


ORIGINAL RESEARCH

Marmots from space: assessing population size and habitat use of a burrowing mammal using publicly available satellite images

Alyona Koshkina^{1,2} , Irina Grigoryeva^{2,3}, Viktor Tokarsky⁴, Ruslan Urazaliyev^{1,2}, Tobias Kuemmerle^{5,6}, Norbert Hölzel¹ & Johannes Kamp¹

¹Institute of Landscape Ecology, University of Münster, Heisenbergstr. 2, 48149, Münster, Germany

²Association for the Conservation of Biodiversity of Kazakhstan (ACBK), Beibitshilik 18, Office 406, 010000, Astana, Kazakhstan

³Karaganda State University named of E.A. Buketov, Universitetskaya 28, 100028, Karaganda, Kazakhstan

⁴V. N. Karazin Kharkiv National University, Kharkiv, Ukraine

⁵Geography Department, Humboldt University Berlin, Unter den Linden 6, 10099, Berlin, Germany

⁶Integrative Research Institute on Transformations in Human-Environment Systems (IRI THESys), Humboldt University Berlin, Unter den Linden 6, 10099, Berlin, Germany

Keywords

Agriculture, burrowing rodents, Eurasian steppe, farmland abandonment, population trend, post-Soviet land-use change, species distribution modelling

Correspondence

Alyona Koshkina, Institute of Landscape Ecology, University of Münster, Heisenbergstr. 2, 48149 Münster, Germany. Tel: +77719025576; Fax: +77172910044; E-mail: alyona.koshkina@acbk.kz

Editor: Ned Horning

Associate Editor: Margarita Mulero-Pazmany

Received: 17 April 2019; Revised: 1 November 2019; Accepted: 21 November 2019

doi: 10.1002/rse2.138

Remote Sensing in Ecology and Conservation 2020, **6** (2):153–167

Abstract

Social, burrowing mammals such as prairie dogs, ground squirrels or marmots are keystone species in grassland ecosystems. Grasslands have been converted into cropland or pastures globally, yet it remains virtually unknown how this has affected the biogeography of burrowing mammals, as efficient, broad-scale survey methods are lacking. We aimed to test whether structures created by burrowing rodents can be reliably detected on publicly available, very-high-resolution satellite images, in order to assess rodent distribution and abundance. We identified burrows of Bobak marmot (*Marmota bobak*), a keystone burrowing steppe rodent, on 1300 randomly selected plots of 1 km diameter (78.53 ha) across the species' range (~950 000 km²) in Kazakhstan and southern Russia using Google Earth and Bing images. We then used burrow occurrences and species distribution models to map marmot distribution. We assessed how marmot occurrence and density vary across land-use types. We also combined satellite-based burrow densities and ground-survey data to derive a new population estimate for the species across Kazakhstan. We mapped a total of 7425 burrows from the satellite imagery. Field visits at a subsample of burrows suggested that burrow occurrence was detected reliably. Broad-scale marmot distribution was mainly determined by summer rainfall, land use and elevation. Occurrence probability was highest on arable croplands, followed by abandoned croplands and grazed steppe. The current Bobak marmot population size for Kazakhstan was estimated at 6.1 (±2.4) million individuals. Our results demonstrate that publicly available, very-high-resolution images can be used to reliably map the distribution of burrowing mammals across large geographic scales. The observed and predicted distributions indicate that the Bobak's range has remained almost unchanged in Kazakhstan since the 1950s, despite several drastic episode of land-use change. This suggests that burrowing mammals can be remarkably resilient to land-use pressure, questioning prevailing narratives of population collapse in these species following agricultural expansion.

Introduction

Social, burrowing mammals shape and maintain grassland ecosystems globally (Dickman 1999; Zhang et al. 2003;

Davidson et al. 2012). Species such as prairie dogs (*Cynomys* spp.), pikas (*Ochtona* spp.), ground squirrels (*Spermophilina*) and marmots (*Marmota* spp.) are ecosystem engineers and keystone species in grasslands (Smith and

Foggin 1999; Davidson et al. 2012). They affect soil structure, increase soil drainage and turnover (Fleming et al. 2014) and influence nutrient cycling and plant productivity (Pang and Guo 2017). Burrowing mammals also increase landscape heterogeneity (Abaturov 1984; Davidson and Lightfoot 2007), and thereby regional plant and animal diversity (Ceballos et al. 1999; Davidson and Lightfoot 2008). Where burrowing mammals decline, important ecosystem processes such as soil turnover and water retention may be negatively affected, and multi-trophic interactions disturbed (James and Eldridge 2007; Fleming et al. 2014; Lacher et al. 2019). However, empirical work on burrowing mammals is usually restricted to small study sites, and it remains unclear what drives their distribution and abundance at biogeographic scales.

The lack of broad-scale studies on trends in distribution and abundance of burrowing mammals is worrying (Davidson et al. 2012), as many burrowing mammals are in decline, for example, Mongolian marmot (*Marmota sibirica*), European ground squirrel (*Spermophilus citellus*), Speckled ground squirrel (*Spermophilus suslicus*) and others (Shilova et al. 2010; Davidson et al. 2012). Most of the burrowing mammals are listed as “Least Concern” in the IUCN Red List, although many of these species experienced a significant decline in the past, such as Black-tailed prairie dog (*Cynomys ludovicianus*) or Bobak marmot (*Marmota bobak*), mainly due to overexploitation and habitat loss (Davidson et al. 2012; Hoogland 2013). Agricultural change is an underlying cause of both. The widespread conversion of grassland into cropland affects burrowing mammals through the direct destruction of their burrows (Davidson et al. 2012), a loss of food resources (Ceballos et al. 2010) and because these animals are often persecuted as crop pests (Delibes-Mateos et al. 2011). Livestock grazing can degrade habitat (Ceballos et al. 2010) and grassland rodents are often seen as competitors of grazing livestock (Derner et al. 2006). Conversion of grassland into cropland has been widespread (Song et al. 2018), and livestock breeding has transitioned from low-input to more intensive systems globally (Alexandratos and Bruinsma 2012). How these land-use changes have affected the distribution and abundance of burrowing mammals, however, remains poorly understood.

A key reason for this knowledge gap is that burrowing mammals are notoriously difficult to survey, as their ranges are typically very large (often >100 000 km², Soberón and Ceballos 2011). This means that field surveys are labour intensive and costly (Corlatti et al. 2017; Karaseva and Telitsyna 1996; Table S1). An alternative to field surveys is the use of aerial or satellite images to detect activity signs. Aerial photos were used to detect prairie dog settlements in the US (Dalsted et al. 1981). High-resolution satellite images can also detect prairie dog

colonies (Sidle et al. 2002). Even relatively coarse-scale Landsat images were useful for detecting Hairy-nosed wombat (*Lasiorhinus latifrons*) colonies in Australia (Löffler and Margules 1980), and vole and lemming activity was inferred from MODIS-based NDVI change analyses (Olofsson et al. 2012). The increasing availability of freely accessible, very-high-resolution images on internet platforms such as Google Earth has brought about new opportunities for broad-scale studies in this context. This imagery has been used to survey plant and amphibian habitat on rocky outcrops (Silva and Alves-Silva 2013), Elephant seal (*Mirounga leonina*) colonies (McMahon et al. 2014), termite mounds (Isabelle et al. 2014), wombat burrows in Australia (Swinbourne et al. 2018) and American beaver (*Castor canadensis*) range expansion in the Canadian Arctic (Tape et al. 2018). The potential of Google Earth images to detect burrows of marmots (*Marmota* spec.) was recognized early (Kolesnikov et al. 2011). While the mentioned studies highlight the potential of very-high-resolution images for assessing species distribution, habitat and populations, including burrowing rodents, they all focused on small sites. Approaches that leverage this potential to biogeographical scale (i.e. to areas of 100 000 km² or more) are missing.

We here aim to assess the usefulness of very-high-resolution satellite image archives to study the biogeography of social, burrowing mammals and how it is shaped by agricultural land use. As study species, we used the Bobak marmot (*M. bobak*), a keystone species of the Eurasian steppes (Zimina and Isakov 1980) that builds comparatively large mounds. Furthermore, the species occurs in a globally important and understudied hotspot of land-use change: the Eurasian steppes, a 4.1 million km² region stretching from Eastern Ukraine to the Altai Mountains that is especially rich in burrowing mammals (Wesche et al. 2016). Vast areas of the western Eurasian steppes have historically been converted into cropland. Conversion started in the 19th century, but was especially significant during the Soviet ‘*Virgin Land Campaign*’ from 1953 to 1960, when 35 million ha of steppe grassland were ploughed in Kazakhstan alone (Durgin 1962). These trends were partly reversed after the dissolution of the Soviet Union in 1991, when at least 42 million ha of cropland was abandoned across the western Eurasian steppes as a result of the withdrawal of state support for agriculture and massive rural outmigration (Dara et al. 2018; Lesiv et al. 2018a). In addition, livestock numbers collapsed after 1991, with declines of up to 80% in Kazakhstan (Kamp et al. 2011) and substantially changed grazing patterns (Kerven et al. 2006). Livestock ownership was privatized and nomadic movements ceased in most areas, resulting in a concentration of livestock around settlements (Kerven et al. 2016).

