ISSN 1062-3590, Biology Bulletin, 2022, Vol. 49, No. 9, pp. 1279–1291. © Pleiades Publishing, Inc., 2022.
Russian Text © The Author(s), 2022, published in Zoologicheskii Zhurnal, 2022, Vol. 101, No. 1, pp. 23–36.

An Analysis of the Distribution of the Lizard Genus *Lacerta* in the Northeastern Caucasus (Dagestan, Russia) Using GIS Technologies and Methods for Building Species Distribution Models

M. A. Doronina[a, *], L. F. Mazanaeva[b, **], and I. V. Doronin[a, *]
[a] *Institute of Zoology, Russian Academy of Sciences, St. Petersburg, 199034 Russia*
[b] *Dagestan State University, Makhachkala, 367025 Republic of Dagestan, Russia*
**e-mail: igor.doronin@zin.ru*
***e-mail: mazanaev@mail.ru*

Received November 17, 2020; revised February 17, 2021; accepted February 24, 2021

Abstract—An analysis of the spatial distribution of green lizards of the genus *Lacerta* in Dagestan is given. The distribution ranges of *L. agilis*, *L. media*, and *L. strigata* are specified and detailed. A set of vector (points of records) and raster synthetic maps is created, reflecting the spatial distribution of species. Bioclimatic modeling of habitat suitability is carried out. The minimum overlap of ecological (eco-climatic) niches is noted for *L. media* with all the species studied, and the maximum overlap is observed in *L. agilis* and *L. strigata*.

Keywords: range, *Lacerta agilis*, *Lacerta media*, *Lacerta strigata*, MaxEnt, QGIS
DOI: 10.1134/S1062359022090114

INTRODUCTION

One of the centers of taxonomic diversity of green lizards of the genus *Lacerta* Linnaeus 1758, which includes ten species according to modern concepts (Kornilios et al., 2019), is the Caucasus. Three species of the genus live here—the sand lizard, *Lacerta agilis* Linnaeus 1758, represented by six subspecies[1]; the nominative subspecies of the three-lined lizard, *L. m. media* Lantz et Cyrén 1920; and the Caspian green lizard, *L. strigata* Eichwald 1831, which is considered as a monotypic species (Uetz et al., 2020; www.lacerta.de). If we accept the eastern border of the Caucasus under the scheme of the Critical Ecosystem Partnership Fund (CEPF) (https://wwf.panda.org/discover/knowledge_hub/where_we_work/ black_sea_basin/caucasus/projects/english/), then this list must also include the southern subspecies of the european green lizard, *L. viridis meridionalis* Cyrén 1933, the range of which includes, in particular, the Pontine Mountains. Previously, the populations of the green lizard from the north of Anatolia were identified as the independent narrow-range subspecies *L. v. paphlagonica* Schmidtler 1986 and *L. v. infrapunctata* Schmidtler 1986, which were reduced to junior synonyms of *L. v. meridionalis* (Marzahn et al., 2016).

It should be noted that the Caucasus has been considered one of the most unique territories of Northern Eurasia in terms of biodiversity throughout the history of herpetological research. According to the results of studying the level of endemism of reptiles in the Western Palearctic (Ficetola et al., 2018), the Caucasus is one of the most significant regions. Within its Russian part, the territory of Dagestan and Krasnodar krai can be recognized as "hot spots" of herpetofauna diversity. All three species of green lizards indicated above live there.

The history of the study of lacertids within Dagestan, which occupies the northeastern part of the Caucasus region, dates back almost 200 years and begins with the expedition of Eichwald, who observed "*Lacerta deserti, viridis, velox, muralis* (*agilis L.*)" in 1825 in the Tarki (p. 97, Eichwald, 1834)—most likely he means *Eremias arguta deserti* (Gmelin 1789), *E. v. velox* (Pallas 1771), *L. a. boemica*, and *L. strigata* (Doronin et al., 2017). Krasovsky (1932) first discovered the three-lined lizard on the territory of the republic. Shibanov (1935) indicated the sand lizard in the vicinity of the city of Kizlyar with the following note: "I define the sole specimen of the collection as subsp. *exigua* Eichw, although in some respects it approaches *Lacerta boemica* Suchow, the taxonomic significance of which I currently refrain from assessing" (p. 66). In 1940, Bannikov (1954) conducted herpetological

[1] The status of *L. a. boemica* Suchow 1929 is proposed to be raised to the species level, as in the original publication by G.F. Sukhov, while a number of other Caucasian subspecies are proposed to be related to junior synonyms *L. a. exigua* Eichwald 1831 (Kalabina-Hauf and Ananjeva, 2004; Claudia et al., 2014). A revision of the intraspecific taxonomy of *L. strigata* is also needed.

research in South Dagestan. According to this author, the sand lizard, which he identified as "*Lacerta agilis exigna*" (lap.) (pp. 75, 79), and the Caspian green lizard are sympatric in the area studied and probably "compete, since in places where there are a lot of sand lizards there are few Caspian green lizards, and vice versa. However, it was not possible to notice any distinctions in habitats" (p. 79).

