ORIGINAL ARTICLE

Presence–absence surveys of prey and their use in predicting leopard (*Panthera pardus*) densities: a case study from Armenia

Igor G. KHOROZYAN[1], Alexander G. MALKHASYAN[2] and Alexei V. ABRAMOV[1]

[1]Zoological Institute, Russian Academy of Sciences, St Petersburg, Russia and [2]Ministry of Nature Protection of the Republic of Armenia, Yerevan, Armenia.

Abstract

It is important to predict how many individuals of a predator species can survive in a given area on the basis of prey sufficiency and to compare predictive estimates with actual numbers to understand whether or not key threats are related to prey availability. Rugged terrain and low detection probabilities do not allow for the use of traditional prey count techniques in mountain areas. We used presence–absence occupancy modeling and camera-trapping to estimate the abundance and densities of prey species and regression analysis to predict leopard (*Panthera pardus*) densities from estimated prey biomass in the mountains of the Nuvadi area, Meghri Ridge, southern Armenia. The prey densities were 12.94 ± 2.18 individuals km^{-2} for the bezoar goat (*Capra aegagrus*), 6.88 ± 1.56 for the wild boar (*Sus scrofa*) and 0.44 ± 0.20 for the roe deer (*Capreolus capreolus*). The detection probability of the prey was a strong function of the activity patterns, and was highest in diurnal bezoar goats (0.59 ± 0.09). Based on robust regression, the estimated total ungulate prey biomass (720.37 ± 142.72 kg km^{-2}) can support a leopard density of 7.18 ± 3.06 individuals 100 km^{-2}. The actual leopard density is only 0.34 individuals 100 km^{-2} (i.e. one subadult male recorded over the 296.9 km^2), estimated from tracking and camera-trapping. The most plausible explanation for this discrepancy between predicted and actual leopard density is that poaching and disturbance caused by livestock breeding, plant gathering, deforestation and human-induced wild fires are affecting the leopard population in Armenia.

Key words: Armenia, leopard, linear regression, presence–absence, prey.

INTRODUCTION

Populations of predators, particularly obligatory meat-eating wild cats (Carnivora, Felidae), depend on prey resources. Predator–prey relationships are so finely tuned that data on prey availability can be used to reliably predict predator densities and abundance (Oli 1994; Stander *et al.* 1997; Fuller & Sievert 2001; Carbone & Gittleman 2002; Karanth *et al.* 2004; Hetherington & Gorman 2007). The use of poorly detectable prey or an incomplete spectrum of prey for predictions might underestimate predator densities; thus, a full prey base should be taken into account as much as possible (Gros *et al.* 1996).

Prey scarcity affects felids by decreasing the proportion of productive females, delaying the age of first reproduction, reducing litter size, increasing offspring and adult mortalities, expanding home ranges, intensifying movements and increasing the numbers of transients and dispersing individuals – all of which worsen facets of vi-

Correspondence: Igor G. Khorozyan, Mashtots Ave. 48/17, Yerevan 0009, Armenia. Email: leopard_am@yahoo.com
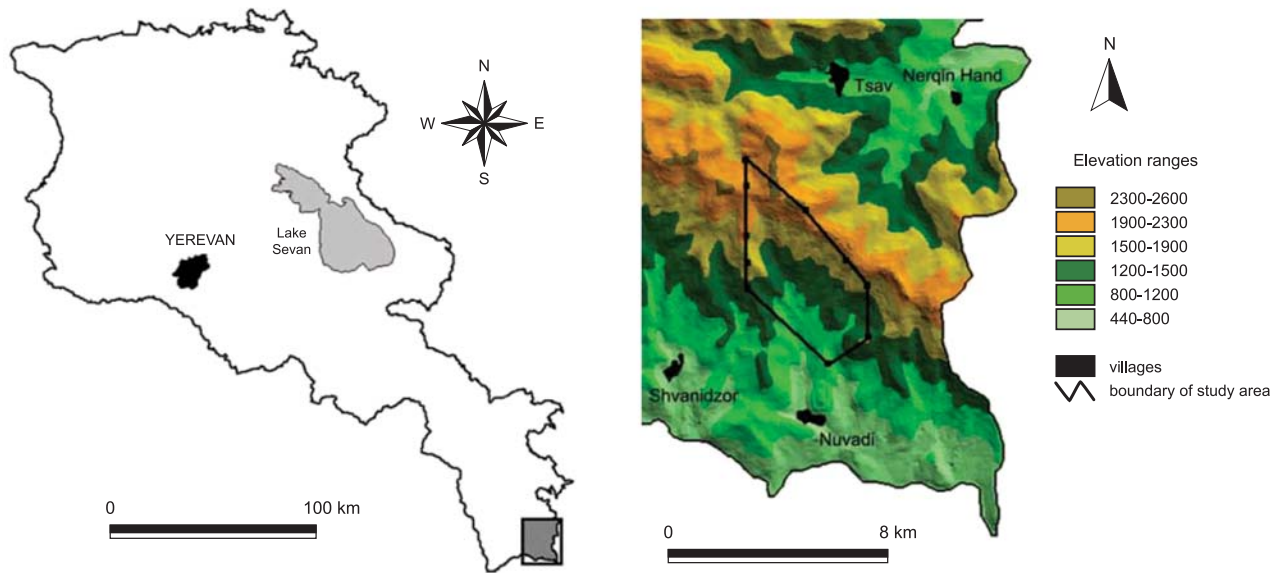
Figure 1 Location of the study area in the extreme south of Armenia.