How these land-use changes shaped the distribution and abundance of marmots across the Eurasian steppes remains unclear, mainly due to a lack of broad-scale surveys. Strong declines in Bobak marmot populations in Ukraine and Western Russia were attributed to steppe conversion and overhunting (Sludsky 1969; Tokarsky 2011), but no study has quantified this. Against this background, we addressed the following research questions:

- 1 Can publicly available, very-high-resolution satellite images be used to map Bobak marmot burrows effectively and reliably?
- 2 What are the factors that determine the distribution of Bobak marmots at biogeographical scales, and how did recent land-use change affect the distribution and abundance of this species?
- 3 What is the range-wide population size of the Bobak marmot, as estimated with satellite-based methods?

Materials and Methods

Study region

Our study region was the current range of the eastern Bobak marmot (subspecies *shaganensis*) (Fig. 2A). The 950 000 km² area comprises northern and central Kazakhstan as well as southern Russia, and is part of the Palearctic steppe biome (Wesche et al. 2016). The climate is continental with very cold winters and short, warm summers: the mean temperature in Kazakhstan's capital Nur-Sultan is -16.5°C in January and $+20.7^{\circ}\text{C}$ in July. There is a strong latitudinal gradient of increasing aridity towards the south caused by declining mean annual precipitation (from *c.* 400 to *c.* 200 mm) and an increasing mean annual temperature (from *c.* 1.2°C in Petropavl to 4.6°C in Zhezkazgan). Dominant soil types are fertile, humus-rich Chernozems in the north and less fertile Kastanozems in the south (Beznosov and Uspanov 1960). Large areas in temporally wet depressions are only marginally suitable for agriculture, as these are dominated by alkaline Solonets or sandy soils (Beznosov and Uspanov 1960; Kraemer et al. 2015). The natural mesic to xeric steppes are dominated by *Stipa*, *Festuca*, *Koeleria* and *Agropyron*, with an increasing proportion of wormwood (*Artemisia*) towards the south (Brinkert et al. 2016).

Digitization of marmot burrows on satellite images

We digitized all visible marmot burrows across 1300 randomly selected circles (= sample plots) of 1 km diameter (78.53 ha), with a minimum distance of 10 km between

sample plots on Bing (www.bing.com/maps) and Google Earth (www.maps.google.com) imagery (Figs. 1 and 2A). Digitization took place from March to December 2016 and thus mirrors image availability at this time. We derived, via copyright labels, main providers of the Google Earth images and the associated satellites and their spatial resolution. These were Quickbird (0.65 m resolution, panchromatic), WorldView (0.31 m), CNES Pleiades 1A (0.7 m) and SPOT 6 and 7 (1.5 m) as well as SPOT 5 (2.5–5 m). We estimate that for *c.* 90% of the sample plots, we had images with a resolution of 2 m or higher. Marmot burrows are *c.* 4–10 m in diameter (i.e. the area covered by freshly excavated soil; the mound itself can be >20 m wide), and were thus detectable on all images we used. We used the open layer plugin in QGIS v2.16.2 and selected the most recent imagery, or that of higher resolution where multiple layers of images were available. We also collected the acquisition year and month of satellite images from metadata displayed in Google Earth. Generally, Kazakhstan was covered to a large extent with high-resolution imagery at the time we digitized the marmot burrows (Lesiv et al. 2018b). Metadata on acquisition month and year for the Bing images were collected from <https://mvxel.dev.openstreetmap.org/bing/>. The distribution of the acquisition year for all images used is provided in Figures S3 and S4. Sixty per cent of the available images were from the years 2012 and 2013, and 92% from the years 2010–2014 (Fig. 2A). We used only snow-free images.

We first randomly selected 1000 sample plots across the whole project area. After the presence of burrows was mapped in these plots, 300 additional sample plots were placed into the most densely settled area to increase the sample size at the upper end of the local densities. We sampled across the latest available map of the distribution range of the Bobak marmot from 1969 (Sludsky 1969; Tsytsulina et al. 2016), adding a 50-km buffer to allow for possible range extension since then (Fig. 2A).

Identification of marmot burrows was based on colony structure and shape, the size of mounds and inter-burrow distances as characteristic features (Vinogradov and Leontieva 1985; Rummyantsev 1989). Occupied Bobak marmot burrows in steppe are detectable on satellite images as light spots with sharp contours (Fig. 1). The area around the burrow entrance is usually paler than the surrounding land due to the extracted light-coloured soils and permanent removal of vegetation (Fig. S1). Abandoned colonies can be distinguished from active ones as the burrows appear as darker spots compared to the surrounding vegetation, due to the overgrowing of mounds with the vegetation that is usually different in composition and traits from the surrounding vegetation communities (Vinogradov and Leontieva 1985, Fig. S2).

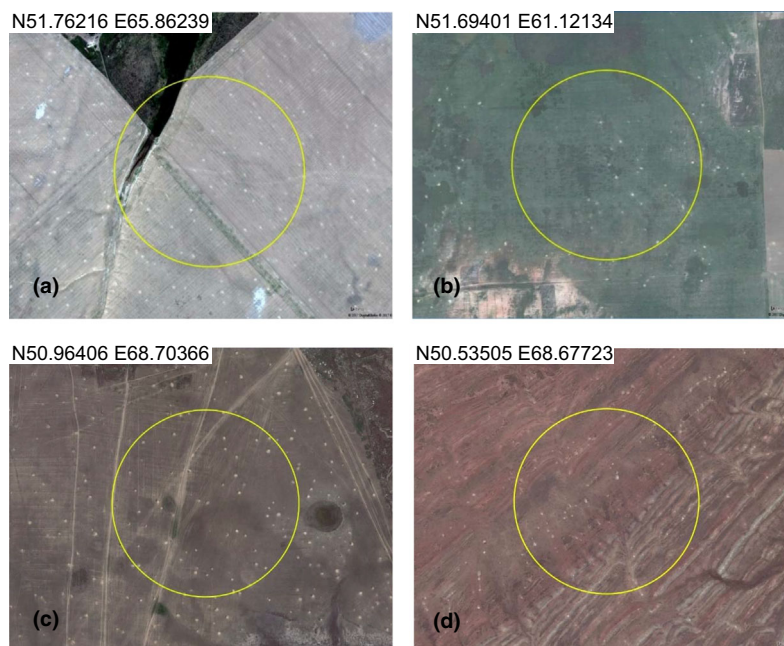


Figure 1. Examples of marmot burrows on (a) arable cropland, (b) abandoned cropland, (c) grazed steppe and (d) moderately or ungrazed steppe as visible on the high-resolution images. The circles represent sample plots of 78.53 ha each. Image scale is 1:9000.

Vinogradov and Leontieva (1985) classified marmot burrows by mound size into large (diameter >20 m), medium (10–20 m) and small (<10 m). Large and medium burrows are used as permanent burrows and for hibernation, whereas small burrows are temporary summer burrows (Vinogradov and Leontieva 1985). Small burrows may also not have a mound of bare ground and therefore may not be visible in our imagery. All sampling plots were inspected at an identical scale of 1:9000 to prevent over- and underestimation of marmot burrows presence and number due to varying image resolution. At this scale, used burrows should be readily visible (Vinogradov and Leontieva 1985, Fig. 1). We assume that the burrows we digitized corresponded mainly to permanently used burrows. The number of burrows was counted separately for each land-use type within the circle. For all sampling plots, we also estimated the dominating land-use type within a 5-km radius surrounding the sample plot (Fig. 1, Text S1). Three observers took part in the analysis, and the first author implemented a final consistency check across all 1300 plots.

Ground-truthing burrow detection success

Earlier work suggested that burrows are generally detectable on the type of imagery we used (Kolesnikov et al. 2011). Nevertheless, detection probability could vary with land cover (burrows on bare ground might be easier to

see on satellite images than burrows in denser vegetation), image characteristics and digitizing person. We therefore validated our satellite-based survey with field records of marmot occurrence. We obtained ad hoc, georeferenced records of marmot presence (occupied burrows) that were collected during wildlife surveys in central Kazakhstan between 2008 and 2015 ($n = 131$), the period for which many of satellite images were acquired (Figs. S3 and S4). In addition, during June 2017, we visited 29 sample plots in the field (including all major land-use types: 11 on arable croplands, 7 on abandoned croplands, 6 on grazed steppe and 5 on ungrazed steppe). Visiting a random sample of all sample plots was not feasible due to logistical constraints and the large extent of our study region, but plots were selected along major environmental gradients. We mapped all burrows with handheld GPS units along strip transects of 1 km length and 200 m width, dissecting each sample plot in the centre. This resulted in 330 field-recorded burrows, 79 on arable croplands, 135 on abandoned croplands, 63 on grazed steppe and 53 on ungrazed steppe. Six plots had no occupied burrows inside the plot, but colonies were recorded nearby. Five of these plots had experienced land-use changes in the previous years (new croplands, change of crops or intensification). We then compared the number of field-recorded burrows in the strip area to the number detected on the satellite image in the identical area to establish land-use-specific detection rates.

