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The striped hyaena *Hyaena hyaena* (Hyaenidae, Carnivora) rediscovered in Armenia

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Abstract. The striped hyaena *Hyaena hyaena* (Linnaeus, 1758) is globally categorised as "Near Threatened" and is nearly extinct in the Caucasus. In Armenia, the last published record dates back to 1925 and the last trustworthy sighting was in the late 1940s. Here, a dead hyaena is described which was found in 2010 near the Nrnadzor village in the extreme south of Armenia. Its skull was investigated, age was estimated by several methods (cementum layers, tooth eruption, fusion of cranial sutures, pulp cavity closure and tooth wear) and sex was determined from the sagittal, occipital and nuchal crests and by genotyping of skin DNA. The specimen was found out to be a female aged ca. 17-18 months. As this is the age of disperal and females play a pivotal role in the social life of this carnivore, the possibilities for recolonization and establishment of hyaena population in the Meghri district of southern Armenia are discussed. This area holds sufficient prey base and suitable arid landscapes for survival of this species. The recent record of another individual's fresh tracks on sand near Nrnadzor supports this hypothesis. Usability of different techniques of sex determination and age estimation in the striped hyaena is considered.

Key words: sex, age, population, Meghri district, Caucasus

Introduction

The striped hyaena *Hyaena hyaena* (Linnaeus, 1758) has a large, but patchy, range extending from East Africa through the Middle East to India and is classified on the IUCN Red List as "Near Threatened" because of persecution, prey depletion and habitat conversion to agricultural lands (Arumugam et al. 2008). This species is mostly scavenger, but also feeds on insects, reptiles, rodents, birds, vegetables and livestock (Heptner & Sludsky 1972, Rieger 1981, Mills & Hofer 1998, Lukarevsky 2001, Singh et al. 2010). Such feeding habits preclude from the establishment of true social behaviour in striped hyaenas, so these carnivores are behaviourally solitary, but forming polyandrous breeding groups (Lukarevsky 2001, Wagner et al. 2007a, 2008). Consequently, they are thinly distributed over the vast tracts of suitable habitats at naturally low densities and are particularly prone to imminent extinction in places where human pressures are high (Mills & Hofer 1998, Lukarevsky 2001, Arumugam et al. 2008).

The striped hyaena is teetering on the brink of extinction in the Caucasus Ecoregion which comprises Armenia, Azerbaijan, Georgia, Russian North Caucasus and parts of north-eastern Turkey and north-western Iran (Williams et al. 2006). Historically, its distribution area in this region was spread from the Arax River basin (Armenia, Azerbaijan) through semi-deserts and plains of eastern Georgia and Azerbaijan northwards to the lower part of the River Samur and Makhachkala town in Russia's Republic of Dagestan (Ognev 1931, Heptner & Skudsky 1972). Currently, this species still survives in eastern Georgia (Iori Upland, Vashlovani National Park), several parts of Azerbaijan (northern

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vicinity of the Mingechaur Reservoir, Zuvand Upland, possibly Nakhichevan Republic), disputed lands of Karabakh and, presumably, also in Dagestan (foothills of the Samur and Gyulgerichay basins) (Gajiev 2000, Aristov & Baryshnikov 2001, Yarovenko 2003, Williams et al. 2006, E. Askerov, pers. comm.). Occurrence of hyaena in the adjoining parts of Turkey is dubious (Kasparek et al. 2004). Firouz (2005) writes that hyaenas do not live in north-western Iran, but Misonne (1959) indicated their presence in the Moghan Steppe.

In Armenia, hyaena records were always sporadic and spatially confined to semi-deserts, arid foothills and riparian scrublands of the Ararat Valley in the west, Meghri district in the south and Shamshadin and Ijevan districts in the north-east (Ognev 1931, Dal 1954, Heptner & Skudsky 1972). Even though hyaenas were frequently killed in the 1860s near the capital of Yerevan, by the end of the 19th century this carnivore had become nearly extinct in the country (Vereschagin 1959). The last published record dates back to 1925 and comes from the Artashat district, Ararat Valley (Dal 1954). To our knowledge, the last trustworthy sighting was in the late 1940s in the western vicinity of Yerevan city (H. Ghazaryan, pers. comm.). Even large abundance of small livestock kept in Armenia before the 1990s by ethnic Azerbaijani did not allure hyaenas. So, the population estimates given by Mills & Hofer (1998) as fewer than 50-100 individuals in Armenia and fewer than 150-200 in the Caucasus (excluding the Turkish and Iranian parts) are unrealistically high.

