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ZOOLOGY

Using Thin-Layer Chromatography of Fecal Bile Acids to Study the Leopard (*Panthera pardus ciscaucasica*) Population

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Abstract—Thin-layer chromatography (TLC) of fecal bile acids has been used to confirm visual identification of scat samples found in Armenia in 2004–2005 and attributed to the leopard (*Panthera pardus ciscaucasica*). The results of TLC do not differ significantly from those of visual identification, confirming the reliability of the latter method. Taking into account the frequency and distribution of fresh scats, two priority areas for leopard conservation have been identified: the Central and Khachadzor districts of the Khosrov Reserve and the Nuvadi-Shvanidzor area in eastern Meghri Ridge.

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The leopard (*Panthera pardus ciscaucasica*) is the only species of large cats that has survived in the Caucasus. In the early historical period, the leopard was widespread in this region, and its range extended to the Ciscaucasian plains (Vereshchagin, 1959). Until the mid-19th century, the leopard could be often encountered in Caucasian forests, brush thickets, and hardly accessible rock massifs with little snow, provided these areas were inhabited by its prey: the chamois (*Rupicapra rupicapra*), bezoar goat (*Capra aegagrus*), West Caucasian tur (*Capra caucasica*), East Caucasian tur (*Capra cylindicornis*), roe deer (*Capreolus capreolus*), and wild boar (*Sus scrofa*) (Dinnik, 1914; Geptner and Sludskii, 1972; Sludskii, 1973).

In the mid-19th century, the leopard population began to decline. In some areas, these animals disappeared because of hunting, deterioration of food resources, and habitat loss. Judging from changes in the number of trophies, the leopard was exterminated in the former Kubanskaya Okhota (Imperial Kuban Hunting Grounds) by the early 1920s; on the Black Sea slope of the Greater Caucasus, in Karachai-Cherkessia, and in the Teberda Reserve by the late 1950s (Nasimovich, 1941; Kotov and Ryabov, 1963; Geptner and Sludskii, 1972; Sludskii, 1973; Penzikov, 1986); and in northern Armenia by the mid-1970s (Khorozyan and Abramov, 2005). Since the 1980s, only two leopards were taken in the whole North Caucasus (Spasskaya and Saidalieva, 1983; Lukarevsky et al., 2004). A resident leopard population has survived only in Armenia and Azerbaijan. Its present-day range in Armenia covers the Meghri, Bargushat, and Zangezur ridges, from the Khosrov Reserve to the Iranian border; in Azerbaijan, it is confined to the Talysh Ridge in the southeast and the Zangezur Ridge in Nakhichevan (Khorozyan et al., 2005). According to preliminary estimates, the total population size does not exceed 30 ind., with 10–20 ind. inhabiting Armenia (Khorozyan and Abramov, 2005; Khorozyan et al., 2005). The leopard is on the Red Lists of all Caucasian republics as an endangered species.

The study of leopard by means of direct observations is difficult because of its great rarity and stealthiness. It is more feasible to use methods based on the analysis of indirect evidence of its presence, such as scats, footprints, and scrapes. In dry mountain habitat of Armenia, scats are well preserved and remain identifiable for a long time. Moreover, they can provide information on animal diet, distribution, space and habita use, population structure, and individual hormonal and genetic characteristics (Putman, 1984; Kohn and Wayne, 1997; Monfort, 2003). Conversely, footprints and scrapes are poorly detectable on the dry, hard ground and disappear within a short time. In addition, in sparse population scrapes are used mainly as territorial markers in the mating period; i.e., their occurrence is limited in space and time (Lukarevsky, 2001).