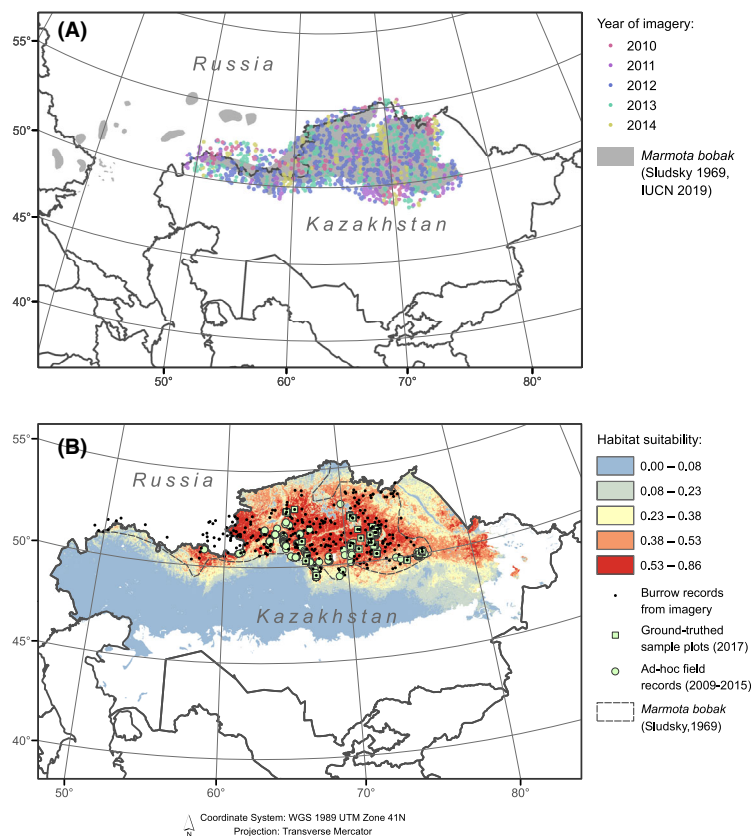


Figure 2. (A) Spatial distribution of the acquisition year of the satellite images used for digitizing burrow location and estimating fine-scale land use across the sampling area. Ninety-two per cent of all satellite images used were from the given years. Grey: IUCN range of *Marmota bobak* (Sludsky 1969; Tsyulina et al. 2016) with a contiguous distribution of *M. b. shaganensis* and fragmented populations of *M. b. bobak*. (B) Habitat suitability across Kazakhstan, based on a MaxEnt species distribution model. Sample plots with detected burrows, which were all used for model building ($n = 308$) are shown as black dots, and records from the two field data sources used for ground truthing are overplotted. The predicted distribution extends well beyond the known extent of occurrence of *M. bobak*. The areas predicted as being of high suitability are indeed inhabited by marmots, but by a different species (Gray Marmot, *Marmota baibacina*).

Evaluating sources of bias

The resolution of the available images could have increased over time as sensor technology improved. The resolution could also differ systematically between the two image sources, Google Earth and Bing. We therefore tested for a relationship of burrow occurrence and density with year, anticipating that if image resolution had increased systematically, burrow occurrence probability and abundance would have increased as well over time. We also modelled burrow occurrence and abundance as a function of image source. We used a binomial generalized linear model (GLM) with a logit link (with detection vs. non-detection as dependent variable), and a negative binomial GLM with a log link (with the number of burrows detected on satellite images as dependent variable). Models were fitted in R (v3.6.1). We assessed model fit with Nagelkerke's R^2 (Nagelkerke 1991). Predictive

performance was assessed with the area under the curve (AUC) of the receiver operating characteristic curve (ROC) packages '*fmsb*' [Nakazawa and Nakazawa 2014] and '*pROC*' [Robin et al. 2011]). For multimodel inference, we used Akaike's Information Criterion (AIC) and compared all models with up to four variables using the '*dredge*' function in the R package '*MuMIn*'. We considered models with $\Delta\text{-AIC} < 2$ as receiving good support from the data.

Predicting marmot distribution

To predict the broad-scale distribution of Bobak marmots, we used maximum entropy (MaxEnt) modelling (Phillips et al. 2004). As occurrence data, we used the 308 sample plots with detected marmot occurrence, irrespective of the number of burrows detected per sample plot. We used 11 predictors describing climate, land use/cover

(hereafter: land use), topography and vegetation productivity. We projected all layers to UTM zone 42N, aggregated to a common 1-km resolution (for details see Table S2), and clipped them to the area that was sampled for burrows (i.e. the latest available spatial extent-of-occurrence information). An overview of the predictor specifications is given in Table S2.

As our sampling plots were chosen at random, but not stratified according to the area of the land-use types, the sampling effort per land-use category was uneven. Uneven sampling effort can affect the prediction of maximum entropy models (Kramer-Schadt et al. 2013). To account for this, we used a sampling-bias grid (Fourcade et al. 2014). The grid was set up using a Gaussian Kernel Density technique implemented in the ArcGIS SDMtoolbox (Brown 2014). We fitted models using MaxEnt version 3.3.3k with only hinge features selected (Elith et al. 2010) and 5000 iterations, and used a 15-fold cross-validation and the AUC value to assess model fit. We then predicted areas suitable for marmots across our study area and converted the continuous MaxEnt output into binary maps of suitable versus unsuitable habitat, based on the maximum training sensitivity plus specificity threshold (Liu et al. 2013).

Marmot habitat selection in relation to land use

As marmot occurrence might vary within the coarse land-use types of our region-wide map (e.g. due to varying grazing intensity or soil type; Zimina and Isakov 1980; Savchenko and Ronkin 2018), we additionally assessed land-use types at the plot level. Key variables, such as fine-scaled land-use (e.g. grazing intensity and cropland abandonment), are not available as spatially exhaustive GIS layers. However, they might be important drivers of marmot occurrence and abundance at the scale our study was conducted. We therefore sampled these variables at the level of the sample plots.

For all sample plots that were used for burrow digitization, we visually estimated the proportion of arable cropland, abandoned cropland, grazed steppe, ungrazed steppe, hayfields, forest and wetlands across the plot area (Fig. 1, Text T1). We then used GLMs in the same framework as described above to relate marmot occurrence and abundance to this fine-scale land use. Marmots prefer certain soil types, and we therefore extracted soil type and soil texture for each plot based on 1:2 500 000 soil map (Beznosov and Uspanov 1960). Fire is an important driver of vegetation patterns in steppes and might influence marmot presence through changed vegetation structure (Collins and Calabrese 2012; Davidson et al. 2012). We therefore extracted fire frequency (i.e. the number of

times a plot had burned in 2001–2015), using the MODIS (MODerate resolution Imaging Spectroradiometer) burned area product (<http://modis-fire.umd.edu>). We added soil type and fire frequency as covariates to the GLMs.

Estimating Bobak marmot population size in Kazakhstan

Using our distributional map, burrow densities from the sample plots, and field data, we estimated the total population of Bobak marmots in Kazakhstan. First, the mean number of burrows per sample plot (\pm SE) detected on satellite images was calculated for each of the four main land-use classes ‘arable cropland’, ‘abandoned cropland’, ‘grazed steppe’ and ‘ungrazed steppe’ within the area sampled in Kazakhstan. We included unoccupied plots to correct for varying occupancy rates per land-use category (Table 2). We then corrected for the fact that not all burrows were detected on satellite images that were found during field surveys: we multiplied the mean number of burrows per sample plot with the mean proportion of burrows detected in the field per land-use type (Table 2). This yielded a corrected mean number of burrows per sample plot, separately for all land-use types (Table 2).

To arrive at a land-use-specific estimate of marmot abundance (and not only burrow numbers) per sample plot, we had to consider that each marmot family in our study area consists on average of three animals after hibernation (i.e. before reproduction; Kolesnikov 2011) and uses one wintering burrow and a number of permanent and non-permanent summer burrows (Bibikov 1989, Fig. S5). We established a land-use-specific mean number of burrows used by one family in the field based on the sample plots used for ground truthing through direct observations (Table 2). To estimate plot-specific numbers of individuals per land-use category, we multiplied the corrected number of burrows per sample plot by 3 (see above), and subsequently divided this figure by the mean number of burrows used per family ($n = 104$ studied family home ranges across the 29 sample plots), separately for each land-use type.

To obtain a final population estimate, we multiplied the mean marmot abundance per sample plot across all habitats with the area predicted as suitable across Kazakhstan (from the MaxEnt model, Fig. S6). We excluded a region predicted as suitable, but known to be inhabited by the Gray marmot (*M. baibacina*), not Bobak marmot (Sludsky 1969). We calculated the lower and upper bound of the population estimate by subtracting, respectively, adding, the standard errors to all means used in the calculation.