According to the earlier accounts (e.g., Dinnik 1914) then oft-quoted by other authors, hyaenas in the Caucasus and particularly in Armenia had been intensively wiped out for their alleged habit to kill children who slept outdoors. As Vereschagin (1959) claimed, direct persecution of hyaenas spurred by human antipathy was the principal cause of their large-scale decline in the region. Gajiev (2000) also blamed the depletion of food resources (carrion), principally goitered gazelles *Gazella subgutturosa* (Güldenstädt, 1780), for the rarity of hyaenas. On the other hand, habitat loss can be the primary cause of hyaena disappearance in Armenia as during the 20th century the Ararat Valley and the Shamshadin and Ijevan districts were almost completely transformed into vineyards, orchards, gardens and crop fields (our data).

In this paper, we describe a dead striped hyaena found in 2010 in the Meghri district, southern Armenia and provide some insights into species ecology and conservation in the country (Fig. 1; WWF 2010, Erickson-Davis 2011).

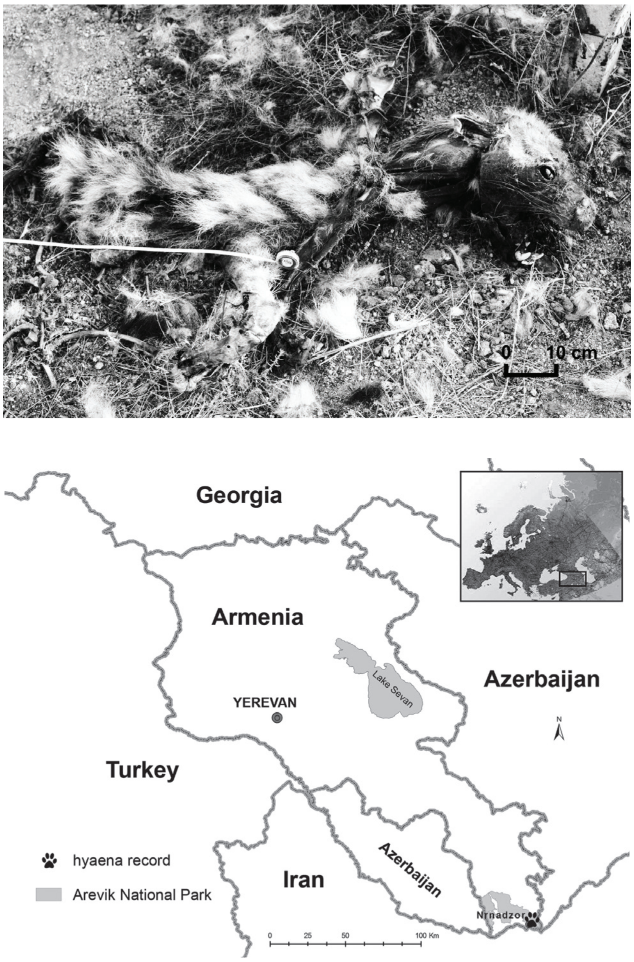

Fig. 1. *Dead striped hyaena* Hyaena hyaena *found near the Nrnadzor village (up) and location of this record (down). Authors: A. Malkhasyan (up), T. Melkumyan (down).*

Material and Methods

Thirteen measurements of the skull of the specimen were taken by Vernier calipers with accuracy 0.05 mm and tabulated (Table 1) for comparative analysis against the cranial measurements of 25 striped hyaenas published by Ognev (1931) and Pocock (1941). The hyaena skull is shown in Fig. 2.

Sexing of the specimen was done using the (1) measurement of the posterior region of the sagittal crest and the degrees of development of the occipital and nuchal crests; and (2) analysis of skin DNA. The posterior region, occipital and nuchal crests appear to be the only cranial parameters differing between males and females of the striped hyaena, a sexually monomorphic species (Buckland-Wright 1969). According to Fig. 5 in Buckland-Wright (1969), male skulls generally have larger posterior region (10-19 cm^2) than female skulls (9-14 cm^2), so the overlap between females and juvenile males is evident.