Correct species identification of scats found in nature is an important component of ecological studies. It may be performed visually, by biochemical (TLC of fecal bile acids) or genetic (DNA analysis) methods (Dalen et al., 2004; Nagata et al., 2005), or using specially trained dogs (Smith et al., 2001; Harrison, 2006). Visual identification is not always reliable, especially in areas inhabited by several sympatric species, and should be confirmed by other methods (Prugh and Rit-

Table 1. Distribution of leopard, lynx, and wolf scats identified by TLC and unidentified scats in four areas surveyed in Armenia

Species	Nuvadi-Shvanidzor, eastern Meghri Ridge (296.9 km^2)	Western and central Meghri Ridge (209.7 km^2)	Central and Khachadzor districts of Khosrov Reserve (207.9 km^2)	Sisian area, Zangezur Ridge (168.0 km^2)	Total*
Leopard	13	1	5	Not found	19/63.3
Lynx	3	1	Not found	Not found	4/13.3
Wolf	2	Not found	Not found	Not found	2/6.7
Unidentified	3	Not found	1	1	5/16.7
Total*	21/70.0	2/6.7	6/20.0	1/3.3	30/100

* Figures above (below) the line show the number (proportion, %) of scats found between April 2004 to November 2005.

land, 2005). TLC of fecal bile acids is widely used for the identification of carnivores and, in particular, large cats in South America (Jimenez et al., 1996; Capurro et al., 1997; Fernandez et al., 1997; Taber et al., 1997; Cazon and Suhring, 1999), North America (Major et al., 1980; Johnson et al., 1984), and Equatorial Africa (Ray and Sunquist, 2001).

In this study, we present the results of TLC application to the identification of Caucasian leopard (*P. pardus ciscaucasica*) scats and discuss various aspects of the use of this method in studies of the leopard population in Armenia.

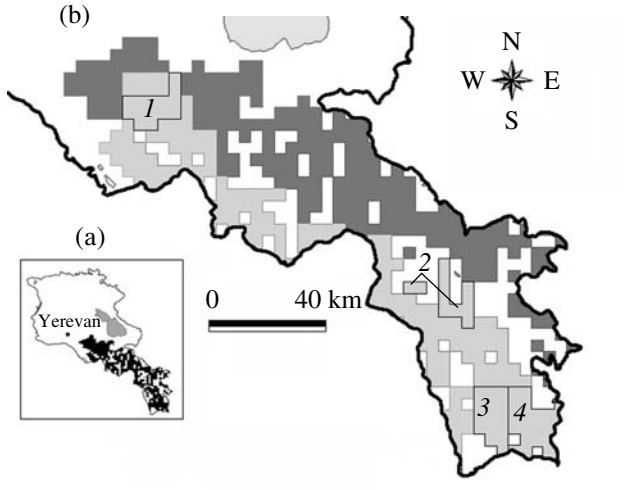

Fig. 1. (a) Leopard range in Armenia and (b) location of surveyed areas: (*1*) Central and Khachadzor districts of the Khosrov Reserve, (*2*) Sisian area, (*3*) western and central Meghri Ridge, and (*4*) Nuvadi-Shvanidzor. Pixel size 4 × 4 km. Light pixels show areas permanently or temporarily inhabited by leopards, and dark pixels show areas not inhabited or occasionally visited by them.

MATERIALS AND METHODS

To estimate the possibility of identifying scats of the leopard and other large carnivores inhabiting the same areas in Armenia (the lynx *Lynx lynx* and wolf *Canis lupus*) by means of TLC, we initially analyzed samples of known origin taken from four leopards (pedigree nos. 330, 295, 306, and 289) and two lynxes (nos. 327 and 220) kept in the Exotic Feline Breeding Compound Inc. (Rosamond, California) and two wolves from the Yerevan Zoo (Armenia). Scats of the brown bear (*Ursus arctos*), which also occurs in the areas inhabited by the leopard, can be easily distinguished visually and are not considered in this study. Characteristic features of leopard scats include pointed ends, segmented (lobular) structure, and a maximum diameter of about 2.7 cm (2.0–3.0 cm); defecation sites are usually distributed along the ridgetops (Khorozyan and Malkhasyan, 2002; Khorozyan, 2003).

At the initial stage, we also estimated possible effects of weather and air temperature on the efficiency of TLC analysis. Each sample was divided into two equal parts. One part was immediately dried and used in experiments, whereas the other part was placed on a metal grid and exposed outside the window of our laboratory to weather for 30 days before analysis.

