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Distribution and Population Status of the Endemic Rock Hyrax Sub-species (*Procavia capensis capillosa*) of the Bale Mountains, Ethiopia

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ABSTRACT

Hyraxes are diurnal mammals limited in their distribution in Africa and the Middle East. *Procavia capensis capillosa* is endemic to Bale Mountains, and its ecology is not studied. The present investigation deals with the distribution and population ecology of this subspecies through field observations and point counts following simultaneous double observer method. This subspecies is distributed from Gaysay Valley through the base of Tulu Dimtu towards southeast to Rira and at the northern edge of the Harenna forest in altitude ranges of 2774 m – 4134 m a.s.l. The population density of *P. c. capillosa* in the recorded sites ranged from 25.4 $\pm$ 4.2 to 1696.4 $\pm$ 172.3 individuals/km^2. Among them, adults constituted 70.5% and juveniles 21.2%. Out of the sexed hyraxes, 57.7% was females and 42.3% was males. Colony size ranged between 4–86 individuals with larger colonies during the wet season. Hyrax colony consists of one territorial male, one to several adult females and sub-adults and juveniles of both sexes. One to several males occupies colony peripheries. High proportion of females and juveniles in the counted population of the rock hyrax indicate a healthy population, which can sustain if intensive human interactions are controlled in these mountain ranges.

Key Words: Bale Mountains National Park; Population Ecology; Population Structure

INTRODUCTION

Bale Mountains is part of the eastern Afromontane hotspot of Ethiopia (Myers et al. 2000), which harbours species that are Ethiopian endemics, and endemics to the Bale Mountains ranges. These mountain stretches form the largest continuous area above 3000 m a.s.l. in Africa, supporting the most extensive Afro-alpine and sub-Afro-alpine vegetation on the continent (Miehe and Miehe 1994).

Hyraxes are found only in Africa and in the Middle East (Olds and Shoshani 1982). The Order Hyracoide consists of one extinct Family, Pliohyracidae and one extant Family, Procaviidae. The extant family comprises of three living genera; viz. *Procavia*, *Heterohyrax* and *Dendrohyrax*. Members of the genera *Procavia* Storr, 1780 is strictly rock dwelling and considered to have evolved first in Africa before the Oligocene, some 40 million years ago (Walker 1975). *Heterohyrax* Gray, 1868 is rock dwelling and partially arboreal bush hyrax, whereas *Dendrohyrax* Gray, 1868 is strictly arboreal (Stuart and Stuart 2007). *Procavia* represented by *P. capensis* and *Heterohyrax* represented by *H. brucei* live in rock outcrops, piles of boulders and fractured cliff faces in Bale Mountains National Park (BMNP) (Yalden et al. 1996). The subspecies, *P. c. capillosa* Brauer, 1917 is confined to high altitudes (2800–3500 m), isolated from the more northerly population by the Wabi Shebele River (Yalden et al. 1986), and is endemic to the Bale Mountains.

Being slow moving and with only few defensive mechanisms against predators, rock hyraxes depend on rocky outcrops, which provide them protection from extreme weather conditions and predators, access to safe foraging areas and good vantage points (Fairall et al. 1983). Rock hyraxes are not subjected for any detailed

studies in Ethiopia, other than a basic ecological investigation in Tigray, Northern Ethiopia (Girmay et al. 2015). It was in this context that the present research was initiated to study rock hyrax to address the distribution and population status of the endemic subspecies in the BMNP.

THE STUDY AREA

Bale Mountains National Park lies along the eastern edge of the Great Ethiopian Rift Valley at altitude ranges 1,500–4,377m a.s.l., with an extent of 2200 km^2 within the geographical coordinates 6º29'–7º10' N and 39º28'–39º57' E (Figure 1). The headquarters of BMNP is in Dinsho, which is 400 km from Addis Ababa, the capital of Ethiopia. This Park is listed as one of the UNESCO 200 worldwide Bio-Regions.

Rainfall in this Park is characterized by the long rainy season from March to October, followed by the dry season from November to February. Precipitation around Dinsho, the Headquarters averages 1,219 mm annually. Temperature shows altitudinal gradient within the Park from –3 to 24 ºC at lower altitudes, and from –15 to 26 ºC at higher altitudes during the dry season (Sillero-Zubiri 1994).