Sukhov (1948) was the first to publish maps of the ranges of green lizards of the fauna of the Soviet Union, citing all three species for Dagestan. Subsequently, new data on the distribution of green lizards in the region were obtained by Khonyakina (1970, 1972), who, like Shibanov, indicated the morphological characters that are common to *L. a. boemica* and *L. a. exigua* for the studied individuals of the sand lizard (the sample from the vicinity of Makhachkala) (p. 89, Khonyakina 1970). To date, we do not have reliable information about the habitat of the second subspecies in the region, although its range occupies the northern part of the republic on a number of maps (Szczerbak, 1966; Bischoff, 1988; Kalyabina-Hauf and Ananjeva, 2004; etc.), and it was included in the list of herpetofauna of Dagestan in zoogeographical analysis (Mazanaeva and Tuniyev, 2011). There is the possibility that *L. a. exigua* can be found in the valley of the Kuma River, where the sand lizard is known in the adjacent territory of the Chernozemelsky district of Kalmykia (Kireev, 1981).

Roytberg et al. (2000) summarized previous studies of chorology and published the cadaster of Dagestan lizard finds that is the most complete to date. Mazanaeva and Orlova (2014), making a brief review of the taxonomic and ecological diversity of the saurofauna, classified *L. agilis* and *L. strigata* as widespread species in the region. According to their data, the Caspian green lizard has colonized the subarid and mesophytic habitats of the lowlands and foothills, penetrating in some places into the intramountain regions and high mountains. The sand lizard occupies mesophytic habitats of meadow–steppe and forest–steppe landscapes in the lowlands, but in the mountains it adheres to dry habitats. *L. media* inhabits dry mountain steppes and the zone of upland xerophytes in the highlands; in the intramountain regions, it inhabits post-forest meadows, forest–steppe, and mountain forests.

Information on the landscape–zonal distribution of green lizards in intramountainous Dagestan is contained in the study by Mazanaeva and Askenderov (2014): according to their data, the sand lizard is distributed in the shale region, where it inhabits steppe and forest–steppe areas, and in the subalpine belt, it inhabits slopes of southern exposure with a height of up to 2300 m a.s.l. The Caspian green lizard inhabits the steppe and forest–steppe belts there up to a height of 1200–1300 m, while in the limestone region, it inhabits the same areas as the sand lizard. The three-lined lizard was noted in the shale region in the steppe and forest–steppe belt of the gorge of the Kurakh River (up to 1400 m), and in the limestone region, it was noted in the same belts, as well as in upland xerophytes of gorges of up to 1500 m. The results of studying the range of *L. media* on the territory of Dagestan were published by Mazanaeva and Askenderov (2016): they revealed four isolated populations of the species in semiarid basins of large mountain rivers—Samur, Kurakh, Andi Koisu, and Avar Koisu.

The publications listed above are based on the empirical method of studying the geographical distribution of species. Currently, arealogical (chorological) studies in zoology have absorbed a significant arsenal of GIS programs (see Lisovsky et al., 2020). Unfortunately, among domestic publications, herpetogeographic (according to the terminology of Borkin and Litvinchuk (2013)) studies using GIS are still clearly not enough. Following ornithologists (Koblik et al., 2011), we can say that "Applied areaology is our weak point" (Ananjeva et al., 2019). At the same time, some foreign publications often give distorted and even erroneous ideas about the distribution of green lizards in the Caucasus (for example, Honegger, 1981; Troidl, A. and Troidl, S., 2000, 2001; Ahmadzadeh et al., 2013; etc.). Most likely, one of the reasons for this is errors in determining their species and subspecies. We revealed the latter when working with the collections of the British Museum of Natural History (www.nhm.ac.uk/our-science/collections.html), the Dresden Zoological Museum, the Senckenberg Museum of Natural History (www.sesam.senckenberg.de/), etc., in the Global Biodiversity Information Facility (GBIF) Database (www.gbif.org).

The goal of this publication is to analyze the distribution of green lizards on the territory of Dagestan using geographic information systems and to create a set of models for the potential spatial distribution of species using ecological niche modeling methods.