In Armenia, scats were collected in four areas between April 2004 and November 2005 (Table 1, Fig. 1). For each area, we calculated the relative index of leopard abundance, i.e., the number of scats (identified visually or by TLC) per 10 km of route survey (Karanth and Kumar, 2002; Henschel and Ray, 2003) (Table 2).

Table 2. Relative abundance indices of leopard calculated from the numbers of scats identified visually (N_{vis}) and by TLC (N_{tlc}) per 10 km of route surveys

Area	Route length (D, km)	N_{vis}	N_{tlc}	Index of abundance		Significance of difference between I_{vis} and I_{tlc}
				$I_{vis} = N_{vis} \times 10/D$	$I_{tlc} = N_{tlc} \times 10/D$	
Nuvadi-Shvanidzor	331.3	21	13	0.63	0.39	$\chi^2 = 0.565$, $df = 1$, $P = 0.452$
Western and central Meghri Ridge	46.9	2	1	0.43	0.21	$\chi^2 = 0.756$, $df = 1$, $P = 0.385$
Khosrov Reserve	94.6	6	5	0.63	0.53	$\chi^2 = 0.086$, $df = 1$, $P = 0.769$
Sisian area	123.3	1	0	0.08	0	$\chi^2 = 0.800$, $df = 1$, $P = 0.371$
Total	596.1	30	19			

The maximum diameter of scat was measured in site with a caliper to an accuracy of 0.05 mm. Some scats collected in winter contained plant material (grass and juniper needles). They were excluded from analysis, because plant pigments and fiber have an effect on the concentration of fecal bile acids (Quinn and Jackman, 1994).

TLC analysis was performed by the method developed by Cazon and Suhring (1999) specifically for analyzing scats of wild cats. Samples were placed in plastic bags with silica gel and stored until complete desiccation. Thereafter, the material was ground into powder in a porcelain mortar, and a 1-g aliquot of the powder was suspended in 20 ml of a benzene–methanol mixture (1 : 1) and incubated at room temperature for 3 h with constant stirring. The mixture was filtered, evaporated to a final volume of 5 ml, and the resulting solution (40 μl) was applied onto a $60F_{254}$ TLC plate (Merck, Germany) coated with a 0.2-mm silica gel layer. The chromatogram was developed in a toluene–acetic acid–water mixture (5 : 5 : 1.5), air dried, and visualized in a mixture of anisealdehyde and glacial acetic and concentrated sulfuric acids (0.5 : 50 :1). The plate was then examined to record the color and intensity of bile acid bands. Bile acid standards were chromatographed together with test samples in order to calculate the *Rf* values (the ratio between the distances of bile acid and solvent migration on the plate) and to perform a comparative analysis of the TLC profiles of all samples. To estimate intra- and interspecific variation in the TLC profiles of bile acids, each sample after drying and grinding was divided into several 1-g aliquots (one to three, depending on its size), which were analyzed independently.

Data were processed statistically using standard χ^2 test and Student's *t*-test (Quinn and Keough, 2002).

RESULTS

The analysis of samples weathered for 30 days did not reveal any significant effect of weather and air temperature on the effectiveness of TLC and the structure of chromatographic profiles.

Scats of the leopard, lynx, and wolf proved to differ in the profiles of fecal bile acids (Fig. 2). In the leopard, it was characterized by high contents of deoxycholic acid (*Rf* = 0.23, yellowish brown band) and chenodeoxycholic acid (*Rf* = 0.23, light purple band) and a medium content of dehydrocholic acid (*Rf* = 0.30, reddish band). The first two bands adjoined each other and partially overlapped, with the zone of overlap having a