Vegetation in BMNP is of Afro-alpine and sub-Afro-alpine types. The flora of the alpine zone is with over 163 highland endemics, out of which 27 are restricted to Bale Mountains only (Birdlife International 2006). Vegetation zones in BMNP are northern grasslands, northern woodlands, heath (ericaceous) moorlands, treeless Afro-alpine habitat, and the southern Harenna Forest. Sixty seven mammal species are known from Bale Mountains, of which 20 are endemic to the country and six are endemic to the highlands in Bale Mountains (Bekele and Yalden 2013).

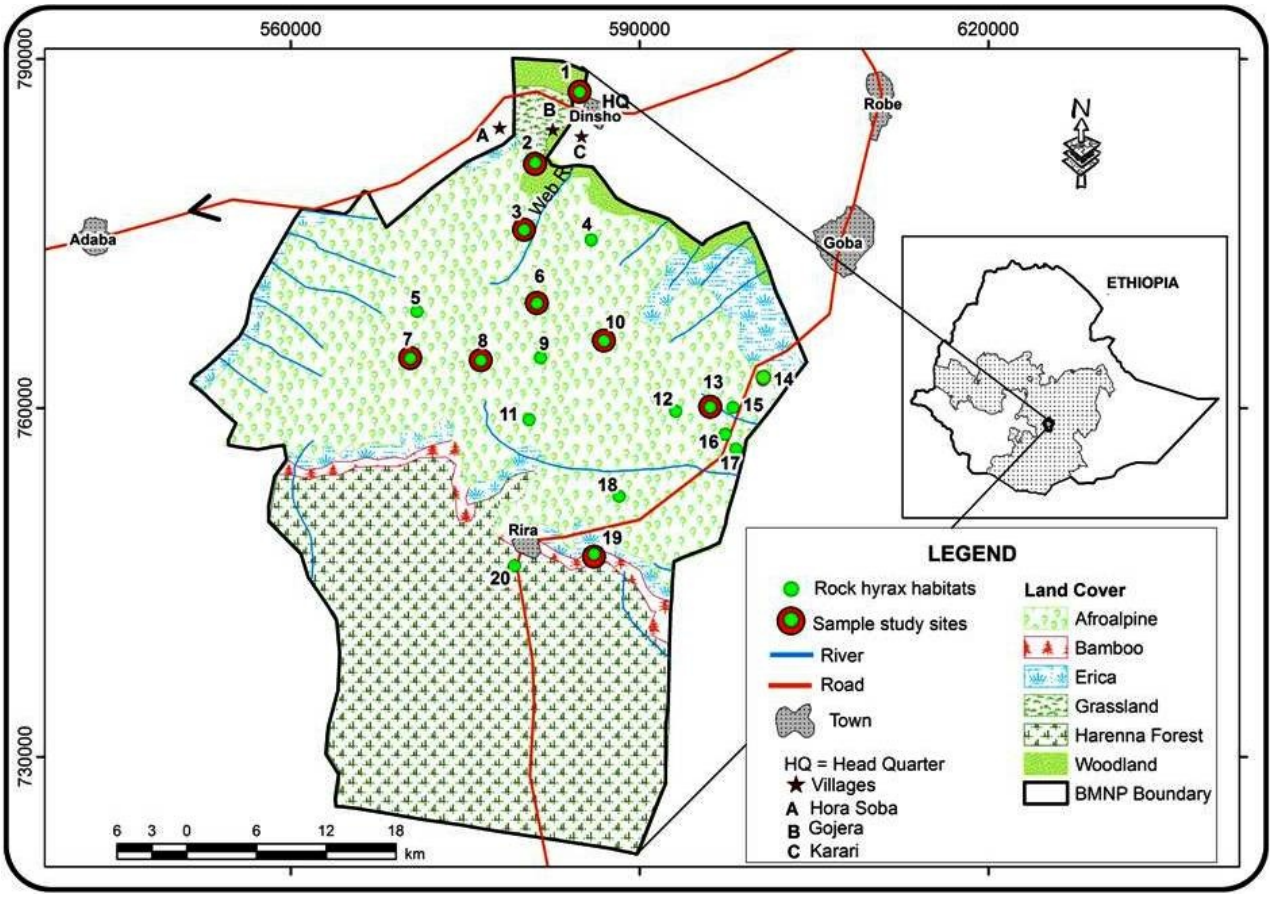

Figure 1. Map of Bale Mountains National Park showing distribution of vegetation types and potential habitats of *Procavia capensis capillosa* (Site 1–20) (Sites 1 = Gaysay Valley, 2 = Adelay Ridge, 3 = Web Valley, 4 = Small Batu, 5 = Goda Senga, 6 = Meraro, 7 = Morebawa, 8 = Keyrensa, 9 = Hujuba, 10 = Worgona Valley, 11 = Rafu, 12 = Large Batu, 13 = Garba Guracha, 14 = Angesu, 15 = Togona Valley, 16 = Sanetti Plateau (EWCP campsite), 17 = Mt. Konteh, 18 = Sanetti Plateau (below Tullu Deemtu), 19 = Harenna Escarpment (around Yadot River) and 20 = Harenna Forest (towards Rira Town) . The nine sample study sites (1, 2, 3, 6, 7, 8, 10, 13 & 19) are highlighted.

METHODS

The present research was conducted during August, 2010 to February, 2013. Data were collected during August to October, 2010 and August to October, 2012 (wet seasons) and December, 2010 to February, 2011 and December, 2012 to February, 2013 (dry seasons).

Distribution of Rock Hyrax

Data on the spatial distribution of the rock hyrax were collected by intensive field observations. Additional data were collected through questionnaire interviews with Park Ecologists, Scouts and local community. All reported sightings of the hyrax in the Park were recorded. Evidences such as calls, fresh pellets and the whitish crystalline hyracium on rocky surfaces were also used for the presence and distribution of the species (Isbell and Chism 2007, Andreas et al. 2008). Locations of the rock hyrax distribution were recorded using a Global Positioning System.

Population Census

Based on the information gathered during a reconnaissance survey, the following nine sample sites were randomly stratified from the identified hyrax habitats to conduct population census: Gaysay Valley (Site 1), Adelay Ridge (Site 2), Web Valley (Site 3), Meraro (Site 6), Morebawa (Site 7), Keyrensa (Site 8), Worgona Valley (Site 10), Garba Guracha (Site 13) and Harenna Escarpment (Site 19).

Data Collection