Fig. 2. *The skull of the striped hyaena found in Armenia. Author: I. Khorozyan.*

The posterior region was measured as the area of the sagittal crest above the bregma-lambda line (Fig. 1 in Buckland-Wright 1969) on six pdf files of skull images (three left-side view and three right-side view), using the Measuring Tool in Adobe Acrobat 9 Pro, ver. 9.0.0. The occipital and nuchal crests are more pronounced in males than in females, but no quantitative comparative analysis is done (Buckland-Wright 1969).

The skin was rubbed from inside with coarse salt to avoid maggot infestation, rolled up and stored in a paper envelope filled with silica gel beads to ensure ventilation and desiccation. Sex of the specimen was determined from skin DNA using a Qiagen tissue and stool kit with a modified protocol with negative control to check for contamination and pipetting error (Murtskhvaladze et al. 2010). The primers DBX intron 6 (forward: ATGCTGCAGTTTTTCCAGA, reverse: TACGCTGGGTCTTAGTT), DBY intron 7 (forward: GGTCCAGGAGAGGCTTTGAA, reverse: TGCCATTGTTTAAAAGGAAGGTCT), SE47 (5′-CAGCCAAACCTCCCTCTGC-3′) and SE48 (5′-CC CGCTTGGTCTTGTCTGTTGC-3′) were used for amplification (Yamamoto et al. 2002, Hellborg & Ellegren 2004, DeMatteo et al. 2009). Polymerase Chain Reaction (PCR) was conducted in 7μL total volume at the following cycling regime: initial at 95 °C for 15 min; a touchdown of 20 cycles at 94 °C for 45 sec; at 60 °C for 30 sec (with a stepwise decrease by 0.3 °C at each cycle); and at 72 °C for 1 min. Additional 20 cycles were made at 94 °C for 45 sec; at 48 °C for 1 min; at 72 °C for 1 min and, finally, at 60 °C for 30 min. Amplified DNA was run on ABI 3300 gene sequencer using the HI-Deionised Formamide and GeneScan™-500 LIZ® Size Standard, Applied Biosystems. Genotypes were screened using Genemapper 3.5 software package, PerkinElmer. All loci were genotyped three times to avoid genotyping errors and false allele amplification (Murtskhvaladze et al. 2010).

Age was determined from (1) counts of dental cementum layers (annuli) in the roots of upper canines; (2) tooth eruption patterns; (3) fusion of cranial sutures; (4) pulp cavity width-tooth width percentage; and (5) tooth wear. In carnivores, the actual age is usually equal to the number of dark and narrow annuli plus one as the first-year annulus has been seldom visible along the very edge of the tooth (Klevezal 1988, Zapata et al. 1997, Roulichová & Anděra 2007). Dark and narrow annuli are laid one per annum during the periods of slow growth, e.g. in winter, and the broad and translucent light-coloured bands are formed during active growth (Spinage 1973). Both canines were extracted from the upper jaw and the lingual sides of their roots were ground lengthways by hand on the abrasive paper at coarseness 80, then smoothed at coarseness 320 and finally polished at very fine coarseness 1200. The sections were examined under an Olympus SZX16 research stereo microscope at its maximum magnifications from 6.3× to 11.5×, then under the 30× magnifying glass. For comparison, Roulichová & Anděra (2007) indicated 25× magnification as sufficient. To make photographic images of the sections, they were scanned on the HP ScanJet 4890 Photo Scanner at resolutions 2400 dpi and 4800 dpi and then modified in Adobe PhotoShop CS2 (Fig. 3).

Tooth eruption was linked to hyaena age as described by Mills (1982) and Van Horn et al. (2003). Permanent dentition has been attained at 13-18 months in the spotted hyaena *Crocuta crocuta* (Erxleben, 1777) (Van Horn et al. 2003) and at ca. 15 months in the brown hyaena *Hyaena brunnea* (Thunberg, 1820) (Mills 1982), so the same timing was assumed also for the striped hyaena. According to tooth eruption patterns, hyaenas can be aged as cubs (age class 1, teeth erupt and change completely from deciduous to permanent, 0-15 months), subadults (age class 2a, period from attaining permanent dentition to becoming sexually mature or adult, 15-30 months), young adults (age class 2b, 30 months-4 years) and adults of age classes 3 to 5 (increase in attrition of teeth, especially premolars, > 4 years) (Mills 1982).

Fusion was studied in sutures which in the striped hyaena obliterate first (closure index = 3.2-4.0 or 80-100 % in relation to the sagittal suture which has the highest index 4.0) (Schweikher 1930). These sutures were sagittal, medial and lateral between the pterygoid wing and the process (index 4.0 for each), lambdoidal (3.4), coronal, basilar or spheno-occipital synchondrosis, spheno-temporal and dorsal maxilla-palatine (3.2 for each).