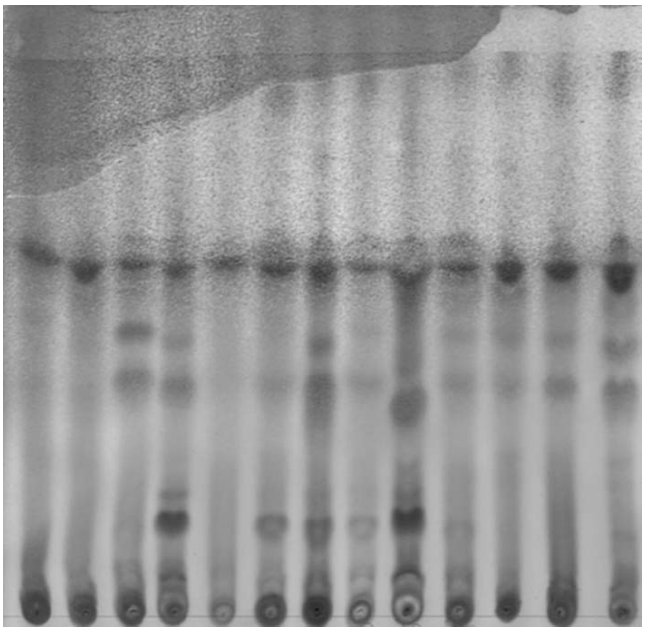

Fig. 2. TLC profiles of fecal bile acids from (*1*) leopard, (*2*) lynx, and (*3*) wolf scats collected in nature.

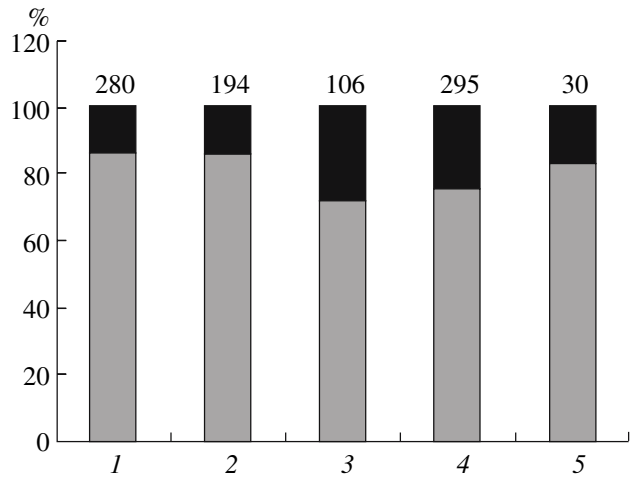

Fig. 3. Comparative data on success (gray areas) versus failure (black areas) in identification of wild cats by means of TLC in different studies: (*1*) *Panthera onca* and *Puma concolor* (Taber et al., 1997); (*2*) *Panthera onca* and *Puma concolor* (Fernandez et al., 1997); (*3*) *Puma concolor* and *Lynx rufus* (Johnson et al., 1984); (*4*) a community of African rainforest carnivores, including *Panthera pardus* and *Profelis aurata* (Ray, 1996; Ray and Sunquist, 2001); and (*5*) *Panthera* pardus, Lynx lynx, and *Canis lupus* (this study). Figures above bars show the number of samples studied.

greenish tint. In lynx scats, deoxycholic and chenodeoxycholic acids were at medium levels, while the content of dehydrocholic acid was slightly higher. Wolf scats contained a large amount of unidentified bile acid ($Rf = 0.64$) and relatively small amounts of deoxycholic and dehydrocholic acids. A distinct cholesterol band ($Rf = 0.58$) was found in all chromatograms.

Table 1 shows the results of species identification of scats collected in nature ($n = 30$). Leopard scats were found mainly in the Nuvadi-Shvanidzor area, in the eastern part of the Meghri Ridge, and fewer samples came also from its eastern and central parts and from the Central and Khachadzor districts of the Khosrov Reserve. Lynx and wolf scats were collected in two areas of the Meghri Ridge but not in the Khosrov Reserve. In 16.7% of samples, the concentrations of bile acids were insufficient for their reliable species identification by TLC.