Prior to the actual data collection, field assistants and scouts were trained on morphological and behavioural features to distinguish the approximate age and sex of the rock hyraxes, rock hyraxes from bush hyraxes and to conduct the census. To estimate the total population, data obtained from the sample sites were extrapolated to the total area of rock hyrax potential habitats in BMNP.

Based on the extent of the sample study sites and number of rock hyrax colonies in the respective sites, each sample site was subdivided into smaller colony sites, and point counts were made by direct double observer method (Barry and Mundy 1998, Walker et al. 2008). Observation points were selected around each census site based on the view and maximum accessibility, and hyraxes were counted by each of the observers. Counts were done in the morning (06:30h – 09:30h) and late afternoon (16:00h – 18:00h) hours, when hyraxes were active and bask on rocky surfaces, or actively forage. Observations were made by unaided eyes and/or using a 10×42 Bushnell binoculars, for five days per month, both during the wet and dry seasons. Individual rock hyraxes were identified to their respective age groups as adults, sub-adults and juveniles on the basis of their relative body size (Wimberger et al. 2009). Mean of the counts of the two observers was taken as the population of each site. When two or more cliffs, kopjes, caves or gorges were found in close proximity and mixing-up of the hyraxes suspected, counting was conducted simultaneously in each colony site to avoid double counting. All observations were made from a distance of 20-40 m based on accessibility of the site and habituation of hyrax to observers. The mean of hyraxes counted by the two observers in all counting points in a particular sample site were pooled together to make the total population of that sample site (Barry and Mundy 1998).

Juveniles among the hyraxes were identified from sub-adults and adults by their relatively darker brown fur. The sex of adult rock hyraxes was determined by careful observation of the shape and size of the exposed upper incisors using binoculars when they were calling, grooming or watching. Adult males were distinguished from adult females by their larger, pointed, tusk-like upper incisors separated one from the other by about the width of a tooth (Rifai et al. 2000), which is shorter and blunter in females. Adult males have relatively thick neck. Some adult females were also distinguished from adult males by their nipples visible when their belly was exposed while basking on rocky surfaces, while grooming, when they were followed by juveniles, and during suckling. Approximate age and sex as adult male, adult female, sub-adult male, sub-adult female and unidentified juvenile were assigned to those individuals observed.