ability (Fuller & Sievert 2001). Prey abundance is the key factor determining the structure of female home ranges, whereas availability of females is most important for male home ranges (Stander *et al.* 1997). Thus, prey abundance determines felid requirements in space. However, space itself is also an important factor because solitary life and the generally exclusive home ranges of same sex individuals in most felids force their populations to occupy large tracts of good habitats above some threshold to maintain viability. For example, leopard (*Panthera pardus* L., 1758) populations require a minimum threshold value of 412 km^2 to remain viable (Smallwood 2001). This is why small and densely populated countries have problems in maintaining viable leopard populations, even though prey densities can be high in some areas (Shoemaker 1993).

It is important to predict how many individuals of *P. pardus* can survive in a given area on the basis of prey sufficiency and to compare predictive estimates with the actual number on the ground. If the predicted carrying capacity significantly exceeds the actual abundance, then factors other than prey availability might play a key role in determining felid densities, for example, human-caused mortalities or habitat loss (Woodroffe 2001). However, even in this case cats are likely to be more susceptible to dwindling prey resources than to direct human effects because they are able to withstand quite high human densities under favorable conservation and management policies (Karanth & Stith 1999; Linnell *et al.* 2001). Interspecific

competition is another possible cause of lower predator densities, but prey availability is again regarded as a priority determinant (Laurenson *et al.* 1995).

The leopard population in Armenia is critically endangered, numbering no more than 10–15 individuals, and is at least partially dependent on immigrations from northern Iran (Khorozyan *et al.* 2005). Whether this small population size is a result of natural or human factors has never been examined. Prey scarcity might be one of the most likely reasons of leopard rarity in Armenia. To test this hypothesis, it would be reasonable to assess the biomass of the key prey species, predict leopard densities from the leopard density–prey biomass relationships and compare the predicted and actual leopard densities.

The goal of the present study was to compare the predicted and actual density and abundance of endangered leopards in the Nuvadi area, which is a priority leopard conservation area in southern Armenia. We achieved this by: (i) estimating the density, abundance and biomass of the key prey species, bezoar goat (*Capra aegagrus* Erxleben, 1777), wild boar (*Sus scrofa* L., 1758) and roe deer (*Capreolus capreolus* L., 1758), through direct observations, presence–absence modeling and photo-capture rates; and (ii) predicting leopard abundance and density from total prey biomass and comparing it with the actual density/abundance obtained from camera-trapping and tracking.

MATERIALS AND METHODS

Field surveys were conducted in a 25 km^2 plot to the north of the Nuvadi village on the Meghri Ridge, in the extreme south of Armenia, from May 2006 to March 2007 (Fig. 1). This area, spanning from 39°01' N to 38°56' N and from 46°24' E to 46°28' E, has been the wildest part of the entire 296.9 km^2 block of the Nuvadi area, which is designated as a priority leopard conservation area, where all trails used by wildlife intersect. The terrain is very rough, rocky and mountainous, and is covered mostly with xerophilous juniper (*Juniperus* spp.) sparse forest and, in the deep canyons, with dense shrubs and patches of mesophilous broadleaf forest. In the south, sparse forest changes to arid grassland. The boundary of the study plot was defined by lines connecting the outermost survey and camera-trap station points.