Leopard, wolf, and lynx scats hardly differed from each other in a number of parameters, primarily in their maximum diameter, although it is regarded as the most conservative and specific for the leopard (Ray and Sunquist, 2001). The difference in weight between scats of the leopard, lynx (6.5 ± 2.7 g) and wolf (4.3 ± 1.2 g) was nonsignificant ($P > 0.1$). Unidentified samples weighed more than leopard scats, 8.3 ± 1.6 vs. 5.0 ± 0.8 g, with the difference being statistically significant ($t = -1.83$, $df = 22$; $P < 0.05$) The maximum diameters of leopard scats (2.8 ± 0.1 cm), lynx scats (2.7 ± 0.0 cm), wolf scats (2.6 ± 0.1 cm), and unidentified scats (2.8 ± 0.1 cm) did not differ statistically ($P > 0.1$). According to the scale of dummy variables for the age of scats (1, fresh; 0.5, relatively fresh; 0, old), the samples of leopard, lynx, and wolf scats (0.9 ± 0.0, 0.9 ± 0.1, and 0.8 ± 0.3, respectively) were fresher than unidentified samples (0.5 ± 0.2), but the difference lacked statistical significance ($P > 0.05$). Likewise, elevations at which these scats were found did not differ significantly: leopard, 1471.4 ± 126.6 m a.s.l.; lynx, 1540.0 ± 312.0 m; wolf, 1621.0 ± 714.0 m; and unidentified species, 1507.8 ± 310.1 m ($P > 0.1$).

DISCUSSION

The approach used in this study has shown that the use of TLC for the analysis of leopard, lynx, and wolf scats allows successful identification of these species, which inhabit the same mountain areas in Armenia. Scats of each species contain increased concentrations of a certain bile acid, namely, deoxycholic acid in the leopard, dehydrocholic acid in the lynx, and an unidentified acid ($Rf = 0.64$) in the wolf. A high content of deoxycholic acid in leopard scats has been noted previously (Ray, 1996; Ray and Sunquist, 2001).

In our study, the TLC method proved to be 83.3% effective, which corresponds to its effectiveness observed in other studies on scats of wild cats, irrespective of the number of samples (Fig. 3). Failure in species identification of scats is usually explained by an insufficient size of samples or their weathering (Ray, 1996). In our study, however, unidentified samples exceeded identified samples in weight, and a comparative analysis of fresh and artificially weathered samples did not reveal any significant differences between the corresponding TLC profiles of bile acids. Likewise, the age of scats collected in nature was not a critical factor, as the unidentified group included two old, one relatively fresh, and two fresh samples. Apparently, leopard scats may naturally contain low concentrations of bile acids, as is the case with the puma (*Puma concolor*), a morphologically and ecologically close species (Johnson et al., 1984).

The results of TLC analysis allow us to estimate the reliability of visual identification of leopard scats. In this study, all cases of erroneous attribution of lynx and wolf scats to the leopard (revealed by subsequent TLC analysis) concern samples from two areas of the Meghri Ridge. All samples from the Khosrov Reserve (except for one unidentified sample) have proved to be leopard scats, although the lynx and wolf are more abundant in the reserve than on the Meghri Ridge. A probable explanation is that the feeding niches and habitats used by these predators in the Khosrov Reserve virtually do not overlap: the leopard's main prey is the bezoar goat *C. aegagrus*, the wolf preys on wild boar and livestock, and the lynx hunts European hares (*Lepus europaeus*) and rodents (Khorozyan and Malkhasyan, 2002). The wolf and lynx are common species in the reserve due to the abundance of their prey, whereas the leopard is very rare, as the local wild

goat population is endangered because of poaching and habitat loss. On the Meghri Ridge, the leopard preys on the bezoar goat, Indian porcupine (*Hystrix indica*), wild boar, and roe deer; the wolf preys mainly on wild boar; and the lynx, on roe deer. Thus, these predators include the same species in their diets and share the same habitats, including trails, which increases the probability of errors in visual identification of their scats.

The relative abundance index of leopard was calculated for each area on the basis of visual and TLC identification of scats. The results obtained by either method were compared, and differences between them proved to be statistically nonsignificant (Table 2). On this basis, we conclude that visual identification of leopard scats is sufficiently reliable and can be effectively used in field studies.