Due to the lack of complete visible morphological and behavioural features to distinguish sex of rock hyraxes, it was not possible to determine the sex of most hyraxes in the field. Hence, rock hyraxes were live-trapped using locally made and previously tested string snare traps, and traditional wooden traps, baited with cabbage and/or fresh grass, placed at the mouths of crevices and along the walking paths (Wimberger et al. 2009) set before sunrise. Traps were closely monitored from early in the morning until 10:00h, then from 16:00h until sunset.

Trapped hyraxes were marked by cutting hair from a distinct spot at their back and released in the same place from where they were trapped immediately after taking body measurements (of only five individuals of each age and sex category), and recording sex on the basis of the genitalia and the presence or absence of teats (Barry and Mundy 1998). Body mass (kg), hind foot length from the tip of the middle toe to the end of the heel with the foot bent at an angle of 90^{o} to the tibia (cm), height at shoulder (cm), body length when lying on its side from the tip of the nose to the end of the vertebrae (cm) and girth measured directly behind the shoulder (cm) were recorded.

A given colony was considered as aggregation of two or more spatially associated individuals, in visual, auditory and/or olfactory communication with each other, basking on the same rock outcrop usually in close proximity (<15 m, and generally much closer) and move in the same direction (Barry and Mundy 2002). Colony size was recorded during the emergence from their shelter in the morning, as members of each colony share the same sleeping hole, and during basking and foraging. Colony composition was determined after careful observation of sex and approximate age. Peripheral males around a colony were included within the 'colony' for the purposes of analysis (Arcese et al. 1995). Each rock hyrax colony was recognized by the colony size and harem composition. The largest number recorded during any ten minutes in a particular colony site was recorded and the mean of the two observers was taken as the size of that colony.

Data Analyses

Data were analyzed using SPSS software for windows version 17. One way ANOVA was used to compare population size among the study sites and between wet and dry seasons. Sex ratio and age structure were computed using Chi-square and descriptive statistics. Colony size among the different study sites during wet and dry seasons was compared using student's t-test.