The pulp cavity width-tooth width percentage is known to decrease sharply during the first two years of life from over 80 % down to 20-30 % because of progressive inward dentine accumulation and to level off at older ages. Therefore, this percentage can be used to discriminate ages or age classes in carnivores, at least before the age of two years or so (Kauhala & Helle 1990, Zapata et al. 1997). The radiographs were obtained by orthopantomography, i.e. panoramic X-ray scanning of the jaws, using an Orthophos 3 system (Sirona Dental Systems GmbH) at voltage 60 kV, power 10 mA and scale 1 : 1. The left and right M_1 were the best visible teeth on radiographs which were used for pulp cavity and tooth width measurements. The measurements were done on gum line on light-exposed radiographs by Vernier calipers with accuracy 0.05 mm and averaged between a right and left M_1.
Tooth wear was investigated primarily in carnassials P^4 and M_1, canines and all premolars (except the vestigial P^1) which are mostly affected by bone-cracking habits of hyaenas (Van Horn et al. 2003, Ferretti 2007, Van Valkenburgh 2007). Tooth wear allows to estimate the following age classes in striped hyaenas: cubs (< 6 months), juveniles (6 months to 1 year), young adults (1-3 years) and adults (> 3 years) (Wagner et al. 2008).

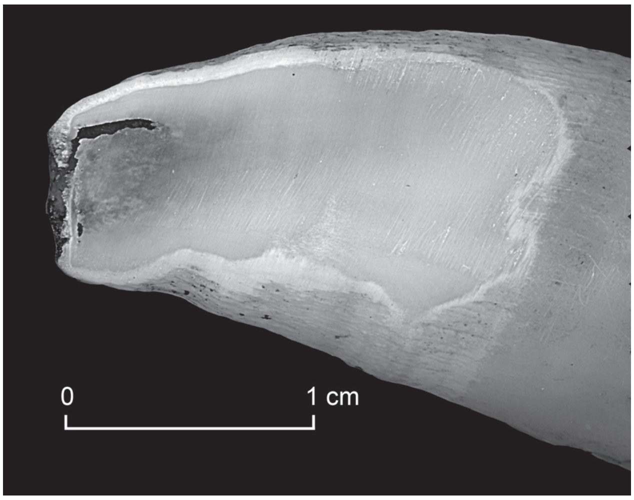

Fig. 3. *A canine root section from the striped hyaena. Author: I. Gabrielyan.*

Results

Record site

The corpse of a striped hyaena entangled in the orchard's barbed-wire fence was found on October 1, 2010 at elevation 592 m in the Kyariz Canyon to the east of the Nrnadzor (formerly Nuvadi) village in the Meghri district, southern Armenia (Fig. 1). Geographically, the record site is confined to the foothills of the southern slopes of the Meghri Ridge.