Results

Burrow detection

A total of 7425 marmot burrows were digitized over the 1300 sample plots. Burrows occurred on 20.6% of the plots. Across the unfragmented range in Kazakhstan, 6247 burrows were digitized over 941 sample plots, with a mean number of burrows of 24.6 (± 21.8 SD, range 1–150) per sample plot (Table 2). The number of burrows detected on identical sample plots by different digitizers was highly correlated, suggesting that plot detection is largely independent of observer ($n = 20$ plots, Spearman's $\rho = 0.910$, $P < 0.001$, Fig. 3).

No false negatives with respect to sample plots occurred, that is, no burrows were detected on sample plots that were classified as free of burrows on satellite images. All false positives were related to colonies abandoned due to the recent land-use change (where remnants of colonies, or occupied burrows were always found near the sample plot). There was a strong correlation between the number of burrows detected on satellite images and in the field ($n = 29$ plots, Spearman's $\rho = 0.892$, $P < 0.001$, Fig. 3) suggesting that marmot presence in a plot can be reliably identified on satellite images. However, only $39 \pm 24\%$ SD of the burrows recorded in the field were detected on satellite images, with variation across land-use types, suggesting many burrows are overlooked on satellite images (Fig. 3).

There was some evidence for an influence of image source and month (but not image year) on the detection of burrows, but model fit was poor. Satellite images from Bing were slightly more likely to have burrows detected compared to those from Google Earth (binomial GLM, $\beta = -0.254$, $P = 0.014$, $R_N^2 = 0.01$). Burrows were slightly

more likely to be detected on images taken in June to August than they were on images taken on other times of the year (binomial GLM with quadratic term fitted for month, $\beta_1 = -0.657 \pm 0.206$ SE, $\beta_2 = -0.043 \pm 0.206$ SE, $P = 0.022$, $R_N^2 = 0.01$). There was no evidence for an influence of image source, year or month on the density of detected burrows (negative binomial GLMs, image source: $\beta = -0.500 \pm 0.400$ SE, $P = 0.213$, $R_N^2 = 0.012$; month: $\beta = -0.002 \pm 0.054$ SE, $P = 0.963$, $R_N^2 = 0.0001$, year: $\beta = -0.025 \pm 0.068$ SE, $P = 0.719$, $R_N^2 = 0.0008$).

Broad-scale Bobak marmot distribution

Our MaxEnt models suggested that *c.* 44 million ha (58% of the total steppe area in Kazakhstan) are suitable for the Bobak marmot. The area predicted as suitable largely matched the historical distributional range of the species (Fig. 2B). The mean AUC for the MaxEnt models was 0.857 ± 0.029 SD, suggesting a good discriminatory ability. The most important variables in the MaxEnt model were summer rainfall, explaining 48.1% of the variation in marmot occurrence, followed by land-use type (18.1%) and elevation (16.8%) (Fig. S7). Both summer rainfall and elevation had hump-shaped relationships with marmot presence, peaking at *c.* 130 mm rainfall and 250 m elevation.

Bobak marmot occurrence and abundance in relation to land-use type

Our fine-scale GLM-based analyses showed that the single-best GLM explaining burrow occurrence contained land use (dominating land-use type inside the sample plot), soil type, soil texture and fire frequency, and had a fair discriminatory ability ($w_i = 0.808$, $R_N^2 = 0.289$, AUC = 0.797). Adding dominant land use around a

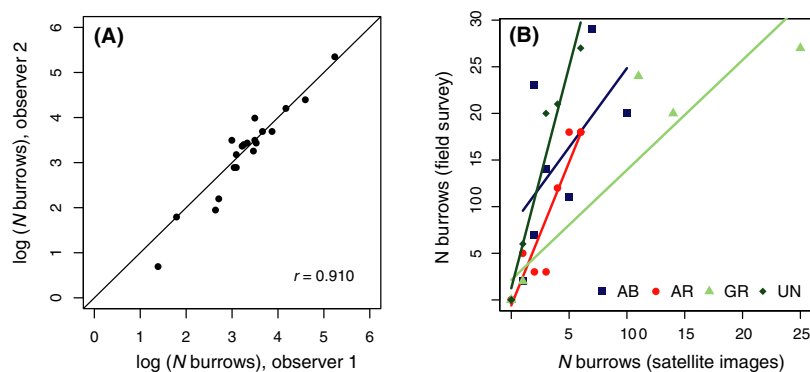


Figure 3. (A) Number of burrows digitized by two independent observers using 20 identical sample plots and (B) number of marmot burrows detected on satellite images compared with the number found on the ground, separately per habitat category for 29 sample plots. Lines are linear regressions fitted separately per land-use type (AR – arable cropland, AB – abandoned cropland, GR – grazed steppe, UN – ungrazed steppe).

sample plot as covariate considerably improved model fit ($\Delta\text{AIC} = 2.98$, $R_N^2 = 0.801$, $\text{AUC} = 0.801$). All other models performed substantially worse ($\Delta\text{AIC} > 8$, Table 1A). Occurrence probability was highest on arable cropland, followed by abandoned cropland and strongly grazed steppe, and lower on hayfields and moderately or ungrazed steppe. Occurrence probability was also higher at sample plots surrounded mainly by abandoned cropland (Fig. 4). Dark Kastanozems as well as southern Chernozems were preferred soil types. Marmots preferred loamy soil texture, and avoided sandy soils (Fig. 4). Burrow occurrence had a near-linear negative relationship with fire frequency, without an obvious threshold (Fig. 4). There was no clear evidence for an effect of land use, soil and fire regime on burrow density, with an intercept-only model performing best (Table 1B).

Bobak marmot population estimate

The mean number of burrows per sample plot (including unoccupied plots) as detected on satellite images varied from 3.8 in ungrazed steppe to 9.1 in arable cropland across Kazakhstan, and from 22.0 to 34.8 when unoccupied plots were excluded (Table 2). The mean number of burrows a family used was 5.2 based on field observations (Table 2). The estimated mean density of marmot individuals after hibernation ranged from 9.9 individuals/km² in grazed steppe to 18.6 individuals/km² on abandoned cropland, reflecting both genuine density differences and varying detection probability of burrows in different habitat types (Fig. 3). The total population estimated for Kazakhstan was 6.1 million individuals, with a lower bound of 4.4 million and an upper bound of 8.7 million.

This estimate is considerably higher than all previous, expert-based estimates since the 1950s (Fig. 5).

Discussion

Burrowing mammals are keystone species in steppes, but difficult to survey across large areas. Focussing on the Eurasian steppes, which have experienced drastic land-use changes recently, we here demonstrate how high-resolution satellite images can be used to assess distribution, habitat use and population size of burrowing steppe rodents at biogeographical scales. Using the Bobak marmot as an example, our analyses highlight that the mounds of larger burrowing rodents can be detected reliably on high-resolution satellite imagery. Across our study region, marmot distribution was mainly determined by summer rainfall, land use and elevation. The predicted range matched historical, expert-based extent-of-occurrence maps well, while providing substantially more spatial detail. Marmots were overall remarkably resilient to land-use change, despite major episodes of land-use change in the 20th century. We also found marmots to not only occur in steppes, with the species being most abundant on arable croplands, followed by abandoned croplands and grazed steppe. Combining our satellite-based and ground-based data yielded a new population estimate of 6.1 (± 2.4 SE) million individuals across Kazakhstan, which suggests marmots have not declined as much as previously assumed. More broadly, our analyses highlight how publicly available satellite images can help to provide important baseline data for understanding the ecology of steppe rodents and for conservation planning aimed at maintaining their key functional roles.

Table 1. GLMs relating (A) burrow detection (occurrence) on digitized satellite images and (B) burrow density (burrows/ha) in sample plots with burrows to habitat features

Model	Intercept	Land use	Surr. Land use	Soil type	Soil texture	Fire	df	LogLik	AIC	ΔAIC	w_i
(A)											
1	0.109	+		+	+	-0.352	19	-492.00	1022.70	0.00	0.808
2	0.202	+	+	+	+	-0.359	24	-488.28	1025.67	2.98	0.182
3	-1.133						1	-610.76	1223.52	200.82	0.000
$w_{+}(j)$		0.99	0.19	1.00	1.00	1.00					
(B)											
1	-1.045						2	-174.81	353.66	0.00	0.664
2	-1.009					-0.057	3	-174.69	355.47	1.81	0.269
5	-1.066	+					6	-174.00	360.32	6.65	0.024
$w_{+}(j)$	0.29	0.02	<0.01	<0.01	0.29	0.04					

For estimating occurrence, we fitted binomial GLMs with a logit link (logistic regression). For estimating abundance, we used negative binomial GLMs with a log link. Models are sorted by AIC, with + indicating that the variable was included in the model, and $w_{+}(j)$ indicating relative variable importance across all models. All models whose Akaike weights sum up to 0.95 are shown, as well as an intercept-only model for comparison. Variables are fire frequency (i.e. the number of fires in the period 2001–2015, “fire”), land use at the sample plot, dominating land in its surroundings (5 km around the sample plot), soil type and soil texture.