Multiple presence–absence surveys represented 30 daily routes (2–15 per site) walked during nine survey periods along the wildlife trails on mountaintops and in gorges. As the surveys were independent, surveys during which we detected animals did not affect the directions of subsequent surveys. Direct detections, that is, observations and vocalizations of the leopard's staple prey species (bezoar goat, wild boar and roe deer) were documented and the cluster size, sex/age composition, time and location were fixed by a GPS Magellan 310 (Magellan Navigation Inc., San Dimas, CA, USA). All cases of possible double-counts of the same individuals were recorded. A cluster was considered to be a group of individuals of a species observed together (Pérez *et al.* 2002; Lannoy *et al.* 2003). The study area consisted of four sites, each represented by two to five localities. The sites were large enough to assume population closure (no movements in and out of the localities during the study, as found from regular prey monitoring), which is essential for presence–absence modeling using PRESENCE 2.0 software (Hines 2006). We chose the sites on the basis of their topographic distinctness, assuming independence for the studied species, and that species known *a priori* to be common should be surveyed more intensively over fewer sites than vice versa (MacKenzie & Royle 2005; MacKenzie *et al.* 2006).

Prey density (D_{prey}, individuals km^{-2}) was calculated as:

$$D_{prey} = \frac{N_{prey}}{A} = \frac{1}{A}\left(\sum_{i=1}^{n}\frac{C_i}{p_i}\right) \qquad (1)$$

where N_{prey} is the prey abundance (individuals), A is the size of the study area (km^2), C_i is the count statistic, that is, the number of directly detected (observed or heard) individuals of the species in the i-th survey, and p_i is the detection probability deriving from direct detections in the same i-th survey (MacKenzie *et al.* 2005, 2006). In our case, $n = 30$ surveys and $A = 25$ km^2. The minimum and maximum values of C_i were assigned as if all individuals of the same sex/age category detected in the same place were counted repeatedly and once, respectively.

The detection probability was estimated using the single-season subprogram of PRESENCE 2.0 (Hines 2006). In the input spreadsheet, we inserted '1' if the species was detected in a given survey, '0' if it was not detected and '–' if no survey was conducted. We ran seven pre-defined models that considered p_i as either constant or survey specific across the arbitrarily chosen 1–3 groups with different p_i values in them, or we considered p_i to be heterogeneous because of variation in species abundance among sites (Table 1; MacKenzie *et al.* 2006). Goodness-of-fit of the best model was tested using the overdispersion parameter $\hat{c}$ calculated in the PRESENCE 2.0 output (MacKenzie & Bailey 2004).

In the single-season subprogram we also obtained the naïve and actual estimates of site occupancy by prey. The naïve estimate indicates the ratio of the number of sites with detections to the number of all surveyed sites, assuming that non-detections are equivalent to true absence. The actual estimate indicates the ratio of the number of sites with detections to the number of all surveyed sites while non-detections indicate non-detections at presence (false absence) and true absence. The subprogram was run with 15 000 bootstraps, with at least 10 000 required for the best performance (D. I. MacKenzie, unpublished data). The best output models were those that had the lowest value of Akaike's Information Criterion (AIC) and the highest AIC weight (≤1).

To estimate the number of surveys (n_{power}) required to reach the desired probability of detecting ≥1 individual of a prey species in the study area ($power_{area}$), we used Eqns 2 and 3:

$$power_{area} = 1 - (1 - p_i)^n \qquad (2)$$

$$n_{power} = \frac{\log_{10}(1 - power_{area})}{\log_{10}(1 - p_i)} \qquad (3)$$

where p_i is the detection probability deriving from direct detections in the i-th survey (see Eqn 1) and n is the number of surveys (Stauffer *et al.* 2002). We set $power_{area}$ at 90% or 0.9 (Fig. 2).
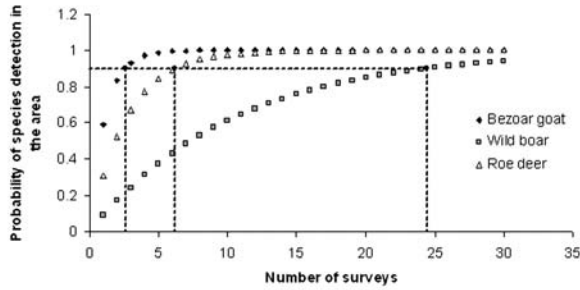
Figure 2 Distribution of the probabilities of detecting at least one individual (*power_area*) of the bezoar goat (*Capra aegagrus*), wild boar (*Sus scrofa*) and roe deer (*Capreolus capreolus*) in the study area in relation to the numbers of surveys (*n_power*).