The relevance of the study is emphasized by both the nature protection aspect (*L. media* is included in the Red Book of the Russian Federation[2] (Darevsky, 2001) and Dagestan (Mazanaeva and Orlova, 2009)) and the epidemiological aspect (green lizards, including those in the Caucasus, play an important role in maintaining natural vector-borne disease foci in humans and domestic animals (Balashov, 2009; Kidov et al., 2016)). The data obtained can also be used to clarify the ways of lizard spread: due to physical and geographical conditions (less development of mountain glaciation, lower elevations compared to the Western and Central Caucasus, peculiarities of the location of high-altitude plant belts), the paths of fau-

[2] According to the Order of the Ministry of Natural Resources and Ecology of the Russian Federation as of March 24, 2020, no. 162 "On Approval of the List of Wildlife Objects Listed in the Red Book of the Russian Federation" (registered on April 2, 2020, no. 57940), only *L. media* populations of the Black Sea coast were included in the new list of protected taxa of Krasnodar krai.

nistic exchange between the North Caucasus and Transcaucasia went through the territory of the republic (Mazanaeva and Tuniyev, 2011), moreover, clearly in both directions. In addition, Dagestan stands out among other regions of the Caucasus and Europe (if its southern border is drawn along the Main Caucasian Range) by the presented variety of climate types according to Köppen-Geiger (Peel et al., 2007), which makes this territory an extremely convenient platform for bioclimatic modeling.

MATERIALS AND METHODS

The materials for this study were the collections of the Zoological Institute of the Russian Academy of Sciences (St. Petersburg, ZISP), the Zoological Museum of Moscow State University (Moscow, ZMMU), Karazin Kharkov National University (Kharkov, MNKhU), National Museum of Natural History (Washington, NMNH), our own field research 1970–2020, and published data. The field collections of the second author covered all the administrative regions of Dagestan, which, together with published data and information from the collections, allows us to speak of a sufficient amount of data for reliable constructions.

Determination of the geographical coordinates (decimal coordinates up to the fourth place after the decimal point) and the height of the points of recording lizards in field conditions was carried out using a GPS navigator (Garmin). When working with museum collections and published sources, interactive maps (www.wikimapia.org and www.maps.google.ru) were used, and their localization was determined based on the known biotopic preferences of lizards. A location that was at least 1 km away from the nearest one was taken for one point, which is due both to the specifics of working with GIS and to the data on individual movements of green lizards (Tertyshnikov et al., 1976). Descriptive statistical calculations were conducted using the Statistica V program 7.0.

The distribution of recording points throughout the region is shown on maps created using the Quantum GIS (QGIS) v. 3.10.2 (www.qgis.org/ru/site/). They demonstrated the point (discrete) method of mapping, which is the first stage in the study of the geographical distribution of species. At the second stage, the grid (raster) method or the method of formal squares was implemented in QGIS (terminology according to Voronov et al., 2002); it consisted in distinguishing an area with assigned sizes (squares with a side corresponding to 15 km of the locality, i.e., with an area of 225 km^2), within which at least one point is known; we also built the so-called heatmaps with color gradation of the number of finds of each species and the number of species in the standard square. When ranking the territory, we used the following color designation: white, no finds within the conventional square; blue, 1 point; green, 1–5 points; red, 5–10 points. On the heat map of the distribution of the number of lizard species, the white color of the square indicates the absence of finds in it, the blue color marks the presence of one species, the green color marks the presence of two species, and the red color marks the presence of three species.

Note that the grid method was used in our time to create the latest version of the atlas of amphibians and reptiles of Europe (Sillero et al., 2014; https://www.seh-herpetology.org/distribution-atlas), maps of green lizard ranges in the Red Books of Krasnodar krai (Ostrovskikh, 2017; Tuniyev and Ostrovskikh, 2017; Tuniyev, B.S. and Tuniyev, S.B., 2017; Tuniyev, S.B. and Tuniyev, B.S., 2017) and South Ossetia (Tuniyev and Lotiev, 2017, 2017a). The compilers of the first report (Zamotailov et al., 2017) noted that the areaological information on specially protected taxa published in the Red Book must contribute to the most reliable assessment of the nature conservation significance of various territories in the region. In this regard, the grid method, which includes the color designation of critical habitats, is especially convenient, since significance estimates are often distorted precisely by point maps of the ranges of poorly studied species, which often do not reflect the real ecological range (covering the colonized habitats) of a taxon within its geographic regional range. In the third edition (Butaeva et al., 2017), this approach was explained by environmental considerations like a reluctance to publish the exact locations of taxa that are subject to commercial capture, but, at the same time, giving essays for all rare and endangered representatives of the herpetofauna that contain precise localization, which eliminates this motive.