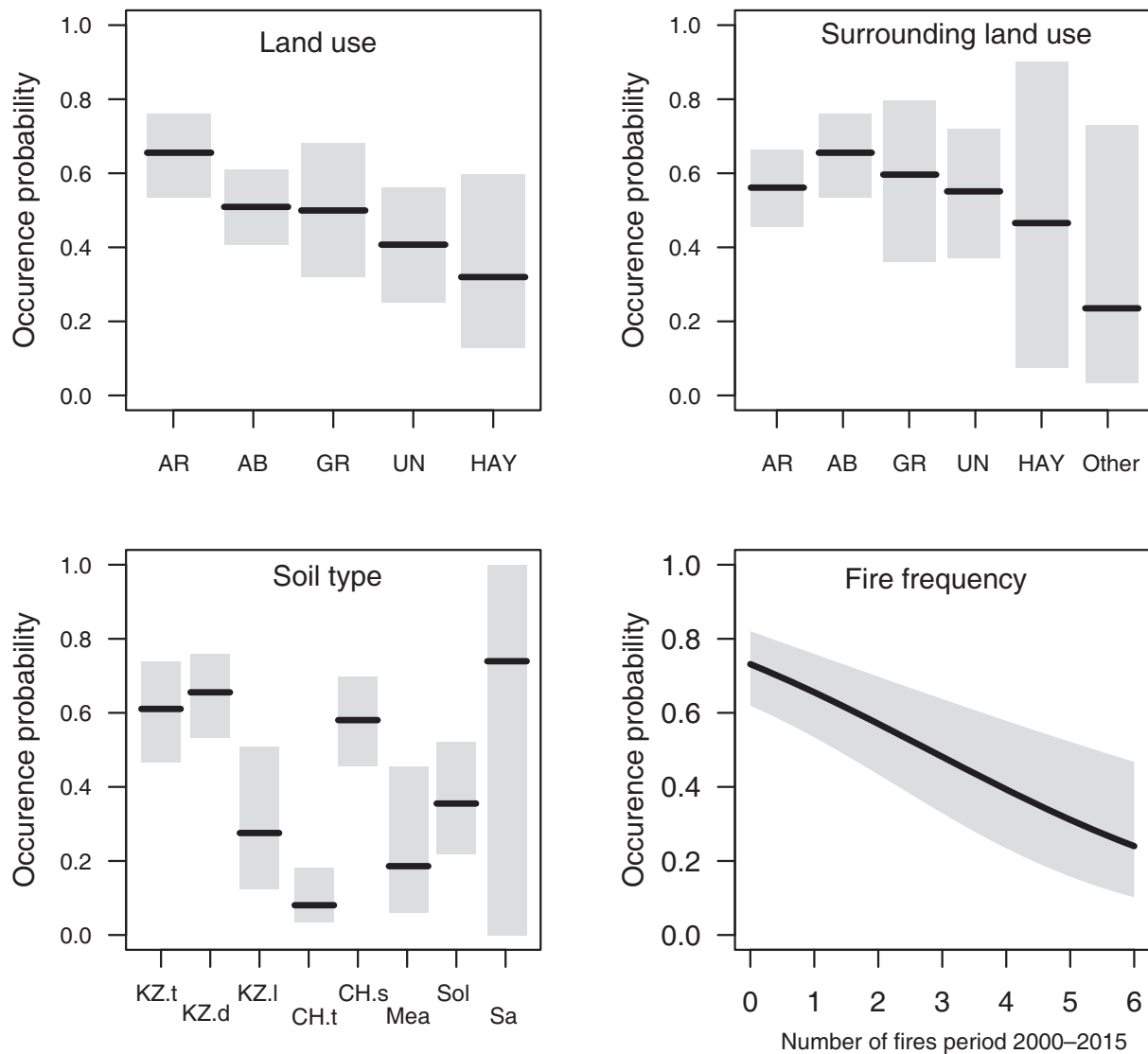


Figure 4. Predicted occurrence probability of marmot burrows using a binomial GLM with logit link. Fitted values ± 1 SE are plotted. Land-use types: AR – arable croplands (wheat), AB – abandoned croplands, GR – strongly grazed steppe, UN – ungrazed or moderately grazed steppe, HAY – hay fields; soil type abbreviations follow the Soviet classification: KZ.t – Typical Kastanozem, KZ.d – Dark Kastanozem, KZ.l – Light Kastanozem, CH.t – Typical Chernozem (Black Earth), CH.s – Southern Chernozem, Mea – Meadow Soil, Sol – Solonets soil, Sa – Sands.

Identifying marmot burrows from space worked remarkably well. Past attempts to use remote sensing images for mapping marmots and other burrowing rodents mainly relied on aerial photos and very small study sites (Vinogradov and Leontieva 1985; Sidle et al. 2002; Kolesnikov 2011), and we here show that such approaches can be scaled up to biogeographic scales. Importantly, image provider, acquisition time and observer did not significantly affect burrow detection. The resolution of Google Earth and Bing imagery was high enough to detect burrow presence, further emphasizing the potential to assess burrowing animals across large areas. Our satellite-based

approach was particularly powerful when combining the on-screen digitization of burrows on satellite images with a very limited field campaign, which allowed us to correct for detection probability (here *c.* 40%). Combining our approach with more detailed studies of colony structure, and perhaps using object-oriented algorithms to detect marmot burrows automatically as suggested by Kolesnikov (2011) may further improve accuracy and make studies even less labour intensive. Given that burrowing rodents with large mounds are common in all major grasslands of the world, our approach seems promising and might be readily transferred to other grassland systems.

Table 2. Key variables for explaining burrow occurrence and abundance in sample plots, separately for main land-use classes

Land-use classes	Sample size (digitized plots, area 0.79 km ²)	Proportion of digitized plots with burrows (occupancy rate)	Number of burrows per sample plot digitized from satellite images (mean ± SE)	Density of burrows per hectare as digitized from satellite images (mean ± SE)	Ratio burrow numbers on satellite images: burrows during field survey (detection rate)	Mean number of burrows/family based on the field survey ± SE
Abandoned cropland	216	0.32	7.12 ± 0.92	0.34 ± 0.40	0.33 ± 0.06	4.44 ± 0.84
Arable cropland	286	0.39	9.05 ± 0.92	0.31 ± 0.02	0.45 ± 0.11	4.88 ± 1.09
Grazed steppe	123	0.23	8.12 ± 1.86	0.45 ± 0.07	0.65 ± 0.11	4.81 ± 1.43
Ungrazed steppe	276	0.13	3.79 ± 0.93	0.40 ± 0.07	0.18 ± 0.02	6.75 ± 0.44
Average (mean ± SE)	225	0.27	6.85 ± 0.53	0.35 ± 0.02	0.40 ± 0.05	5.15 ± 0.48

Table includes only the data for four main land-use classes within the area of Kazakhstan. Variables that were used for the population estimate are marked in grey.

Yet, our study also highlighted a number of challenges for mapping burrowing rodents from space. First, burrows of different species could be confused (Swinbourne et al. 2018), although the field campaign suggested that this was not a problem in our case. The only similar structures on the Kazakh steppe are created by large ground squirrels (e.g. *Spermophilus fulvus*), but inter-burrow distances were lower and the mound of bare soils much smaller in ground squirrels (Fig. S8). Second, detectability of burrows varied across land-use types. Although this was not a problem for assessing marmot presence, this variation highlights the value for additional ground data for going beyond occurrence predictions to estimate abundance. Third, marmot colonies might be unoccupied due to recent hunting or disease events.

Including recently abandoned colonies would possibly lead to an overestimation of distribution and population size, but our field visits suggested that abandoned burrows are very scarce. Recently abandoned burrows show less contrast to the surrounding vegetation and a blurred outline (Vinogradov and Leontieva 1985). Old abandoned burrows are normally even darker than the surrounding vegetation (Vinogradov and Leontieva 1985, Fig. S2). In contrast, occupied burrows appear bright due to the excavated soil (Fig. S2). Therefore, occupancy rates can be estimated reliably if up-to-date imagery is available.

The satellite images that we used for digitization were mainly acquired between 2010 and 2016, with the vast majority from 2012 and 2013 (Figs. S3 and S4). While this period matches well the time period for which our field data were collected, it is considerably earlier than the time of the targeted ground-truth survey in 2017. It is therefore possible that during on-screen digitization, burrows that were abandoned between 2012 and 2016 were included. On the contrary, the higher number of burrows detected in the field compared to the satellite images might indicate that new burrows were built between image acquisition and on-screen digitization. However, marmots are known to use burrows over decades (Zimina and Isakov 1980). Building a new, large nesting burrow is energy-demanding, and young individuals would usually occupy old burrows when starting their own family or refurbish existing ones. An experimental comparison of Corona spy satellite images from the 1960s shows that many burrow locations have indeed remained unchanged for at least 45 years (Munteanu et al. submitted). It is very rare that permanent burrows are newly created, and the burrows we missed were likely mainly smaller, secondary burrows.