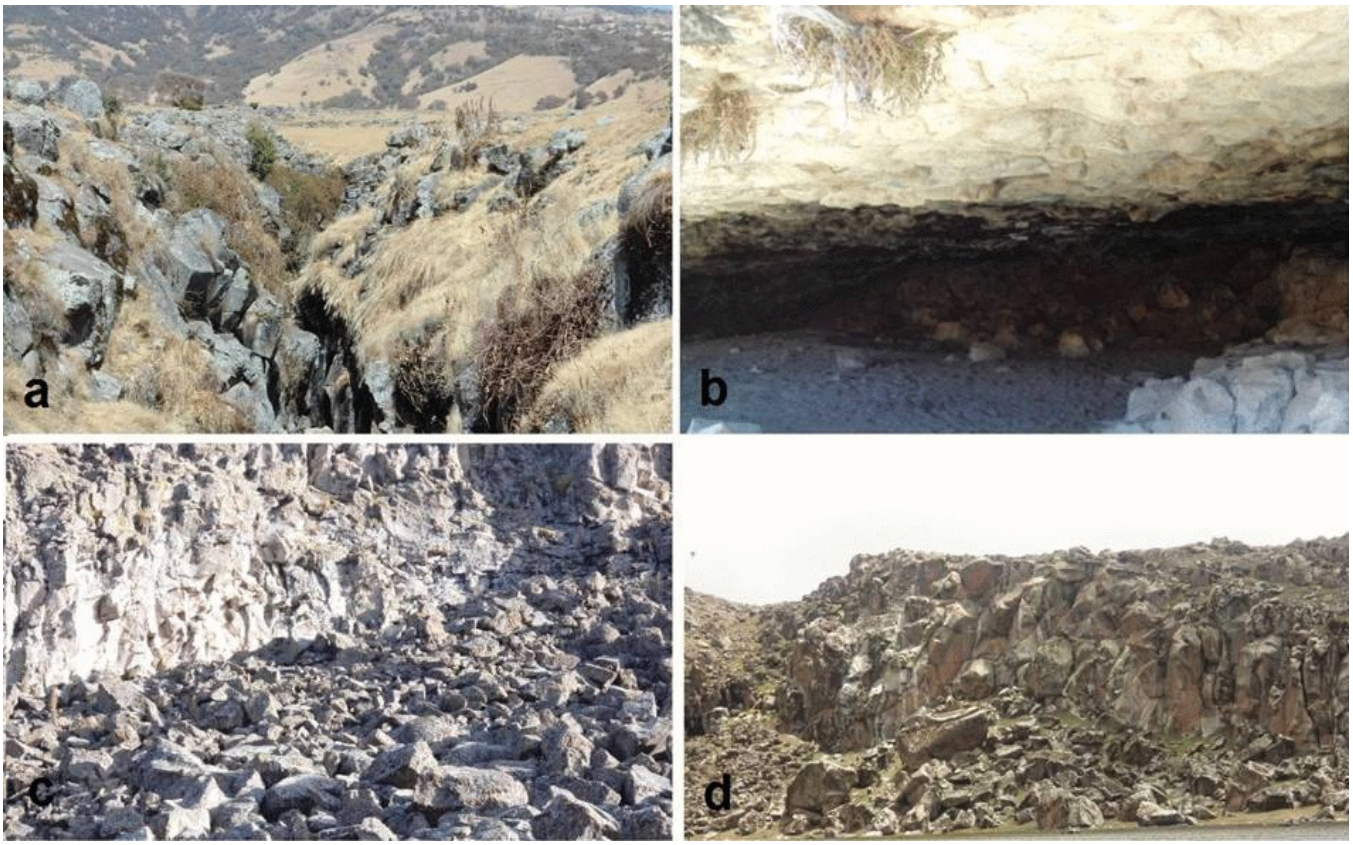

Figure 2. *Procavia capensis capillosa* habitats, (A) A gorge at Gaysay Valley, (B) Cave in Web Valley, (C) Rock boulders at Garba Guracha, and (D) Cliffs at Sanetti plateau (Photo: Gebremeskel Teklehaimanot, January and February 2012).

RESULTS

Distribution

Procavia c. capillosa is distributed from Gaysay Valley (3050 m) through the base of Tulu Dimtu towards southwest (4134 m) to Rira, and the northern edge of the Harenna forest (2774 m). Isolated populations occur in Morebawa, in the west of Keyrensa in a small cliff and kopjes and in Small Batu, along the way from Sanetti plateau to Dinsho (see Figure 1). This subspecies inhabits cliffs, rocky piles (kopjes), caves, plains with kopjes, and valleys with crevices (Figure 2), where vegetation cover of *Erica* shrubs and grasses occur. Such habitats are found in Adelay Ridge, Upper Web Valley, Meraro, Goda Senga, Keyrensa, Rafu, Worgonna Valley, Garaba Guracha and Sanetti Plateau in BMNP. Distribution of rock hyrax also extends to Togona Valley, Angesu, base of Tulu Dimtu and Harenna escarpment.

They were seen in interconnected cliffs and rocky piles with crevices around *Erica* dominated shrubs and rocky habitats in open areas, while less or absent in cliffs and kopjes in forests. Interconnected cliffs and *Erica* shrubs are abundant in the Web Valley, Kyrensa and Sanetti plateau at the base of Tulu Dimtu. These areas harbour rock hyrax populations. Rocky areas spread over wide ranges are present in Garba Guracha with numerous holes in which rock hyraxes shelter. One rock hyrax colony of 8–10 individuals inhabits burrows and rocky piles at the northern tip of the Harenna forest near (10–15 m) the main road that leads from Goba to Delo Mena.

Two colonies in Gaysay Valley were located in a gorge through which Danka River flows underneath, and where large number of livestock grazes regularly. In this area, construction activities were seen and settlements were expanding towards the rock hyrax colony sites. Two rock hyrax colonies were also sheltered in caves in the Web Valley. Some of the rock hyrax colonies in Web Valley, Meraro, Keyrensa, Goda Senga, Rafu, Garba Guracha and Sanetti plateau were in the vicinity of human settlements.

Population

An extent of 50.24 km^2 of the hyrax habitat was sampled during the present study out of the potential 168.5 km^2 in BMNP. A mean of 30,003 rock hyraxes were counted in the nine sample study sites. More individuals were counted in Keyrensa (10,568) during the wet season and the least counted (13) was in Gaysay Valley during the dry season (Table 1). There was significant difference in the population size of rock hyraxes among the sampled study sites ($F_{8\ 121}$ =156.4, P<0.05). There were 33,383 ±3419.7 individuals during the wet season and 26,623 ±2918.3 during the dry season counts. Populations in different sites during wet and dry seasons were significantly different ($F_{1\ 38.7}$ = 198, P<0.05). The highest population density recorded was 1696.4 ±172.3 individuals km^{-2} in Garba Guracha and the lowest was 25.4 ±4.2 individuals / km^{-2} in Gaysay Valley. Extrapolation of the hyraxes counted to the extent of hyrax potential habitats in BMNP has revealed the total population to be 100,629 individuals.