At the third stage, we carried out ecological and climatic GIS modeling of lizard ranges using 19 environmental parameters (Bio 1–19 predictors, see Table 2), which reflect data on the temperature and precipitation of the territory (Busby, 1991), as well as on the heights, which allow interpolation of the observed data from 1950 to 2000 (Current) (Hijmans et al., 2005). These data were obtained from the Worldclim Database (http://www.worldclime.org) at a resolution of 30 arcseconds or ~1 km per pixel near the equator.

At the initial stage, the significance of all bioclimatic variables was assessed. Subsequently, predictors that correlated with each other were excluded to build the model. To do this, we calculated the Pearson correlation coefficient for all pairs of predictors using ENMTools (Warren et al., 2010). We excluded a variable from a correlated pair with $|r| > 0.7$, which was considered less biologically important based on known preferences for the species studied (Szczerbak et al., 1976; Ahmadzadeh et al., 2013; Kafash et al., 2019; authors' data). The resulting data set contained six bioclimatic predictors: Bio 2 (temperature mean diurnal range, max–min), Bio 6 (minimum temperature of coldest month, ×10, °C), Bio 7 (temperature

Table 1. Distribution of points of recording lizards of the genus *Lacerta* on the territory of Dagestan by information sources

Species	Information source							
	total number of points	authors' observations, % of the total amount	collection data, % of the total amount	literature data, % of the total amount	3 + 4	3 + 5	4 + 5	3 + 4 + 5
1	2	3	4	5	6	7	8	9
L. agilis	78	34 (43.6)	4 (5.1)	7 (9)	1 (1.3)	25 (32.1)	4 (5.1)	3 (3.8)
L. media	30	0	0	0	4 (13.3)	21 (70)	0	5 (16.7)
L. strigata	253	154 (60.9)	22 (8.7)	18 (7.1)	3 (1.2)	35 (13.8)	7 (2.8)	14 (5.5)
Total	361	188 (52.1)	26 (7.2)	25 (6.9)	8 (2.2)	81 (22.4)	11 (3.1)	22 (6.1)

Table 2. Altitude distribution of points of recording lizards of the genus *Lacerta* on the territory of Dagestan

Species	*n*	Distribution range, m above sea level	Mean value (μ)	Standard deviation (σ)	Coefficient of variance (*CV*, %)
L. agilis	78	–30–2300	914.61	737.09	80.59
L. media	30	560–1710	1278.66	253.91	19.85
L. strigata	253	–30–1780	281.60	356.70	126.66
Total	361	–30–2300	501.23	575.18	114.75

annual range, ×10, °C), Bio 8 (mean temperature of wettest quarter of the year, ×10, °C), Bio 10 (mean temperature of warmest quarter of the year, ×10, °C), Bio 14 (precipitation of driest month, mm), Bio 15 (precipitation seasonality, CV), and Bio 19 (precipitation of coldest quarter of the year, mm).

The ENMTools v. 1.4.3 program was used to remove the localities that were close to each other and located in the same square (1 × 1 km). Modeling was performed using the MaxEnt program (Maximum Entropy Species Distribution Modeling) v. 3.4.1 (www.cs.princeton.edu/~schapire/maxent/), which extrapolates the spatial distribution of species using the maximum entropy method (Elith et al., 2011). With its help, maps of the most likely areas of distribution (habitat suitability) of lizards were created and the contribution (in %) of each factor to the construction of the model was determined.

To parameterize the models correctly, we evaluated the performance of various combinations of ten MaxEnt adjustment options (from 0.5 to 5.0 in 0.5 steps; see Vences et al., 2017). The most suitable version of the model was parameterized with a regularization factor of 1.0 (30 repetitions). We used the default settings, i.e., all space object classes, the maximum number of iterations (500) and the maximum number of background points (10000) were involved (Phillips and Dudík, 2008). To test the models obtained, 25% of the points were used. We applied jackknife analysis to estimate the relative contribution of variables to the MaxEnt model.

The reliability of the model was assessed using the built-in function for constructing the AUC curve (area under receiver operating characteristic (ROC) curve), which reflects the sensitivity of the species to parameters and its specificity. An AUC index value that is greater than 0.75 and close to one indicates a high degree of significance (Elith, 2002). MaxEnt maps were visualized using the DIVA-GIS v. 7.5.0 (www.diva-gis.org) (Scheldeman and van Zonneveld, 2010).