Camera trapping took place in the same study area from August 2006 to April 2007 and comprised eight sampling occasions. Initially, we used 26 units of DeerCam DC-300 passive photo-traps (Non Typical, Park Falls, WI, USA); however, we used 24 units in October 2006 to January 2007 and six units in January to April 2007. As camera-trapping was targeted to capture leopards and then to identify them by matching spot patterns on flanks, we set up the devices as two units per camera-trap station, positioned up to 20 m apart on the opposite sides of the trail to photograph both flanks of each animal. The units were mounted mostly on trees, and some on boulders. The locations of the camera stations were not stationary and the stations were moved down from an altitude of 1964.6 ± 120.8 m (mean ± standard error [SE]) for the first sampling occasion (August–October 2006) to 1169.3 ± 66.7 m for the sixth–eighth occasions (January–April 2007), following animal migrations down to the foothills in response to deep snow at higher elevations. Films that shot more than 10 frames during a sampling occasion were removed, developed and printed, and new films were placed into the cameras. The devices were set for a camera delay of 30 s (normal sensor sensitivity) and the date and time were printed on the pictures.

The sampling effort for the camera-trapping was 4188 trap nights. We obtained 543 pictures of 13 mammalian species. We identified a species in each picture, recorded the time and date, and registered it as either a dependent or independent capture. We defined independent captures as: (i) consecutive photographs of different individuals of the same or different species; (ii) consecutive photographs of individuals of the same species taken more than 0.5 h apart by the same photo-trap or two traps at the same camera station; and (iii) non-consecutive photos of indi-

viduals of the same species (O'Brien *et al.* 2003). We measured overall sampling effort (in trap-nights) as the sum of nights that all units were exposed in the wild during the sampling occasions and calculated sampling efficiency (relative abundance index [RAI]) as the number of independent pictures of a species per 100 trap-nights (O'Brien *et al.* 2003; Mohd. Azlan & Sharma 2006).

Prey biomass (B_{prey}, kg km^{-2}) was calculated as:

$$B_{prey} = D_{prey}W_{prey} \qquad (4)$$

where W_{prey} is the average live body weight (kg) of the prey species (Lannoy *et al.* 2003). Values of W_{prey} were retrieved from previous studies and W of roe deer was assumed to be similar to that of red muntjac (*Muntiacus muntjak* Zimmermann, 1780) (Karanth & Sunquist 1995; Khorozyan & Malkhasyan 2002; Hayward *et al.* 2006). The biomass of another leopard prey species, the Indian porcupine (*Hystrix indica* Kerr, 1792), could not be calculated as described above because this rodent went undetected during our surveys as a result of its nocturnal and crepuscular life; however, this species was frequently camera-trapped. We examined the relationship between independently obtained values of B and RAI for the bezoar goat, wild boar and roe deer with the intention of using the relationship to predict porcupine biomass. We used a *t*-test and an ANOVA *F*-test to choose the best-fit regression model, with a statistically significant ($P < 0.05$) model fit, coefficient and intercept (Quinn & Keough 2002). We used the mean ± SE values of the equation coefficient and intercept to estimate B of the porcupine and we used Eqn 4 to calculate its D, using $W = 8$ kg (Karanth & Sunquist 1995).
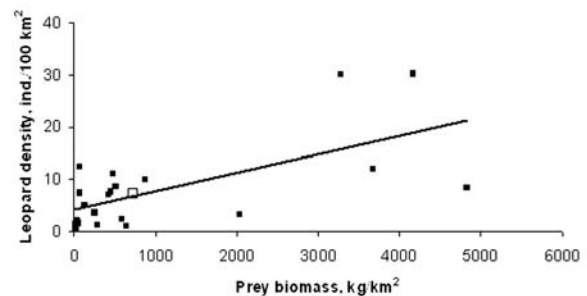

Figure 3 Linear relationship between total prey biomass and leopard (*Panthera pardus*) densities across the global range. The leopard density predicted in the present study is indicated by the white quadrat.

A database of leopard densities and prey biomasses (*n* = 21), kindly provided by C. Carbone (Institute of Zoology, London, UK), was used to predict leopard density from existing prey biomass in our study area. Most of this database was used as input data for Carbone and Gittleman (2002). The best-fit model was defined as shown above and by its comparison with reduced major axis regression (O'Brien *et al.* 2003). We used total biomass of the bezoar goat, wild boar and roe deer to predict leopard densities (individuals 100km^{-2}), taking the mean ± SE values of the equation coefficient and intercept and the lower and up-

per bounds of their 95% confidence intervals (Fig. 3).

Leopard numbers and density in the study plot were estimated from camera-trapping and from surveys of territorial marking behavior conducted in 2004 to 2007.

All statistical procedures were carried out in SPSS 13.0 (SPSS 2004) and MS Excel 2003 (Microsoft 2003) software.

