A. buselaphus swaynei*, *A. buselaphus cokii*, *A. buselaphus lelwel* and *A. buselaphus major*), which were intermixed and did not form monophyletic clades (Supplementary Fig. 4).

Discussion

We aimed to provide an updated estimate of the population size and genetic diversity of the two relict populations of Swayne's hartebeest in Ethiopia. We estimated the total population of Swayne's hartebeest to be c. 1,528 individuals,

TABLE 2 Density and ratio of Swayne's hartebeest and livestock per km² in Senkele Swayne's Hartebeest Sanctuary and Maze National Park during the dry and wet seasons.

Block	Habitat type	Dry season			Wet season		
		Hartebeest	Livestock	Livestock/hartebeest	Hartebeest	Livestock	Livestock/hartebeest
Senkele Swayne's Hartebeest Sanctuary							
A1	Grassland	17.5	336.0	19.2	10.3	455.7	44.2
A2	Grassland	0.0	222.6		7.5	325.0	43.3
A3	Grassland	0.3	193.5	644.9	3.0	451.4	150.5
A4	Grassland	5.6	75.7	13.5	10.4	151.2	14.5
A5	Grassland	4.7	26.2	5.6	8.9	47.2	5.3
A6	Grassland	34.0	0.8	0.02	16.7	16.8	1.0
A7	Grassland	0.9	358.2	398.0	6.6	512.7	77.7
<i>Mean ± SD</i>		18.3 ± 18.4	173.3 ± 144.0	180.0 ± 275.7	9.1 ± 4.2	280.0 ± 207.0	48.1 ± 52.6
Maze National Park							
B1	Grassland	25.5	131.7	5.2	27.7	63.9	2.3
B2	Grassland	18.6	0.0	0.0	0.6	0.0	0.0
B3	Rugged bushland	8.1	252.4	31.2	0.6	3.3	5.6
B4	Rugged bushland	2.6	0.0	0.0	0.5	0.0	0.0
B5	Rugged bushland	4.9	0.0	0.0	0.4	0.0	0.0
B6	Rugged bushland	1.9	0.0	0.0	0.9	0.0	0.0
B7	Grassland	3.0	75.4	25.3	17.1	69.7	4.1
B8	Sloppy bushland	1.5	57.3	38.6	0.3	31.6	136.3
B9	Grassland	5.0	182.6	36.5	9.0	94.4	10.5
B10	Plain bushland	0.0	170.8		0.0	118.8	
<i>Mean ± SD</i>		7.0 ± 8.4	87.0 ± 92.4	12.4 ± 11.0	5.7 ± 9.6	38.2 ± 45.2	6.7 ± 4.7

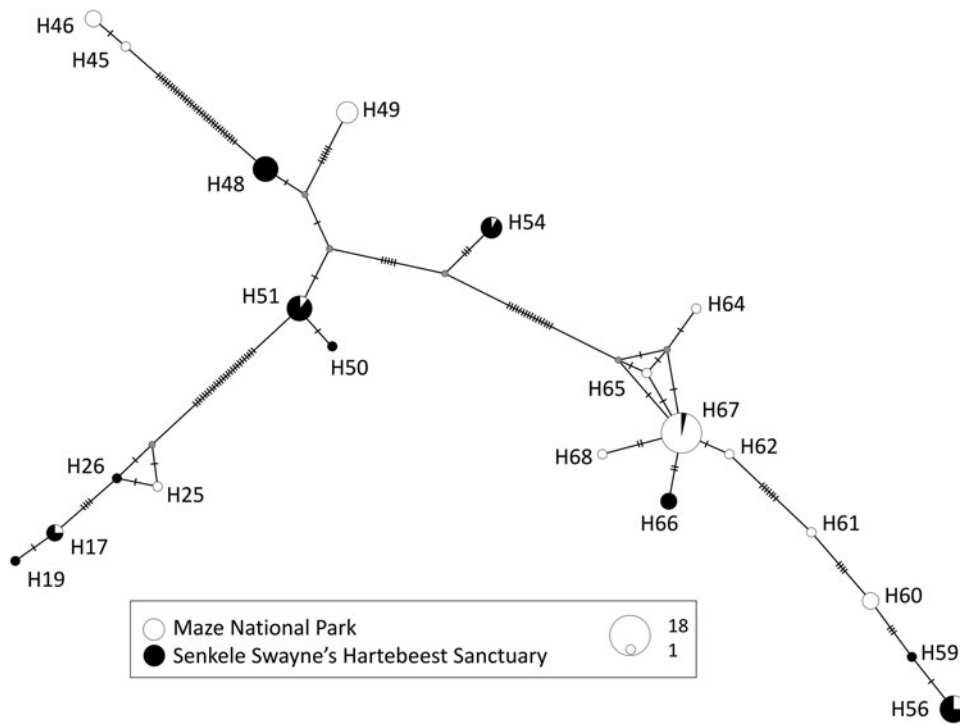


FIG. 2 Median-joining mtDNA haplotype network of Swayne's hartebeest from Maze National Park and Senkele Swayne's Hartebeest Sanctuary. H17–H68 indicate individual haplotypes. The number of hatch marks indicates the number of mutations between two haplotypes. Numbers of identical haplotypes are indicated by circle-size (1–18 identical haplotypes).