Among the individuals observed, 70.5% was adults, 8.3% was sub-adults and 21.2% was juveniles (Figure 3). There were 23,623 ±2624.2 adults, 2870 ±919.5 sub-adults and 6830 ±1190.9 juveniles during the wet season. During the dry season there were 18,681 ±1307.8 adults,

Table 1. Mean counts and density of *Procavia capensis capillosa* in different counting sites.

Counting sites	Area (km^2) of census site	No. of colony sites	Mean count	Density (Mean ± SE) /km^2
Gaysay Valley	0.59	2	15	25.4 ± 4.2
Adelay Ridge	2.94	7	636	216.3 ± 21.4
Web Valley	14.90	12	7401	496.7 ± 38.9
Meraro	5.86	10	4304	743 ± 45.7
Morebawa	0.97	3	303	312.4 ± 24.3
Keyrensa	12.85	15	9618	748.5 ± 74.7
Worgona Valley	4.93	5	811	164.5 ± 20.4
Garba Guracha	2.75	3	4665	1696.4 ± 172.3
Harenna Escarpment	4.44	6	2250	506.7 ± 76.8
Total	50.24	63	30,003	597.2 ± 53.2

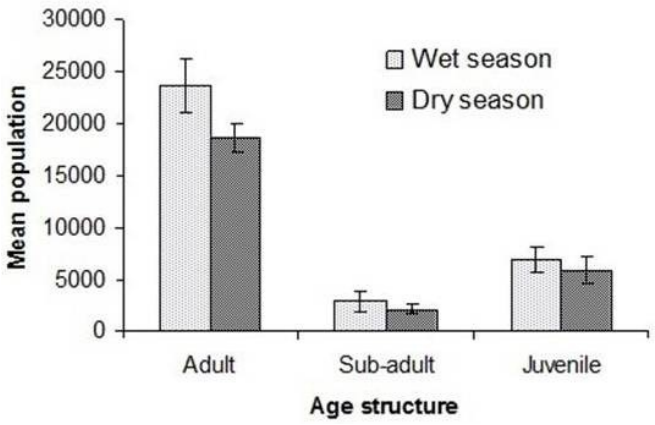

Figure 3. Age structure of *Procavia capensis capillosa* recorded during wet and dry seasons (Mean ± SE).

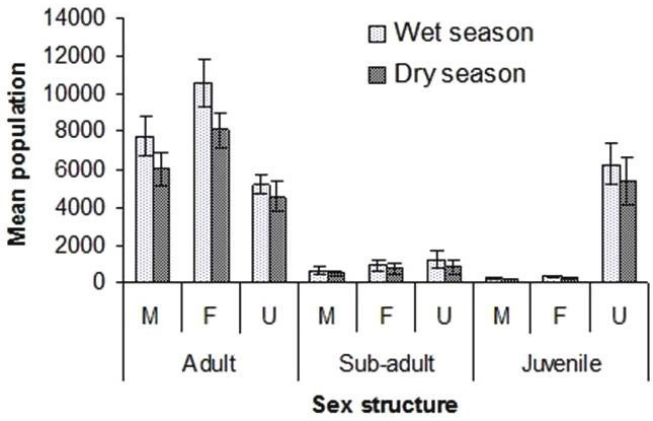

Figure 4. Sex structure of *Procavia capensis capillosa* recorded during wet and dry seasons (Mean ± SE) (M= Male, F= Female, U= Unidentified sex).

Table 2. Biometric data of *Procavia capensis capillosa* trapped from different habitats in Bale mountains. Age and sex classes were defined as: mature males – adult males with fully erupted permanent dentition; young males – sub-adult males with incomplete permanent dentition; juvenile males – immature males that lack permanent dentition; mature females – females with fully erupted permanent dentition; young females – sub-adult females with incomplete permanent dentition; and juvenile females – immature females that lack permanent dentition (Milner and Harris 1999).