RESULTS

The model implying constant probabilities of direct detection (p_i) across the surveys and sites and consider-

Table 1 Occupancy models developed for the bezoar goat (*Capra aegagrus*), wild boar (*Sus scrofa*) and roe deer (*Capreolus capreolus*) in the Nuvadi area, southern Armenia, using PRESENCE 2.0 software

Model	AIC	ΔAIC	AIC weight	Model likelihood
Bezoar goat				
One group, constant *p*	47.23	0.00	0.866	1.000
Two groups, constant *p*	51.23	4.00	0.117	0.135
Three groups, constant *p*	55.23	8.00	0.016	0.018
One group, survey-specific *p*	62.00	14.77	0.001	0.001
Abundance-induced heterogeneity	86.45	39.22	0.000	0.000
Two groups, survey-specific *p*	124.00	76.77	0.000	0.000
Three groups, survey-specific *p*	186.00	138.77	0.000	0.000
Wild boar				
One group, constant *p*	23.91	0.00	0.867	1.000
Two groups, constant *p*	27.91	4.00	0.117	0.135
Three groups, constant *p*	31.91	8.00	0.016	0.018
One group, survey-specific *p*	62.00	38.09	0.000	0.000
Two groups, survey-specific *p*	124.00	100.09	0.000	0.000
Abundance-induced heterogeneity	131.27	107.36	0.000	0.000
Three groups, survey-specific *p*	186.00	162.09	0.000	0.000
Roe deer				
One group, constant *p*	27.75	0.00	0.867	1.000
Two groups, constant *p*	31.75	4.00	0.117	0.135
Three groups, constant *p*	35.75	8.00	0.016	0.018
One group, survey-specific *p*	65.82	38.07	0.000	0.000
Abundance-induced heterogeneity	123.45	95.70	0.000	0.000
Two groups, survey-specific *p*	127.82	100.07	0.000	0.000
Three groups, survey-specific *p*	189.82	162.07	0.000	0.000

p, detection probability; AIC, Akaike's Information Criterion; ΔAIC, difference between the AIC of a given model and the minimum AIC.

ing all animals living within the study area as one group was the best-fit model of detection probability and occupancy of the bezoar goat, wild boar and roe deer (Table 1). The variation expected by the model was higher than the variation in the observed data ($\hat{c} < 1$), most likely because of the small number of surveyed sites. The other models had negligible fit (AIC weights ranging from 0.00 to 0.12) and were rejected; therefore, the weighted averaging technique of p and occupancy across the models were not used (Table 1). The population estimates derived from this model are shown in Table 2. Estimated prey densities and abundance were high in bezoar goat, medium in wild boar and low in roe deer. As the Indian porcupine was not detected during the surveys we assumed $p = 0$ for this species.

The value of n_{power} was very low in bezoar goat (2.58 surveys), intermediate in roe deer (6.21 surveys) and high in wild boar (24.41 surveys) (Fig. 2).

We obtained 416 independent pictures (76.6% of all) of the following mammals: wild boar (96 pictures, 23.1%), bezoar goat (76, 18.3%), red fox (*Vulpes vulpes* L., 1758) (72, 17.3%), European hare (*Lepus europaeus* Pallas, 1778) (48, 11.5%), gray wolf (*Canis lupus* L., 1758) (39, 9.4%), Indian porcupine (35, 8.5%), brown bear (*Ursus arctos* L., 1758) (25, 6.0%), jungle cat (*Felis chaus* Schreber, 1777)

(8, 1.9%), stone marten (*Martes foina* (Erxleben, 1777) (6, 1.4%), roe deer (5, 1.2%), Eurasian lynx (*Lynx lynx* (L., 1758) (3, 0.7%), wild cat (*Felis silvestris* Schreber, 1775) (2, 0.5) and leopard (1, 0.2%). The bezoar goat and wild boar were camera-trapped most commonly both in space and time and were captured on all sampling occasions (100%) and at $47.0 \pm 6.8\%$ (wild boar) and $52.6 \pm 5.1\%$ (bezoar goat) of the camera-trap stations across all occasions. The Indian porcupine was captured on 62.5% of occasions and at $17.5 \pm 5.7\%$ of the camera-trap stations, whereas the roe deer was captured on 50.0% of occasions and at $11.0 \pm 6.1\%$ of the camera-trap stations.