518 in Senkele Swayne's Hartebeest Sanctuary and 1,010 in Maze National Park. The population in the Sanctuary was only slightly higher than the estimated 464 individuals in the 2008 survey (Mamo et al., 2012) and 400 individuals

in the 1974 survey (Lewis & Wilson, 1977). Most likely, the small area of available habitat (55 km²), competition with a large number of livestock, and the absence of permanent water sources are limiting Swayne's hartebeest population in

TABLE 3 Population genetic parameters of Swayne's hartebeest in Senkele Swayne's Hartebeest Sanctuary and Maze National Park. Total number of sites was 475. Alignment gaps were considered as a fifth state (Librado & Rozas, 2009).

Population	Sequences	Haplotypes	Private haplotypes	Haplotype diversity	Nucleotide diversity
Senkele Swayne's Hartebeest Sanctuary	34	12	5	0.89127	0.03897
Maze National Park	39	16	9	0.82051	0.04037
<i>Total</i>	73	22		0.91514	0.04302

the Sanctuary. Carrying capacity could potentially be increased if livestock numbers were reduced and if the hartebeests could access water year-round.

In Maze National Park, the population of Swayne's hartebeest has increased substantially, from 364 individuals in 2008 (Mamo et al., 2012). The increase may in part be a result of the resettlement of 333 households from the area when the Park was established in 2005, and the implementation of new management and conservation strategies to reduce poaching and uncontrolled burning of grasslands.

Of continued concern is the high number of livestock that compete with Swayne's hartebeest for forage. Livestock numbers were 150–200 times greater than the number of hartebeest in the Sanctuary. Studies of food preferences and foraging habits of hartebeest and cattle in Kenya showed a similar selection of grasses (Casebeer, 1970), suggesting a high potential for competition when this resource is limited (Fritz et al., 1996). In addition, livestock in the African Rift Valley harbour ticks that can potentially transmit disease (Bengis & Erasmus, 1988; Olubayo et al., 1993) and could affect the well-being of wildlife (Fyumagwa et al., 2007).

The sex ratio of adult males to adult females, and the proportion of young to adult females, are similar to numbers reported in previous studies (Lewis & Wilson, 1979). Lewis & Wilson (1979) speculated that the greater number of adult females in the Sanctuary could be a result of increased predation on males. The higher proportion of calves and juveniles in Maze National Park compared to the Sanctuary could be because of higher habitat quality there. In addition, the lion *Panthera leo* is the only large predator in Maze National Park but there is a relatively high density of the hyena *Crocuta crocuta* and African wolf *Canis anthus* in Senkele Swayne's Hartebeest Sanctuary (M. Tamrat et al., unpubl. data, 2020).

A species with a small population size is vulnerable to demographic stochasticity and inbreeding depression (O'Grady et al., 2006). The subpopulation of Swayne's hartebeest in the Sanctuary showed lower genetic diversity than the larger subpopulation in Maze National Park. The nucleotide diversity that we recorded is the same as that recorded by Flagstad et al. (2000), although the sampled populations are not the same. The significantly higher genetic diversity in Maze National Park suggests this population

has the highest relevance for the conservation of the species. Our phylogeny of *A. buselaphus* indicates an intermixed northern clade, suggesting potential gene flow among the northern populations (Flagstad et al., 2001). This indicates that mitochondrial sequence data is not sufficient to delimit taxonomic entities and thus our phylogeny cannot be used to infer conservation priorities.

In conclusion, the population of Swayne's hartebeest in Maze National Park seems to be demographically robust, with a four-fold increase since 2008 (i.e. after the establishment of the Park) and a relatively high level of mitochondrial genetic diversity compared to the population in the Sanctuary. In contrast, the latter population has remained low but stable since the 1970s. Whether it is at the carrying capacity of the Sanctuary will require further research. The principal conservation concern for Swayne's hartebeest in both protected areas is the potential for competition with livestock, and this could also increase the risk of disease transmission. One option would be to consider a translocation from Senkele Swayne's Hartebeest Sanctuary to other protected areas within the species' former range, to reduce the vulnerability of this population.

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Author contributions Study design: MT, AA, NCS; fieldwork, data collection: MT; laboratory work, data analysis: MT, AA, DZ, CR; 1988 and 1995 DNA sequence data, genetic analysis and interpretation: ØF; additional analyses, writing: all authors.

Conflicts of interest None.

Ethical standards This research abided by the *Oryx* guidelines on ethical standards. The Ethiopian Wildlife Conservation Authority granted permission to conduct this research in compliance with CITES. The Senkele Swayne's Hartebeest Sanctuary and Maze National Park approved all field procedures. Faecal samples were collected non-invasively without harming or disturbing the animals, and the study meets all animal care policies and adheres to the legal requirements of Ethiopia, Germany and Norway.

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