The distribution of the Bobak marmot appears to be mainly governed by climate variables, especially summer rainfall, as well as land use and elevation. Higher elevations with stony soils and lower and wet depressions with

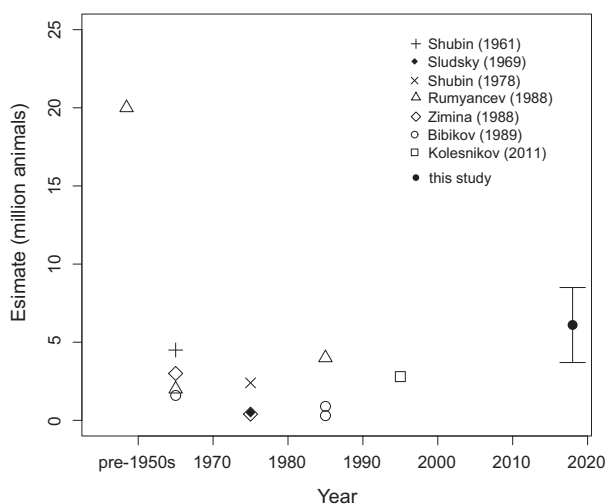


Figure 5. Published, range-wide population estimates for the Bobak marmot since the 1950s and the new estimate from this study. Note that the current estimate was calculated for Kazakhstan only, but that >95% of all Bobak marmots are currently found in Kazakhstan.

a risk of inundation are avoided. This is well in line with prior, more fine-scaled studies (Bibikov 1989). A preference of elevated terrain has also been shown for close marmot relatives such as ground squirrels (Barker and Derocher 2010) and might be associated with their burrowing activity. Many burrowing mammals are distributed in areas with harsh continental climate with cold winters and/or hot arid summers, and gain body mass before hibernation to cope with these conditions (Davidson et al. 2012; Armitage 2013). Nutrient availability prior to long hibernation periods determines the survival of these species through winter probably stronger than predation (Van Horne 2007). In cold, (semi-) arid grasslands, such as the steppes of Kazakhstan, where plant growth is limited to a few months, summer precipitation determines vegetation productivity and therefore influences winter survival of small mammals (Abaturov 1984).

Both our observed range (based on screen digitized and field data) and modelled range (based on species distribution modelling) suggested that the Bobak marmot's range has remained almost unchanged in Kazakhstan since the 1950s. The species disappeared only from the most northern areas, where steppe grasslands have almost disappeared and cropland use is most intensive in Kazakhstan (Dietrich et al. 2012; Dara et al. 2018). This range stability is remarkable given the several drastic episodes of land-use change, most notably the expansion of highly mechanized agriculture, during Soviet times. In fact, Bobak marmot presence was highest on managed and abandoned cropland, not in natural steppes. This might be explained by the generally high site fidelity in social, burrowing rodents (Hare et al. 2007; Van Horne 2007). Furthermore, farming in the steppe region of Kazakhstan is less intensive than in other parts of the world. Fields are rarely ploughed, no-till or minimal till is applied almost everywhere and pesticide use is minimal (Dietrich et al. 2012; Kamp et al. 2015). This likely resulted in a higher persistence of burrows and provided marmots with more nutrient-rich fodder in the form of ruderal arable weeds, which are preferred over crops even in wheat fields (Bibikov 1991; Rummyantsev 1991). However, the fact that occurrence probability was highest on plots with close proximity to abandoned croplands suggests that some proportion of (semi-)natural habitats in the landscape has a positive effect on marmot survival, especially after tillage and an associated shortage in weeds in spring (Bibikov 1991; Rummyantsev 1991). Finally, a factor contributing to the persistence of Bobak marmots is that the species in this region has no significant negative impact on crop yields (Bibikov 1991) and is therefore not persecuted as a pest (Bibikov 1989).

Altogether, this suggests that the Bobak marmot in Kazakhstan was fairly resilient to land-use change, both

the conversion of steppe into cropland during Soviet times and the abandonment of cropland after the break-up of the Soviet Union. While studies on the impact of agricultural land-use change on social, burrowing mammals are scarce (Bibikov 1989; Davidson et al. 2012), they typically suggest a detrimental impact of land-use change. For example, while ground squirrels can survive on croplands and even cause significant crop damage (Feldhamer et al. 2003), their populations often become fragmented and decline after agricultural expansion (Van Horne 2007) and associated persecution (Hoogland 2013). The conditions that allowed the Bobak marmot to persist in croplands for decades are likely to change in the near future though. The currently observed intensification of cropping, with increased herbicide use and an ongoing replacement of outdated Soviet machinery with modern agricultural equipment (Kamp et al. 2011) will cause a reduction in cover of ruderal plants and might negatively impact marmots and other burrowing rodents, possibly leading to the disappearance of colonies. Given that abandoned croplands support a significant part of Bobak population, the ongoing reclamation and recultivation of abandoned cropland (Dara et al. 2018) will result in increasing pressure on Bobak, and might affect colonies in neighbouring croplands. Moreover, wildfires and grazing can significantly alter the habitat of burrowing mammals (Detling 2006; Davidson et al. 2010; Savchenko and Ronkin 2018) and fires have been increasing recently (Dara et al. 2019). On steppes and abandoned fields, frequent fires are likely to result in denser and taller swards, as grasses are favoured over dwarf shrub when stands burn frequently (Dubinin et al. 2011; Collins and Calabrese 2012). This might affect small mammals as approaching predators are more difficult to spot and escape is more difficult in taller vegetation (Hoogland 2013).

We here present a new population estimate that is significantly higher than all previous estimates since the 1960s, suggesting a recovering Bobak population since the 1980s (Fig. 4) after the steep decline in the 1950s. The historic decline was mainly caused by habitat loss and persecution for fur, meat and fat (Bibikov 1989). A recovery might be linked to relaxing hunting pressure. Hunting bags decreased strongly after the break-up of the Soviet Union (Bibikov 1989; Ministry of Agriculture of Kazakhstan 2016). As the area of abandoned cropland within 5 km of a sample plot was an important predictor of marmot occurrence, another reason for an apparent population recovery might be the large-scale abandonment of cropland that allowed marmots to access more productive, "weedy" vegetation. This would be especially important early in the season, as wheat is not sown before mid-May, 1 month after marmots leave their burrows after hibernation (Sludsky 1969). Alternatively, the discrepancy

in estimates might be driven by the use of different mapping methods. Previous estimates were largely based on field surveys with extrapolation over the large areas, or hunting statistics (Bibikov 1989), while the use of satellite imagery and random sampling allows covering all habitats, including those of limited access for terrestrial surveys. Although the uncertainty is considerable, we suggest that the new estimate can be used as a baseline for future population monitoring, and for estimating sustainable hunting quota.

The impact of agriculture on the world's grasslands will likely increase in the future (Alexandratos and Bruinsma 2012; Meyfroidt et al. 2016), with manifold and likely negative consequences for burrowing mammals. We have shown that structures created by burrowing mammals can be reliably mapped with publicly available satellite images in order to assess the distribution, habitat use and abundance of these animals. This suggests our method can contribute to an improved monitoring and management of these keystone species for steppes. As the coverage and availability of free, high-resolution satellite images increases and archives are constantly growing, our approach should be transferable to many burrowing mammals with a sufficient size of burrows and mounds and has considerable potential to track changes in their distributions and populations over large area and back in time.

Acknowledgements

We thank Benjamin Ullrich, Andrey Ateasov, Darya Derr and Baurzhan Isakov for help with fieldwork and digitization. Vadim Kapitonov and Sergey Sklyarenko provided valuable comments on an earlier draft of this article. We are grateful to the National Centre of Space Research and Technologies in Almaty for digitizing the soil map of Kazakhstan, and to Ingrid Stirnemann for producing the fire frequency map. The study was funded by the Volkswagen Foundation, project BALTRAK (Project Ref-No. A112025). We are grateful to two reviewers and the handling editor Ned Horning for very constructive and helpful comments on a previous manuscript version.

Data Accessibility

The raw data are available as Supporting Online Material.

References

Abaturov, B. D. 1984. Mammals as component of ecosystems (on the example of herbivorous mammals in semi-deserts). Nauka (in Russian).