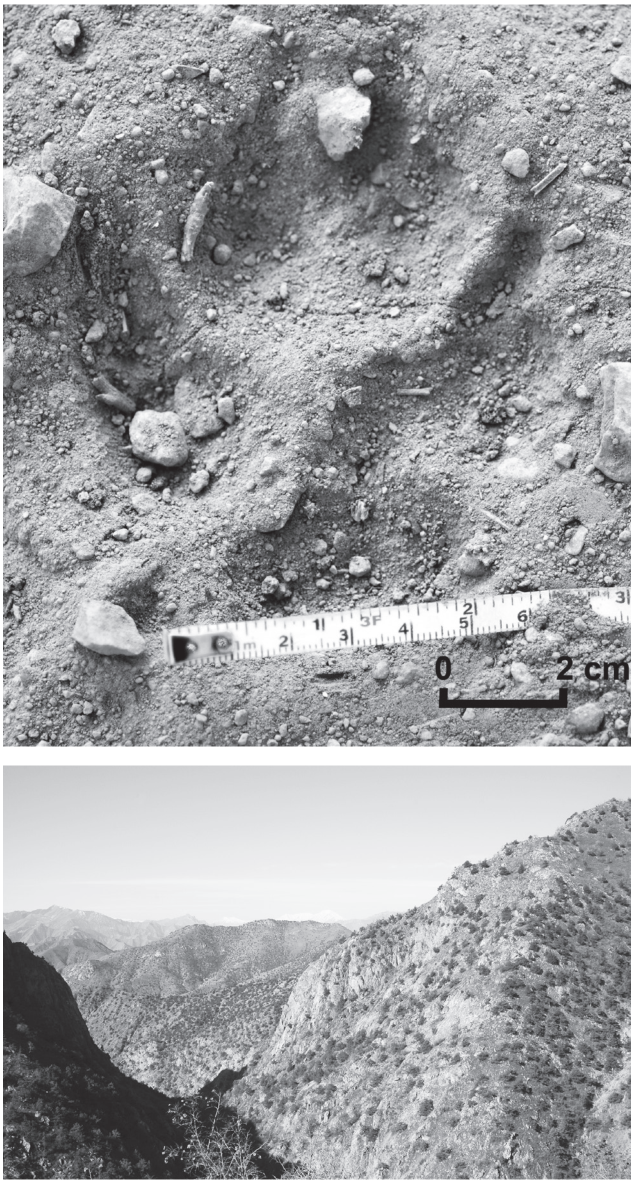

Fig. 4. *A fresh hyaena track recorded on sand near the Nrnadzor village in December, 2010 (up) and suitable habitat for hyaenas in this area (down). Author: A. Malkhasyan.*

The body was obviously scavenged, but still remained fresh for unambiguous identification. The leftovers contained the head, left scapula, right os coxae (innominate bone), limbs, some ribs and scattered pieces of brown-and-white striped fur.
Local landscape is arid grassland (phrygana) dominated by *Artemisia fragrans*, *Amygdalus fenzliana*, *Salsola dendroides*, *Stipa capillata*, *Alhagi pseudalhagi* and other plants.

Age

The cranial measurements showed a very small size of the hyaena skull. The values of the greatest length,

Table 1. *Craniological measurements (mm) of the striped hyaena* Hyaena hyaena *from Armenia and other localities.*

Trait	juvF, this study	No. 2011, adF[1]	No. 7845, adF[1]	No. 3040, sex unkn[1]	No. 3041, sex unkn[1]	No. 10087, sex unkn[1]	No. 10086, sex unkn[1]	No. 11481, sex unkn[1]	adM[2]	adM[2]	adM[2]	adM[2]	adM[2]
Greatest length	229.1	247.2	240.0	235.0	238.7	247.8	232.2	243.7	250.0	244.0	250.0	244.0	247.0
Condylobasal length	212.3		214.0	208.0	204.2	221.1	207.8	224.0	221.0	220.0	219.0	215.0	216.0
Basal length	202.4		198.3	192.5	199.0	204.7	192.7	207.9					
Length of C-P^4	88.2	91.1	89.6	87.0	90.0	91.8	90.0	91.2					
Greatest length of P^4	29.3	28.2	29.1	30.0	30.8	30.2		31.0	30.5	31.0	30.0	31.0	30.0
Length of braincase	68.1	90.2	88.4	85.5	91.3	89.1	86.0	89.5					
Zygomatic breadth	145.0	158.2	153.0	157.0	156.1		143.0	160.2	154.0	164.0	159.0	155.0	153.0
Frontal breadth	68.2	77.6	75.3	74.6	67.9	79.0	69.0	77.1					
Minimal interorbital breadth	30.2	45.8	48.2	48.0	46.3	51.7	44.7	47.0	50.0	49.0	47.0	49.0	49.0
Rostrum breadth	54.0	56.0	50.2	52.3	50.7	54.3	48.2	54.7					
Minimal postorbital constriction	21.1	33.5	37.5	39.0	37.0	39.8	34.2	32.3	36.0	37.0	35.0	37.0	39.0
Breadth between infraorbital foramena	50.2	48.2	48.7	52.2	51.5	54.2	48.3	50.2					
Nasal length with processes	61.3	61.3	67.9	57.2	60.0	69.0	53.8	64.0					
Trait	adM[2]	adM[2]	adM[2]	adM[2]	adF[2]	adF[2]	adF[2]	adF[2]	adF[2]	adF[2]	adF[2]	adF[2]	adF[2]
Greatest length	247.0	243.0	233.0	240.0	248.0	245.0	242.0	245.0	243.0	241.0	245.0	237.0	233.0
Condylobasal length	215.0	212.0	211.0	210.0	210.0	220.0	220.0	216.0	215.0	215.0	211.0	210.0	202.0
Basal length													
Length of C-P^4													
Greatest length of P^4	31.0	29.0	30.0	29.0	29.0	30.0	30.0	30.5	30.0	30.0	30.0	30.0	30.0
Length of braincase													
Zygomatic breadth	159.0	154.0	152.0	149.0	155.0	156.0	153.0	156.0	154.0	152.0	158.0	147.0	149.0
Frontal breadth													
Minimal interorbital breadth	48.0	49.0	48.0	47.0	48.0	47.0	47.0	47.0	50.0	47.0	49.0	47.0	44.0
Rostrum breadth													
Minimal postorbital constriction	38.0	39.0	37.0	35.0	37.0	39.0	35.0	37.0	40.0	38.0	36.0	38.0	36.0
Breadth between infraorbital foramena													
Nasal length with processes													