Age and sex class	No. of hyraxes measured	Body mass, kg (Mean ± SE)	Hind foot length, cm ` (Mean ± SE)	Height at shoulder, cm (Mean ± SE)	Total length, cm ` (Mean ± SE)
Adult males	5	3.9 ± 0.82	7.2 ± 1.4	28.0 ± 3.3	49.5 ± 4.8
Sub-adult males	5	2.7 ± 0.41	5.8 ± 1.0	20.0 ± 2.4	38.7 ± 3.6
Juvenile males	5	1.9 ± 0.88	0.9 ± 0.7	14.3 ± 2.1	22.0 ± 2.3
Adult females	5	3.5 ± 0.50	6.7 ± 1.1	23.2 ± 2.1	44.7 ± 3.9
Sub-adult females	5	2.6 ± 0.22	5.5 ± 1.1	17.6 ± 1.9	35.3 ± 2.8
Juvenile females	5	1.2 ± 0.10	2.6 ± 0.6	10.0 ± 1.6	20.4 ± 1.9

2110 ±420.3 sub-adults and 5892 ±1292.9 juveniles. There was significant difference in the number of adults and juveniles during wet and dry seasons ($\chi^2 = 8.06$, df= 1, $P<0.05$), but not sub-adults ($\chi^2 = 2.2$, df = 1, $P>0.05$). The ratio between sub-adults to adults was 1:8.5 and that of juveniles to adults and sub-adults to juveniles was 1:3.3 and 1:2.6, respectively. More individuals were recorded during the wet season (55.6%) than during the dry season (44.4%) ($\chi^2 = 72.6$, df= 1, $P<0.05$).

Among the sexed individuals, 42.3% was males and 57.7% was females. The ratio between adult male and adult female was 1:1.5, and that between sub-adult male and sub-adult female, and juvenile male and juvenile female was 1: 1.3 and 1: 1.1, respectively. Overall, the rock hyrax population was female biased. However, juvenile sex ratio was around 1:1. Sex distribution among the observed rock hyrax population during wet and dry seasons is given in Figure 4. Biometric data of *P. c. capillosa* are presented in Table 2.

During the wet and dry seasons, 38 (1846 individuals) and 46 (1690 individuals) hyrax colonies, respectively, were recorded (t= 3.27, df= 1, $P<0.05$). The mean colony size was 49 ±9.68 and 37 ±6.44 during wet and dry seasons, respectively (t= 4.21, df=1, $P<0.05$). The colony size also varied from site to site (t= 58.49, df= 42, $P<0.05$). Larger colonies were observed in sites

with more cover and food supply, and when juveniles were present. Each colony consisted of one dominant territorial male, one or more adult females and sub-adults and juveniles of both sexes. One to several adult males was also observed in the periphery of colonies.

DISCUSSION

Presence of *P. c. capillosa* in the BMNP is associated with the presence of mountain cliffs, rocky outcrops and rocky piles having crevices. They prefer open rocky areas or other similar sites where protection from predators and good visibility of the surroundings are ensured. Rock hyrax distribution in BMNP is not continuous, rather patchy and clumped, interrupted by open areas devoid of rocky outcrops and cliffs. Low water demand of hyraxes helps them to live in water-scarce rocky areas and cliffs.

Variations observed in the population size of *P. c. capillosa* in different study sites in BMNP could be due to the differences in the availability of suitable cover and/or forage, in addition to human impacts. The highest population size recorded was in Keyrensa, where there were rocky outcrops and cliffs, with grasses and shrubs in abundance in the vicinity of the shelter. The lowest population count recorded was in Gaysay Valley, where human interference was more and cover was less. These findings show that availability of forage and shelter play important roles in the spatial behaviour and population dynamics of the hyrax as reported in the case of other wild animals (Stephens and Krebs 1986). Population density of *P. c. capillosa* also varied from site to site. Higher density was in sites where rocky areas with crevices, abundance of grasses around, and fewer disturbances. The lowest density was in the area where human interactions were severe. Rock hyrax population density studies elsewhere have revealed 20–100/km² in Mount Kenya (Young and Evans 1993), 73–94/km² in the Matobo National Park, Zimbabwe (Barry and Mundy 1998) and 500–4000/km^2 in the Serengeti National Park, Tanzania (Hoeck 1982). The observed densities in the present findings are higher than that recorded in Mount Kenya, but within the density ranges documented in the Serengeti National Park.