- Alexandratos, N., and J. Bruinsma 2012. World agriculture towards 2030/2050: the 2012 revision. ESA Working paper FAO, Rome.
- Armitage, K. 2013. Climate change and the conservation of marmots. *Nat. Sci.* **5**(5A), 36–43.
- Barker, O. E., and A. E. Derocher. 2010. Habitat selection by arctic ground squirrels (*Spermophilus parryii*). *J. Mammal.* **91**, 1251–1260.
- Beznosov, A., and U. Uspanov 1960. Soils of KazSSR. Academy of Science KazUSSR (in Russian).
- Bibikov, D. I. 1989. Marmots. Agropromizdat (in Russian).
- Bibikov, D. I. 1991. The steppe marmot - its past and future. *Oryx* **25**, 45–49.
- Brinkert, A., N. Hölzel, T. V. Sidorova, and J. Kamp. 2016. Spontaneous steppe restoration on abandoned cropland in Kazakhstan: grazing affects successional pathways. *Biodivers. Conserv.* **25**, 2543–2561.
- Brown, J. L. 2014. SDM toolbox: a python-based GIS toolkit for landscape genetic, biogeographic and species distribution model analyses. *Methods Ecol. Evol.* **5**, 694–700.
- Ceballos, G., J. Pacheco, and R. List. 1999. Influence of prairie dogs (*Cynomys ludovicianus*) on habitat heterogeneity and mammalian diversity in Mexico. *J. Arid Environ.* **41**, 161–172.
- Ceballos, G., A. Davidson, R. List, J. Pacheco, P. Manzano-Fischer, G. Santos-Barrera, et al. 2010. Rapid decline of a grassland system and its ecological and conservation implications. *PLoS ONE* **5**, e8562.
- Collins, S. L., and L. B. Calabrese. 2012. Effects of fire, grazing and topographic variation on vegetation structure in tallgrass prairie. *J. Veg. Sci.* **23**, 563–575.
- Corlatti, L., L. Nelli, M. Bertolini, F. Zibordi, and L. Pedrotti. 2017. A comparison of four different methods to estimate population size of Alpine marmot (*Marmota marmota*). *Hystrix* **28**, 61–67.
- Dalsted, K. J., S. Sather-Blair, B. K. Worcester, and R. Klukas. 1981. Application of remote sensing to prairie dog management. *J. Range Manag.* **34**, 218–223.
- Dara, A., M. Baumann, T. Kuemmerle, D. Pflugmacher, A. Rabe, P. Griffiths, et al. 2018. Mapping the timing of cropland abandonment and recultivation in northern Kazakhstan using annual Landsat time series. *Remote Sens. Environ.* **213**, 49–60.
- Dara, A., M. Baumann, N. Hölzel, P. Hostert, J. Kamp, D. Müller, et al. 2019 (in press). Post-Soviet land-use change affected fire regimes on the Eurasian steppes. *Ecosystems*, 1–14. <https://doi.org/10.1007/s10021-019-00447-w>.
- Davidson, A. D., and D. C. Lightfoot. 2007. Interactive effects of keystone rodents on the structure of desert grassland arthropod communities. *Ecography* **30**, 515–525.
- Davidson, A. D., and D. C. Lightfoot. 2008. Burrowing rodents increase landscape heterogeneity in a desert grassland. *J. Arid Environ.* **72**, 1133–1145.
- Davidson, A. D., E. Ponce, D. C. Lightfoot, E. L. Fredrickson, J. H. Brown, J. Cruzado, et al. 2010. Rapid response of a

- grassland ecosystem to an experimental manipulation of a keystone rodent and domestic livestock. *Ecology* **91**, 3189–3200.
- Davidson, A. D., J. K. Detling, and J. H. Brown. 2012. Ecological roles and conservation challenges of social, burrowing, herbivorous mammals in the world's grasslands. *Front. Ecol. Environ.* **10**, 477–486.
- Delibes-Mateos, M., A. T. Smith, C. N. Slobodchikoff, and J. E. Swenson. 2011. The paradox of keystone species persecuted as pests: a call for the conservation of abundant small mammals in their native range. *Biol. Conserv.* **144**, 1335–1346.
- Derner, J. D., J. K. Detling, and M. F. Antolin. 2006. Are livestock weight gains affected by black-tailed prairie dogs? *Front. Ecol. Environ.* **4**, 459–464.
- Detling, J. K. 2006. Do prairie dogs compete with livestock? Pp. 65–88 in J. L. Hoogland, ed. *Conservation of the black-tailed prairie dog: saving North America's western grasslands*. Island Press, London.
- Dickman, C. R. 1999. *Ecologically-based management of rodent pests*. Australian Centre for International Agricultural Research, Canberra.
- Dietrich, J. P., C. Schmitz, C. Müller, M. Fader, H. Lotze-Campen, and A. Popp. 2012. Measuring agricultural land-use intensity—a global analysis using a model-assisted approach. *Ecol. Modell.* **232**, 109–118.
- Dubinin, M., A. Luschekina, and V. C. Radeloff. 2011. Climate, livestock, and vegetation: what drives fire increase in the arid ecosystems of southern Russia? *Ecosystems* **14**, 547–562.
- Durgin, F. A., Jr. 1962. The Virgin lands programme 1954–1960. *Eur. Asia Stud.* **13**, 255–280.
- Elith, J., M. Kearney, and S. Phillips. 2010. The art of modelling range-shifting species. *Methods Ecol. Evol.* **1**, 330–342.
- Feldhamer, G. A., B. C. Thompson, and J. A. Chapman. 2003. *Wild mammals of North America: biology, management, and conservation*. JHU Press, London.
- Fleming, P. A., H. Anderson, A. S. Prendergast, M. R. Bretz, L. E. Valentine, and G. E. S. Hardy. 2014. Is the loss of Australian digging mammals contributing to a deterioration in ecosystem function? *Mamm. Rev.* **44**, 94–108.
- Fourcade, Y., J. O. Engler, D. Rödder, and J. Secondi. 2014. Mapping species distributions with MAXENT using a geographically biased sample of presence data: a performance assessment of methods for correcting sampling bias. *PLoS ONE* **9**, e97122.
- Hare, J. F., J. O. Murie, J. O. Wolff, and P. W. Sherman. 2007. Ecology, kinship, and ground squirrel sociality: insights from comparative analyses. Pp. 345–355 in J. O. Wolff and P. W. Sherman, eds. *Rodent societies: an ecological and evolutionary perspective*. The University of Chicago Press, Chicago, IL.
- Hoogland, J., ed. 2013. *Conservation of the black-tailed prairie dog: saving North America's western grasslands*. Island Press, London.
- Isabelle, V., A. Marielle, M. B. Basile, M. K. François, B. Geert, V. R. Eric, et al. 2014. Termite mound identification through aerial photographic interpretation in Lubumbashi, Democratic Republic of the Congo: methodology evaluation. *Trop. Conserv. Sci.* **7**, 733–746.
- James, A. I., and D. J. Eldridge. 2007. Reintroduction of fossorial native mammals and potential impacts on ecosystem processes in an Australian desert landscape. *Biol. Conserv.* **138**, 351–359.
- Kamp, J., R. Urazaliev, A. Balmford, P. F. Donald, R. E. Green, A. J. Lamb, et al. 2015. Agricultural development and the conservation of avian biodiversity on the Eurasian steppes: a comparison of land-sparing and land-sharing approaches. *J. Appl. Ecol.* **52**, 1578–1587.
- Kamp, J., R. Urazaliev, P. F. Donald, and N. Hölzel. 2011. Post-Soviet agricultural change predicts future declines after recent recovery in Eurasian steppe bird populations. *Biol. Conserv.* **144**, 2607–2614.
- Karaseva, E. V., and A. Y. Telitsyna. 1996. Field methods for studying rodents: monitoring and marking. Nauka (in Russian).
- Kerven, C., I. I. Alimaev, R. Behnke, G. Davidson, N. Malmakov, A. Smailov, et al. 2006. Fragmenting pastoral mobility: changing grazing patterns in post-Soviet Kazakhstan. Pp. 99–110 in D. J. Bedunah, E. D. McArthur, M. Fernandez-Gimenez, eds. *Rangelands of Central Asia: proceedings of the conference on transformations, issues, and future challenges*. 27 January 2004. Salt Lake City, UT. Proceeding RMRS-P-39. US Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fort Collins, CO. 39.
- Kerven, C., S. Robinson, R. Behnke, K. Kushenov, and E. J. Milner-Gulland. 2016. A pastoral frontier: from chaos to capitalism and the re-colonisation of the Kazakh rangelands. *J. Arid Environ.* **127**, 106–119.
- Kolesnikov, V. V. 2011. Resources and management of Bobak marmot (*Marmota bobak*), Grey Marmot (*M. baibacina*) and Mongolian Marmot (*M. sibirica*) populations. All-Russian Research Institute of Game Management and Fur Farming named after prof. B.M. Zhitkov, Kirov (in Russian).
- Kolesnikov, V. V., N. S. Ketova, and O. V. Brandler. 2011. The possibility of using satellite images to survey marmots. *Theor. Appl. Ecol.* **3**, 17–20 (in Russian).
- Kraemer, R., A. V. Prishchepov, D. Müller, T. Kuemmerle, V. C. Radeloff, A. Dara, et al. 2015. Long-term agricultural land-cover change and potential for cropland expansion in the former Virgin Lands area of Kazakhstan. *Environ. Res. Lett.* **10**, 054012.
- Kramer-Schadt, S., J. Niedballa, J. D. Pilgrim, B. Schröder, J. Lindenborn, V. Reinfelder, et al. 2013. The importance of correcting for sampling bias in MaxEnt species distribution models. *Divers. Distrib.* **19**, 1366–1379.
- Lacher, T. E. Jr, A. D. Davidson, T. H. Fleming, E. P. Gómez-Ruiz, G. F. McCracken, N. Owen-Smith, et al. 2019. The