The bezoar goat is a diurnal species: 39% of the independent photo-captures were recorded in the morning (06: 00–12:00 hours), 41% in the daytime (12:00–18:00 hours) and 14% in the early evening (18:00–21:00 hours) ($n = 76$). The wild boar is crepuscular and nocturnal, but is also active on cool days: 17% of the independent photo-captures were recorded late in the day (15:00–18:00 hours), 50% in the evening (18:00–00:00 hours) and 29% at night (00:00–06:00 hours) ($n = 94$). The small sample size does not allow for any firm conclusions on the activity patterns of roe deer, but 60% of the captures were taken in the morning and during the day and 40% were taken in the evening ($n = 5$). The Indian porcupine is essentially noc-

Table 2 Population parameter estimates (mean ± standard error) of leopard ungulate prey species

Parameter	Bezoar goat	Wild boar	Roe deer
No. direct detections (observations and vocalizations)	54	2	5
No. photo-captures	76	96	5
Relative abundance index (no. independent pictures per 100 trap-nights)	1.81	2.29	0.12
Naïve estimate of occupancy	1.00	0.75	0.50
Estimate of actual occupancy	1.00 ± 0.00	1.00 ± 0.00	0.61 ± 0.29
Detection probability p_i derived from direct detections in a single survey	0.59 ± 0.09	0.09 ± 0.05	0.31 ± 0.12
Average live body weight W_{prey} (kg)	30	47	20
Biomass B_{prey} (kg km^{-2})	388.20 ± 65.40	323.37 ± 73.32	8.80 ± 4.00
Density D_{prey} (individuals km^{-2})	12.94 ± 2.18	6.88 ± 1.56	0.44 ± 0.20
Cluster size (individuals)	8.72 ± 0.94	9.00 ± 3.00	1.60 ± 0.24
Population size N_{prey} (individuals)	269-378	133-211	6-16

turnal and crepuscular: 14% of the independent photo-captures were recorded in the early morning (06:00–09:00 hours), 54% in the evening and 32% at night ($n = 35$).

Sampling efficiency or RAI was ranked among the prey species (Table 2). In the porcupine RAI = 0.84 independent pictures per 100 trap-nights.

The detection probabilities (p) of leopard prey species did not increase significantly with increases in their average live body weight W_{prey} ($R^2 = 0.03$; $R^2_{adj.} = -0.46$; $F_{1,2} = 0.06$; $P = 0.835$), principally because of the outlier point of the large-bodied, but hardly detectable, wild boar. p was strongly, linearly and positively correlated with the percentage of independent photo-captures of species taken at the survey time from 06:00 to 18:00 hours as an indicator of species diurnal activity and exposure to direct detection ($R^2 = 0.96$; $R^2_{adj.} = 0.94$; $F_{1,2} = 50.42$; $P = 0.019$). Actual occupancies of wild boar and roe deer were 33.3 and 22.0% larger, respectively, than the naïve estimates, probably because of their low to moderate detection probabilities (Table 2).

A strong relationship was found between ln-transformed prey biomass B (y) and prey RAI^{-1} (x): $y = (-0.472 \pm 0.026) x + (6.103 \pm 0.124)$; $R^2 = 0.99$; $R^2_{adj.} = 0.99$; $F_{1,1} = 338.94$; $P = 0.035$. Transforming RAI to the number of independent pictures per trap-night (RAI$_1$, variable x_1 is RAI$_1^{-1}$), we produced the equation: $y = (-0.005 \pm 0.000) x_1 + (6.103 \pm 0.124)$. The variable x_1 is the number of days required to take an animal photo-capture. Exponentiation of the x_1-equation shows that prey biomass is more or less constant regardless of x_1, so this regression model has poor predictive power and cannot be used to estimate Indian porcupine biomass. Therefore, we have estimated the total biomass of leopard prey as the sum of the biomasses of the bezoar goat, wild boar and roe deer, and the value obtained is 720.37 ± 142.72 kg km^{-2}.

Leopard density (y) is linearly and strongly correlated with total prey biomass (x): $y = (0.004 \pm 0.001) x + (4.146 \pm 1.759)$; $R^2 = 0.42$; $R^2_{adj.} = 0.39$; $F_{1,19} = 13.66$; $P = 0.002$ (Fig. 3). An increase in prey biomass by 1 kg km^{-2} adds 0.003–0.005 leopards 100 km^{-2} or, proportionally, leopard density increases by one individual when prey biomass is increased, on average, by 25 000 kg in the same 100 km^2 area. The leopard density predicted from the total prey biomass in our study area is 7.18 ± 3.06 (range 4.12–10.23) individuals 100 km^{-2}. The lower and upper bounds of the 95% confidence intervals of these estimates are 1.91 and 12.15, respectively. The reduced major axis regression equation was a bit steeper, $y = 0.005 x + 2.536$, but its coefficient and intercept did not differ statistically from those shown above ($\chi^2 = 0$, d.f. = 1, $P = 0.992$ and $\chi^2 = 0.388$,

d.f. = 1, $P = 0.533$), indicating the reliability of the equation in Fig. 3.