During the present investigation, more individuals were recorded during the wet season than during the dry season in all sites. This was probably due to the birth of pups during the wet season and availability of fresh grass that can satisfy their nutritional demands during this season. Wet season is full of nutritious food items, which could promote breeding of animals and birth of new ones (Marcello et al. 2008). Rock hyraxes show seasonality in breeding activities, and peak birth coincides with the rainy season (Macdonald 1985). Low population during the dry season could also be attributed to juvenile mortality owing to physiological stress and scarcity of nutritious grass, when they move farther and subject to predation. Studies elsewhere during dry periods also showed that hyraxes expose to greater predation as they seek food farther from cover and refuge (Hoeck 1989, Davies 1997). Hyrax populations fluctuate due to predation, droughts and infectious disease (Druce et al. 2006, Parsons et al. 2008). Slow movement of rock hyraxes outside their crevices makes them vulnerable even to aerial predators (Brown et al. 1993).

There were more adults than juveniles and sub-adults in the *P. c. capillosa* population. This might be mainly due to the vulnerability of juveniles and sub-adults to predators than adults. Relatively more juveniles and fewer sub-adults in the studied population can be attributed to the birth of more individuals at first and mortality of juveniles by predation and food shortage stress during the dry season. Juveniles have higher surface area to volume ratio and are more vulnerable to low ambient conditions than adults (Brown and Downs 2005). Dry season is the time of minimal resources and cover in most of the natural habitats, making small mammals to experience considerable physiological stress. In Matobo National Park, Barry and Mundy (1998, 2002) estimated mortality of around 60–75% of juvenile rock hyraxes. Thus, infant mortality might be one of the reasons for fewer sub-adults compared to adults in the present rock hyrax population in the Bale Mountains.

The sex ratio of rock hyraxes in BMNP was female biased. Sex ratio in animals signifies the proportion of each sex that is involved in the breeding process (Robinson and Bolen 1989). High population of females and high proportion of young indicate healthy and increasing status. In polygynous animals such as hyraxes, adult females can mate with more than one males and have offspring, which is favourable for sustainability of the population (Fourie and Perrin 1987a).

The disparity in the sex ratio was more in adults, followed by sub-adults and juveniles. Fewer males among adults and sub-adults might be due to the higher rates of predation of males of these age groups. Territorial males have to stay out of their shelter to watch and defend their territories. Young males are

prone to mortality while being dispersed from their natal kopje to periphery. Through intraspecific agonistic behaviour of the territorial male, non-territorial adult males are excluded from the breeding unit (Hoeck 1982). During such occasions, they may fight and sustain serious wounds, or even die as witnessed in some of the study sites during the present investigation.

Rock hyraxes are social animals living in colonies of various sizes. The colony sizes of *P. c. capillosa* ranged between 4–86 individuals. Such a variation was mainly attributed to differences in the availability of cover and food in different study sites. According to Skinner and Chimimba (2005), rock hyrax colony size varies based on the available extent of rocky habitat and food. Lack of sufficient refuges can be a factor limiting colony size. Large colonies having up to 86 individuals were recorded in the Web Valley, Keyrensa and Garba Guracha, where rocky outcrops and mountain cliffs where abundant.

The colony size was larger during the wet season, as could be expected when food is plentiful and when small groups merge for protection against predation and other disturbances. However, during the dry season, as food becomes scarce due to grazing by livestock, colonies break up to forage in wider areas in smaller family units. The colony size was high when there were juveniles and when rock hyraxes were in association with bush hyraxes as in Web Valley and Garba Guracha sites. Major benefits of heterospecific groups include enhanced vigilance against predators and increased ability to defend resourceful feeding sites. Grouping with other species may reduce predation risk through earlier detection of predators, dilution and confusion effects, and due to cooperative defense (Isvaran 2007).

Although peripheral male rock hyraxes do not form groups in most cases, male bachelor groups of 2–4 were recorded in some of the study sites. This observation contradicts with earlier reports of Fourie and Perrin (1987b) and Hoeck (1982) that peripheral males of hyraxes do not form groups and always sit alone at the periphery of the colony. However, Koren (2006) observed bachelor males among the peripheral males in Ein Gedi Nature Reserve in Israel.

Procavia c. capillosa has wide spacial and altitudinal distribution all over BMNP. Distribution of this subspecies depends mainly on the presence of enough cover that ensures protection against predators in addition to the availability of forage. Population density was associated mainly with the presence of enough shelter and forage. Presence of more adult females and juveniles in the population demonstrates high reproductive potential and sustainability of them in the study area. Repeated census of rock hyrax and assessments on their habitats in BMNP are crucial to address population dynamics and genetic relationships among hyraxes within and around the Park, and other relevant ecological parameters of this subspecies.

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