- functional roles of mammals in ecosystems. *J. Mammal.* **100**, 942–964.
- Lesiv, M., D. Schepaschenko, E. Moltchanova, R. Bun, M. Dürauer, A. V. Prishchepov, et al. 2018a. Spatial distribution of arable and abandoned land across former Soviet Union countries. *Sci. Data* **5**, 180056.
- Lesiv, M., L. See, J. Laso Bayas, T. Sturn, D. Schepaschenko, M. Karner, et al. 2018b. Characterizing the spatial and temporal availability of very high resolution satellite imagery in Google Earth and Microsoft Bing Maps as a source of reference data. *Land* **7**, 118.
- Liu, C., M. White, and G. Newell. 2013. Selecting thresholds for the prediction of species occurrence with presence-only data. *J. Biogeogr.* **40**, 778–789.
- Löffler, E., and C. Margules. 1980. Wombats detected from space. *Remote Sens. Environ.* **9**, 47–56.
- McMahon, C. R., H. Howe, J. van den Hoff, R. Alderman, H. Broolsma, and M. A. Hindell. 2014. Satellites, the all-seeing eyes in the sky: counting elephant seals from space. *PLoS ONE* **9**, 92613.
- Meyfroidt, P., F. Schierhorn, A. V. Prishchepov, D. Müller, and T. Kuemmerle. 2016. Drivers, constraints and trade-offs associated with recultivating abandoned cropland in Russia, Ukraine and Kazakhstan. *Glob. Environ. Change* **37**, 1–15.
- Ministry of Agriculture of Kazakhstan. 2016. Report on the resources and hunting limits for the hunting species for the period 2013–2015 (in Russian).
- Munteanu, C., J. Kamp, M. Nita, N. Klein, B. Kraemer, D. Müller, et al. submitted. Cold War spy satellite images reveal delayed declines of a philopatric keystone species in response to cropland expansion.
- Nagelkerke, N. J. 1991. A note on a general definition of the coefficient of determination. *Biometrika* **78**, 691–692.
- Nakazawa, M., and M. M. Nakazawa. 2014. Package ‘fmsb’. R package.
- Olofsson, J., H. Tommervik, and T. V. Callaghan. 2012. Vole and lemming activity observed from space. *Nat. Clim. Chang.* **2**, 880.
- Pang, X. P., and Z. G. Guo. 2017. Plateau pika disturbances alter plant productivity and soil nutrients in alpine meadows of the Qinghai-Tibetan Plateau, China. *Rangeland J.* **39**, 133–144.
- Philips, Z., L. Ginnelly, M. Sculpher, K. Claxton, S. Golder, R. Riemsma, et al. 2004. Review of guidelines for good practice in decision-analytic modelling in health technology assessment. In *NIHR Health Technology Assessment programme: Executive Summaries*. NIHR Journals Library.
- Robin, X., N. Turck, A. Hainard, N. Tiberti, F. Lisacek, J. C. Sanchez, et al. 2011. pROC: an open-source package for R and S+ to analyze and compare ROC curves. *BMC Bioinformatics* **12**, 77.
- Rumyantsev, V. Y. 1989. An experiment in mapping the distribution of the steppe marmot using aerial photographs. *Mapp. Sci. Remote Sens.* **26**, 294–299 (in Russian).
- Rumyantsev, V. Y. 1991. Steppe marmot on the arable fields of Kazakhstan. *Bull. Moscow Soc. Naturalists Biol.* **96**, 15–28 (in Russian).
- Savchenko, G., and V. Ronkin. 2018. Grazing, abandonment and frequent mowing influence the persistence of the steppe marmot *Marmota bobak*. *Hacquetia* **17**, 25–34.
- Shilova, S. A., V. V. Neronov, O. N. Shekarova, and L. E. Savinetskaya. 2010. Dynamics of colonies of the speckled ground squirrel (*Spermophilus suslicus* Guld., 1770) on the northern boundary of the habitat. *Biol. Bull.* **37**, 532–536 (in Russian).
- Sidele, J. G., D. H. Johnson, B. R. Euliss, and M. Tooze. 2002. Monitoring black-tailed prairie dog colonies with high-resolution satellite imagery. *Wildl. Soc. Bull.* **30**, 405–411.
- Silva, H. R., and R. Alves-Silva. 2013. Predictive-like distribution mapping using Google Earth: reassessment of the distribution of the bromeligenous frog, *Scinax v-signatus* (Anura: Hylidae). *Zootaxa* **3609**, 213–222.
- Sludsky, A. A., ed. 1969. Mammals of Kazakhstan: rodents (marmots and ground squirrels). Science (in Russian).
- Smith, A. T., and J. M. Foggin. 1999. The plateau pika (*Ochotona curzoniae*) is a keystone species for biodiversity on the Tibetan plateau. *Anim. Conserv.* **2**, 235–240.
- Soberón, J., and G. Ceballos. 2011. Species richness and range size of the terrestrial mammals of the world: biological signal within mathematical constraints. *PLoS ONE* **6**, e19359.
- Song, X. P., M. C. Hansen, S. V. Stehman, P. V. Potapov, A. Tyukavina, E. F. Vermote, et al. 2018. Global land change from 1982 to 2016. *Nature* **560**, 639.
- Swinbourne, M. J., D. A. Taggart, A. M. Swinbourne, M. Lewis, and B. Ostendorf. 2018. Using satellite imagery to assess the distribution and abundance of southern hairy-nosed wombats (*Lasiorhinus latifrons*). *Remote Sens. Environ.* **211**, 196–203.
- Tape, K. D., B. M. Jones, C. D. Arp, I. Nitze, and G. Grosse. 2018. Tundra be dammed: beaver colonization of the Arctic. *Glob. Change Biol.* **24**, 4478–4488.
- Tokarsky V. A., ed. 2011. European Bobak marmot: its past and present status. - V. N. Karazin Kharkiv National University (in Russian).
- Tsytsulina, K., I. Zagorodnyuk, N. Formozov, and B. Sheftel. 2016. *Marmota bobak* (errata version published in 2017). *The IUCN Red List of Threatened Species 2016*: e.T12830A115106780. <https://doi.org/10.2305/iucn.uk.2016-3.rlts.t12830a22258375.en>. Downloaded on 09 September 2019.
- Van Horne, B. 2007. Conservation of ground squirrels. Pp. 463–471 in J. O. Wolff, P. W. Sherman, eds. *Rodent societies: an ecological and evolutionary perspective*. University of Chicago Press, Chicago, IL.
- Vinogradov, B. V., and E. V. Leontieva. 1985. Study of marmot burrows in northern Kazakhstan using aerophotographs. Pp.

269–286 in V. E. Sokolov, ed. *Mammals in terrestrial ecosystems*. Nauka, Moscow (in Russian).

Wesche, K., D. Ambarlı, J. Kamp, P. Török, J. Treiber, and J. Dengler. 2016. The Palaearctic steppe biome: a new synthesis. *Biodivers. Conserv.* **25**, 2197–2231.

Zhang, Y., Z. Zhang, and J. Liu. 2003. Burrowing rodents as ecosystem engineers: the ecology and management of plateau zokors *Myospalax fontanierii* in alpine meadow ecosystems on the Tibetan Plateau. *Mamm. Rev.* **33**, 284–294.

Zimina, R. P., and J. A. Isakov 1980. *Marmots. Biocenotic and practical importance*. Nauka, Moscow. 206 (in Russian).

Supporting Information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Text S1. Digitizing land-use types.

Table S1. Cost assessment (in €) for two surveys implemented in Kazakhstan in 2017: (A) ground-truth field study of 29 sample plots and (B) digitizing 1300 sample plots using Google and Bing satellite imagery.

Table S2. Variables used in maximum entropy models of marmot distribution.

Figure S1. Permanently used burrows of Bobak marmots in (A) arable cropland (B) abandoned cropland (C) grazed steppe (D) ungrazed steppe.

Figure S2. Examples of (A) long abandoned overgrown burrows appearing as dark dots on the image, (B) ploughed burrows with blurry edges and less soil contrast (can be both occupied or recently abandoned) at arable

croplands, and (C) occupied burrows with lighter spot in the middle, contrasting with the surrounding vegetation at a fallow land or recently abandoned cropland. Base map: Google imagery.

Figure S3. Acquisition month and year of the satellite images used for digitizing burrow location and estimating fine-scale land use for the 1151 sample plots, separate for the two image sources Bing maps and Google Earth.

Figure S4. Acquisition month and year of the satellite image used for digitizing burrow location and estimating fine-scale land use for the 1151 sample plots, separate per land use category.

Figure S5. Family home-ranges of Bobak marmots (white circles). Larger dots are permanently used burrows and smaller dots are burrows used for cover and as foraging base. The approximate borders of the family plots can be identified by the patterns of the paths that connect burrows. Base map: Google imagery.

Figure S6. Bobak marmot (*Marmota bobak*) range prediction for Kazakhstan based on the maximum training sensitivity plus specificity logistic threshold. Areas predicted as suitable, but out of the range of the Bobak marmot, are excluded.

Figure S7. Response curves for the two most important variables in the Maxent models, holding all other variables constant.

Figure S8. Comparison of burrow size and colony structures of Bobak marmot (A) and Yellow Ground Squirrel (B). Images scale 1:9000. Base map: Bing imagery.

Data S1. Final dataset with digitized sample plots.

Data S2. Ground-truthed sample plots.