We obtained only one leopard photo-capture during the surveys (subadult non-resident male on 8 February 2007), and this sample size was insufficient to estimate predator density using capture–recapture technique. Prior to the present study, on 9 March 2005, we photo-trapped an adult resident male. Intensive tracking has shown that in 2004–2005 the study area was inhabited by one resident male (the photographed individual) and one resident female who actively moved and scraped the ground in the overlapping area during the mating season in winter. Then, in winter 2005–2006 the male left the territory of Armenia for the disputed lands adjacent to Nagorno–Karabakh and was killed. In late autumn 2005 his land tenure was taken over by a subadult male who came in from the west. He had not established his home range by early 2007 (no ground scraping was visible), but kept roaming around. No signs of the presence of any female leopards were found after 2004–2005.

DISCUSSION

Presence–absence modeling using the PRESENCE program is a new approach that has been used to estimate species' detection probabilities and occupancy and has been well verified for a number of taxa (MacKenzie *et al.* 2005, 2006; Linkie *et al.* 2007). However, presence–absence surveys and modeling have rarely been used in ungulates and, to the best of our knowledge, have never been used to assess their abundance as a key factor of predator viability (Tosh *et al.* 2004; MacKenzie *et al.* 2005, 2006; MacKenzie 2006). This technique appears to be an effective and cost-efficient way to estimate the abundance of ungulates and other prey, particularly in the mountains where traditional census approaches, such as line transects, do not work (Pérez *et al.* 2002). In light of the ever-increasing costs of wildlife research and conservation, inexpensive methods like this warrant special attention (Tosh *et al.* 2004).

Alternative methods are needed to detect crepuscular and nocturnal species, which are unlikely to be recorded during the surveys. Camera-trapping allows to estimate species abundance from the photographic rates if the relationship between these rates and abundance is proved by calibration of independent data as reliable. This approach broadens the applicability of camera-trapping to naturally unmarked animals that cannot be individualized from pictures and counted using mark–recapture techniques, particularly prey species (Carbone *et al.* 2001,

2002). Several other studies have also found a linear relationship between independently obtained values of species photo-capture rates and abundance (O'Brien *et al.* 2003; Silveira *et al.* 2003). Moreover, data from camera-trapping can be used for presence–absence modeling in PRESENCE (Linkie *et al.* 2007).

In the present study, the linear regression between photo-capture rates and the density of leopard prey species was statistically significant, but its predictive capacity was inadequate. Such a situation, that is, when statistical rigor does not prevent the appearance of implausible regression models, occurs quite often in wildlife science (Guthery & Bingham 2007), and was the reason why we did not estimate the density and abundance of the Indian porcupine, another important prey for leopards in Armenia.

In ungulates, and possibly in other mammals, predicted and actual densities often do not agree when species occupancies are low (Tosh *et al.* 2004). In our study, the three ungulate species had high occupancy levels so their abundance and biomass estimates should be regarded as accurate (Table 2).

The bezoar goat, wild boar, roe deer and Indian porcupine are the leopard's staple prey species on the Meghri Ridge in southern Armenia (Khorozyan & Malkhasyan 2005; Khorozyan *et al.* 2005, 2007; Lukarevsky *et al.* 2007). The bezoar goat and wild boar live in groups and have the highest biomasses and occupancies, and are the most common and widely occurring prey in the area. Roe deer are more solitary and rare because their favored habitat, humid broadleaf forest with dense shrubs, is patchy and available only in some places along the streams at the bottoms of the canyons. The Indian porcupine appears to be common and lives in small groups in localities with rocky outcrops and grottos.

The ungulate densities estimated in the present study are among the highest in the Nuvadi priority leopard conservation area and possibly in the entire Caucasus Ecoregion (Mallon *et al.* 2007). Our estimate of bezoar goat density is similar to that in the Avarskoe Koisu and Andiiskoe Koisu river basins, Daghestan, Russia's North Caucasus (8–17 individuals km^{-2}) and in the Kirthar National Park, Pakistan (11.8–16.3 individuals km^{-2}) and is much higher than elsewhere in the Caucasus (3.7 in the Urts Ridge, Armenia, and 0.65–0.87 individuals km^{-2} in the headwaters of the Chanty-Argun and Sharo-Argun rivers, Chechen Republic) (Dal 1951; Batkhiev 1989; Edge & Olson-Edge 1990; Weinberg 1999). However, none of these studies calculated detection probabilities to estimate actual abundance, so their density values could be underestimated (P. Weinberg, unpublished data). The population

size of bezoar goats in the Nuvadi area is close to the "guesstimate" made by local people (200–300 individuals; M. Boyajyan, unpublished data).