Explanations: M, male; F, female; ad, adult; unkn, unknown; [1] Ognev 1931 (Caucasus: n = 1, Mesopotamia: n = 1, Central Asia: n = 5); [2] Pocock 1941 (India: n = 18). Empty cells indicate that no measurements were taken. The traits which in Armenian specimen are significantly smaller than the 99 % confidence interval of measurements in the other 25 specimens are marked by bold.

length of the upper tooth row C-P^4, greatest length of the carnassial P^4, braincase length, zygomatic breadth, frontal breadth, minimal interorbital breadth and minimal postorbital constriction were significantly lower than the 99 % confidence intervals (CI) of the measurements taken in other 25 specimens (Table 1). The difference was especially profound in the greatest length (229.1 mm vs 99 % CI = 239.8-245.2 mm), length of braincase (68.1 mm vs 86.5-90.7 mm), minimal interorbital breadth (30.2 mm vs 46.9-48.7 mm) and minimal postorbital constriction (21.1 mm vs 35.9-37.9 mm). Obviously, this skull belonged to a subadult individual < 2 years old. This is also evident from Fig. 1.

Neither canine root section has revealed clear dark cementum annuli what indicated the animal's age as more than one year (canines are permanent, one vague and thin annulus extends along the edge in the bottom of the root), but well before two years when one dark annulus would become clearly visible in all parts of the root (Fig. 3). All teeth in the skull were permanent and the cusps of the carnassials, premolars and canines were slightly worn, so the hyaena was aged as a 15-18-month-old subadult (Fig. 2).

All studied sutures belonging to the skull vault (except the medial and lateral pterygoid sutures classified as miscellaneous bones) were open and did not show the signs of fusion (Fig. 2). According to Schweikher's (1930) approach, their closure index was 0 which indicated continuing brain growth in a young individual.

The pulp width-tooth width ratio was 22.9 %, so the hyaena was aged 17-20 months. That the lowest possible voltage was used to produce light and clear-cut radiographs indicated relative thinness of skull bones and young age of the specimen.

Sex

The posterior region of the sagittal crest was 11.08 cm^2 which fell within the overlap area of male and female hyaena skulls (10-14 cm^2, see Material and Methods). The occipital and nuchal crests in the hyaena skull were intermediately developed. Therefore, using these characters in hyaena sexing in this study was proved inefficient.

Genetic analysis has shown that the specimen is a female, as no alleles in Y chromosome could be amplified and repeated genotyping displayed the homozygosity of the individual.

Ecology and distribution

The hyaena described in this study was proved to be a young adult female aged approx. 17-18 months, i.e. at the age of dispersal. This can give an insight into possible recolonization and likely establishment of hyaena population in southern Armenia. That recolonization of striped hyaenas in the Meghri district is possible was proved by the discovery on December 12, 2010 of fresh tracks on dust in the same locality where the dead specimen was found (Fig. 4). Contrary to other parts of historical hyaena range in Armenia which are fully modified by humans for agricultural purposes, the Meghri district still contains vast tracts of relatively undisturbed arid landscapes suitable for hyaena existence. In 2009, Arevik National Park (344.02 km^2) was established to safeguard protection of southern slopes of the Meghri Ridge and now this park has been considered a premier protected area for large mammals in all Armenia (Fig. 1).