Fresh leopard scats (identified both visually and by TLC) occurred most frequently in the Nuvadi-Shvanidzor area and in the Central and Khachadzor districts of the Khosrov Reserve. Apparently, these areas are permanently inhabited by the leopard and, therefore, should have a priority status with respect to the conservation of this species in Armenia.

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REFERENCES

Capurro, A.F., Novaro, A.J., Travaini, A., and Romero, M.S., Improved Bile-Acid Thin-Layer Chromatography to Identify Feces of Neotropical Carnivores, *J. Wildl. Manag.*, 1997, vol. 61, pp. 1424–1427.

Cazon, A. and Suhring, S.S., A Technique for Extraction and Thin Layer Chromatography Visualization of Fecal Bile Acids Applied to Neotropical Felid Scats, *Rev. Biol. Trop.*, 1999, vol. 47, pp. 245–249.

Dalen, L., Gotherstrom, A., and Angerbjorn, A., Identifying Species from Pieces of Faeces, *Conserv. Genet.*, 2004, vol. 5, pp. 109–111.

Dinnik, N.Ya., *Zveri Kavkaza. Ch. II. Khishchnye* (Caucasian Mammals. Part II: Carnivores), Tiflis: Tipografiya K.P. Kozlovskogo, 1914.

Fernandez, G.J., Corley, J.C., and Capurro, A.F., Identification of Cougar and Jaguar Feces through Bile Acid Chromatography, *J. Wildl. Manag.,* 1997, vol. 61, pp. 506–510.

Geptner, V.G. and Sludskii, A.A., *Mlekopitayushchie Sovetskogo Soyuza. T. 2. Ch. 2. Khishchnye (gieny i koshki)* [Mammals of the Soviet Union, vol. 2, part 2: Carnivores (Hyenas and Cats)], Moscow: Vysshaya Shkola, 1972.

Harrison, R., A Comparison of Detector Dogs, Hair Snares, Cameras, and Scent Stations for Detection of Bobcats, *Cat News*, 2006, vol. 44, pp. 20–22.

Henschel, P. and Ray, J., *Leopards in African Rainforests: Survey and Monitoring Techniques*, Washington, DC: WCS Global Carnivore Program, 2003.

Jimenez, J.E., Yanez, J.L., and Jaksic, F.M., Inability of Thin-Layer Chromatography to Distinguish Feces from Congeneric Foxes by Their Bile Acid Contents, *Acta Theriol.*, 1996, vol. 41, pp. 211–215.

Johnson, M.K., Belden, R.C., and Aldred, D.R., Differentiating Mountain Lion and Bobcat Scats, *J. Wildl. Manag.*, 1984, vol. 48, pp. 239–244.

Karanth, K.U. and Kumar, N.S., Field Surveys: Assessing Relative Abundances of Tigers and Prey, in *Monitoring Tigers and Their Prey*, Karanth, K.U.. and Nichols, J.D., Eds., Bangalore: Centre for Wildlife Studies, 2002, pp. 71–87.

Khorozyan, I., Habitat Preferences by the Endangered Persian Leopard (*Panthera pardus saxicolor* Pocock, 1927) in Armenia, *Zool. Middle East*, 2003, vol. 30, pp. 25–36.

Khorozyan, I.G. and Abramov, A.V., *Spatial Structure of the Persian Leopard Population and Aspects of Its Conservation in Armenia*, in *Mlekopitayushchie gornykh territorii* (Mammals of Mountain Areas), Rozhnov, V.V. and Tembotova, F.A., Eds., Moscow: KMK, 2005, pp. 199–202.

Khorozyan, I. and Malkhasyan, A., Ecology of the Leopard (*Panthera pardus*) in Khosrov Reserve, Armenia: Implications for Conservation, *Sci. Rep. Zool. Soc. "La Torbiera,"* 2002, vol. 6, pp. 1–41.

Khorozyan, I., Malkhasyan, A., and Asmaryan, S., The Persian Leopard Prowls Its Way to Survival, *End. Spec. Update*, 2005, vol. 22, pp. 51–60.