The probability of detecting these species using observations or vocalizations (barking of roe deer bucks) is constant within the species and directly proportional to the level of their diurnal activity, and therefore is highest in diurnal bezoar goats and lowest in nocturnal porcupines (Tables 1 and 2) In addition, the detection probabilities are not biased to large-bodied species, as suggested by Silveira *et al.* (2003).

False absence, that is, non-detection when present, is significant in roe deer and wild boar, which have moderate and low detection probabilities, respectively, but retain high occupancy. Non-detection is caused not only by their crepuscular life, but also by the fact that they live in dense bushes and forested areas, mostly in humid canyons. In contrast, cliff-dwelling bezoar goats are easier to detect, but can also be missed when they merge with the rocky background. The results can be summarized as follows: (i) real boar and roe deer occupancies are significantly greater than the naïve estimates, which assume only true absence and ignore false absence; (ii) many more surveys need to be conducted in the study area to detect one or more wild boars and roe deer (24 and six surveys, respectively) than one or more bezoar goats (≥two surveys) at 90% level of confidence (Fig. 2); and (iii) our findings confirm that habitat characteristics may impinge on wildlife detection probabilities, even in common species (Gu & Swihart 2004).

The relationship between leopard densities and prey abundance is strong and linear across their global range, but variation in prey biomass explains only 42% of variation in leopard densities, suggesting that alternative factors, such as human persecution, competition with other predators or habitat loss, could play a role in shaping the population size of this cat (Fig. 3; Hunter & Balme 2005). More research is needed to assess whether this linear regression levels off at high prey biomass, when further increases in leopard densities have to be regulated by intra-population social processes (Fuller & Sievert 2001).

It is logical to assume that the absence of prey leads to the absence of predators, so the no-intercept linear regression between leopard density and prey biomass would look biologically more meaningful than the full equation depicted in Fig. 3 (Guthery & Bingham 2007). Indeed, the full equation shows that leopard density in our study plot would reach 4.146 ± 1.759 individuals $100\ km^{-2}$ if prey biomass went down to zero. Nevertheless, we adhere to the full regression equation for two reasons. First, any no-intercept model involves subjective extrapolation of data

and assumes that the linear relationship between predictor and response varies beyond the range of observed data, surmising that the intercept does not statistically differ from zero (Quinn & Keough 2002). However, the intercept is often statistically different from zero, as in our case ($P = 0.029$). Second, when only the wild prey base is accounted for, as in our input database of leopard densities and prey biomass, its biomass might be reduced to zero, but the leopard will continue to survive because of a lag-effect and a switch to domestic livestock. However, densities of livestock-killing carnivores, including leopards, have been regulated by human persecution rather than by prey abundance (Lukarevsky 2001).

Camera-trapping revealed the presence of one leopard in 25 km² in 2006–2007 when prey surveys were conducted simultaneously. This value can be translated to four leopards 100 km⁻², which is at the lower end of the predicted leopard densities given the available prey resources. Meanwhile, intensive tracking surveys conducted over the entire 296.9 km² block of the Nuvadi area showed that this is a clear overestimate because there were no signs of other leopards in the area. Thus, adult leopards known to live here in previous years have disappeared (Khorozyan & Malkhasyan 2005).

The actual leopard density in the Nuvadi area is one individual per 296.9 km² or 0.34 leopards 100 km⁻². Why is it so low? Certainly, prey limitation is not a factor of concern because our prediction shows that the existing prey biomass is sufficient for the survival of 4–10 leopards 100 km⁻². As food availability is most important for female leopards which, in turn, determine the status of males (Stander *et al.* 1997), the locally available prey base is favorable for the formation of a core population consisting of resident females and males. The most plausible explanation for the population plight is that poaching and disturbance caused by livestock breeding, gathering of edible plants and mushrooms, deforestation and human-induced wild fires are so high that they exceed the tolerance limits of leopards (Khorozyan *et al.* 2005). The 80 km Kapan-Meghri motorway, which opened in October 2007, clears the way for poachers and other disturbances. This pressure could be counterbalanced by the government's plans to establish a national park, the Arevik National Park, on the Meghri Ridge, in the near future, which will include the Nuvadi priority leopard conservation area.

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