Discussion

The system of spatial, social and genetic interactions in striped hyaena populations is in many aspects uncommon and even unique for mammals. Individuals in the population are spatially grouped, but socially solitary as the inter- and intra-sex associations beyond the breeding period are rare (Wagner et al. 2007a, 2008). The core of the breeding group is an adult female associated with several distantly related or unrelated males who sire most of this female's offspring, but copulations with extra-group males also play a significant role. The closely related females disperse afar to become the nuclei of the groups (Wagner et al. 2007a). The groups are very mobile and do not stay in the same place for more than several days (Lukarevsky 2001). Food availability is a principal driver for distribution of females carrion (staple food for striped hyaenas), being a variable resource in space and time, represents a structural force underlying the movement and spatial distribution of scavengers (Wilson & Wolkovich 2010).

In light of this, dispersal of female striped hyaenas has been a way to mitigate the detrimental effects of inbreeding in small populations and to maximize access to food resources. This is fully true for the southern slopes of the Meghri Ridge where the dead hyaena was found and for south-western parts of Azerbaijan where this individual had to come from (Fig. 1). The source population in Azerbaijan is definitely endangered, small and possibly food-deficient because of the unresolved military conflict over Nagorno Karabakh in which plenty of firearms can provoke uncontrolled hunting. In the meantime, the Meghri Ridge is rich in wild ungulates, namely the bezoar goat *Capra aegagrus* (Erxleben, 1777), wild boar *Sus scrofa* (Linnaeus, 1758) and roe deer *Capreolus capreolus* (Linnaeus, 1758) as potential prey for hyaenas (Khorozyan et al. 2008). There are also anecdotal records of red deer *Cervus elaphus* (Linnaeus, 1758) in this area (Khorozyan 2010a).

Availability of shelters, such as caves and grottos, can be even more important for survival of striped hyaenas than prey (Singh et al. 2010). The southern slopes of the Meghri Ridge are covered by arid sparse forests and grasslands with numerous secluded rocky refugia, so they well fit the hyaenas' requirements for habitats (Fig. 4). Existence of competitors, viz. gray wolf *Canis lupus* (Linnaeus, 1758), golden jackal *C. aureus* (Linnaeus, 1758), brown bear *Ursus arctos* (Linnaeus, 1758), Eurasian lynx *Lynx lynx* (Linnaeus, 1758) and leopard *Panthera pardus* (Linnaeus, 1758) makes shelters an even more important resource for hyaenas in this area. Despite this strong rivalry, hyaenas may benefit by scavenging on prey killed and consumed by these carnivores (Lukarevsky 2001).

Before the new records (dead individual and fresh tracks) have become known, in the Red Data Book of Armenia the striped hyaena was registered as "Regionally Extinct", but now it has to be reconsidered as "Critically Endangered" (Khorozyan 2010b).

As the striped hyaena is strongly associated with arid subtropical landscapes and availability of carrion, it would most likely benefit from current climate change. In 1929-2007, mean annual air temperatures in Armenia have risen by 0.85 °C and mean annual precipitation has decreased by 6 %, with distinct aridisation in summer and no apparent changes in winter. By 2030, air temperatures are forecast to increase by 1-2 °C and precipitation is expected to drop by 5-15 % in all areas of historical hyaena occurrence in Armenia (Ministry of Nature Protection of the Republic of Armenia 2010).

The striped hyaena is a sexually monomorphic species which cannot be reliably sexed from external or cranial parameters. This can be partly caused by abnormally low concentrations of circulating testosterone in males which even bring to unique morphological convergence of male and female genitals in the age of 1-18 months (Wagner et al. 2007b). So, the only viable technique to determine sex in striped hyaenas is genetic analysis. Different methods of hyaena aging have provided similar results, but counts of cementum annuli in canine roots appeared to be the most reliable technique, in corcordance with results of other studies (Spinage 1973, Klevezal 1988, Zapata et al. 1997, Roulichová & Anděra 2007). The pulp cavity width-tooth width percentage is seasonally variable, but in present study the age estimate is expected to be correct as the hyaena died in September when the level of correct age determination from the percentage is maximal (Kauhala & Helle 1990). The highest concern is raised over the utility of tooth wear in age determination of the striped hyaena because of observer bias, individual variability and a natural habit of bone-cracking which will intensify attrition of a hyaena's teeth, mostly premolars and lower molars, disproportionally to its actual age (Ferretti 2007, Van Valkenburgh 2007). In gray wolves which are less specialised in bone consumption than hyaenas, the age determined from tooth wear was overestimated in juveniles by 1-2, sometimes even by 3-4 years (Nowak et al. 2000), so in hyaenids such overestimation can be higher. More research is needed to apply different age determination techniques to hyaenids, particularly the striped hyaena, using the known-age material.

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