Kohn, M.H. and Wayne, R.K., Facts from Feces Revisited, *Trends Ecol. Evol.*, 1997, vol. 12, pp. 223–227.

Kotov, V.A. and Ryabov, L.S., Commercially Valuable Mammals of Piedmont and Mountain Regions of Krasnodar Krai, *Tr. Kavkaz. Gos. Zap.*, 1963, no. 7, pp. 3–226.

Lukarevsky, V.S., *Leopard, polosataya giena i volk v Turkmenistane* (Leopard, Striped Hyena, and Wolf in Turkmenistan), Moscow: Signar, 2001.

Lukarevsky, V., Askerov, E., and Hazaryan, G., Condition of the Leopard Population in the Caucasus, *Beitr. Jagd- und Wildf.*, 2004, vol. 29, pp. 305–319.

Major, M., Johnson, M.K., Davis, W.S., and Kellogg, T.F., Identifying Scats by Recovery of Bile Acids, *J. Wildl. Manag.*, 1980, vol. 44, pp. 290–293.

Monfort, S.L., Non-Invasive Endocrine Measures of Reproduction and Stress in Wild Populations, in *Reproduction and Integrated Conservation Science*, Wildt, D.E., Holt, W., and Packard, A., Eds., Cambridge: Cambridge Univ. Press, 2003, pp. 147–165.

Nagata, J., Aramilev, V.V., Belozor, A., et al., Fecal Genetic Analysis Using PCR–RFLP of Cytochrome B to Identify Sympatric Carnivores, the Tiger *Panthera tigris* and the Leopard *Panthera pardus*, in Far Eastern Russia, *Conserv. Genet.*, 2005, vol. 6, pp. 863–866.

Nasimovich, A., Leopard in the Western Caucasus, *Prir. Sots. Khoz.*, 1941, no. 8, pp. 260–265.

Penzikov, Yu.A., Last Leopards in the Karachai-Cherkess Republic, *Priroda*, 1986, no. 3, p. 96.

Prugh, L.R. and Ritland, C.E., Molecular Testing of Observer Identification of Carnivore Feces in the Field, *Wildl. Soc. Bull.*, 2005, vol. 33, pp. 189–194.

Putman, R.J., Facts from Faeces, *Mammal. Rev.*, 1984, vol. 14, pp. 79–97.

Quinn, T. and Jackman, W.R., Influence of Diet on Detection of Fecal Bile Acids by Thin-Layer Chromatography, *J. Wildl. Manag.*, 1994, vol. 58, pp. 295–299.

Quinn, G.P. and Keough, M.J., *Experimental Design and Data Analysis for Biologists*, Cambridge: Cambridge Univ. Press, 2002.

Ray, J.C., Resource Use Patterns among Mongooses and Other Carnivores in a Central African Rainforest, *Ph.D. Dissertation*, Gainesville: Univ. of Florida, 1996.

Ray, J.C. and Sunquist, M.E., Trophic Relations in a Community of African Rainforest Carnivores, *Oecologia*, 2001, vol. 127, pp. 395–408.

Sludskii, A.A., Distribution and Abundance of Wild Cats in the Soviet Union, *Tr. Inst. Zool. Akad. Nauk KazSSR*, 1973, no. 34, pp. 5–106.

Smith, D.A., Ralls, K., Davenport, B., et al., Canine Assistants for Conservationists, *Science*, 2001, vol. 291, p. 435.

Spasskaya, T. and Saidalieva, M., The Leopard in Dagestan, *Okhota Okhotn. Khoz.*, 1983, no. 12, p. 10.

Taber, A.B., Novaro, A.J., Neris, N., and Colman, F.H., The Food Habits of Sympatric Jaguar and Puma in the Paraguayan Chaco, *Biotropica*, 1997, vol. 29, pp. 204–213.

Vereshchagin, N.K., *Mlekopitayushchie Kavkaza. Istoriya formirovaniya fauny* (Mammals of the Caucasus: History of Fauna Formation), Moscow: Akad. Nauk SSSR, 1959.