To assess the overlap of ecological (environmental–climatic) niches using ENMTools v. 1.4.3, Schoener's (D) index and the standardized Hellinger's I (I) distance were calculated, the value of which is statistically measured from zero (in the case of the complete absence of niche overlap) to one (in the case of their identity); for this reason, this indicator is called the identity test, I-test. It is recommended to use it with all predictors in 100-fold replication (Warren et al., 2010). The high efficiency of using the D index was previously shown based on the example of parthenogenetic and bisexual lizard species of the genus *Darevskia* 1999 (Petrosyan et al., 2019, 2020).

RESULTS

As of September 1, 2020, the cadastre of green lizard finds in Dagestan includes 361 recording points (78 for *L. agilis*, 30 for *L. media*, and 253 for *L. strigata*) (Appendix 1, http://sev-in.ru/ru/zoologiceskii-zurnal). According to the source of information (Table 1), more than half (188 points, or 52.1%) were obtained

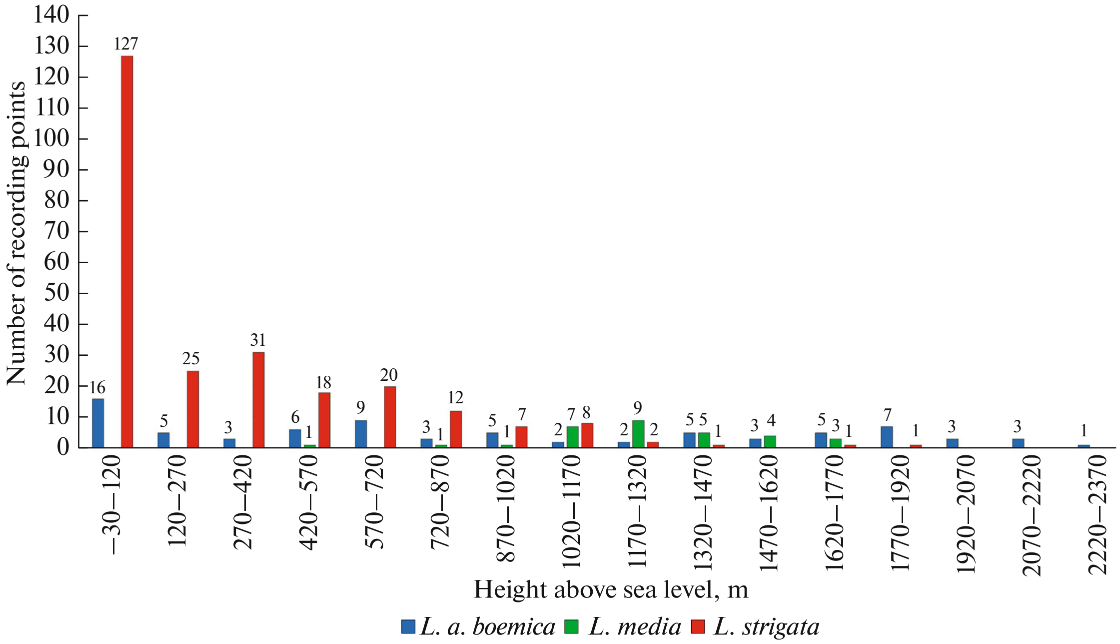

Fig. 1. Altitude distribution of points of recording (n = 361) lizards of the genus *Lacerta* on the territory of Dagestan.

only from the results of the authors' observations and were not previously published. It is indicative that the data on the finds of the three-lined lizard were 100% made public, due to the increased attention of specialists to this species, which is listed in the regional and federal Red Books.

The range of altitudes inhabited by species varies from –30 m for populations of the sand lizard and Caspian green lizard on the coast of the Caspian Sea (the minimum values for these species in general throughout the range) to 2300 m above sea level for the population of the sand lizard in the vicinity of the village of Shari in the Agulskii district (ZISP no. 22021; Kalyabina-Hauf and Ananjeva, 2004; data of L.F. Mazanaeva, 2005, 2007). The altitude distribution of finds is presented in Table 2, from which it follows that, under the conditions of the northeastern Caucasus, according to the average indicators, *L. strigata* (range from –30 to 1780 m, μ is 281.60) can be associated with the plains zone (according to Gurlev, 1972), *L. agilis* (range from –30 to 2300 m, μ is 914.61) can be associated with the zone of foothills, and *L. media* (560–1710 m, μ is 1278.66) can be related to the zone of mountains.

Figure 1 notes the maximum coverage of heights for *L. agilis;* this is the only species that is present in all altitudinal ranges (the interval between divisions = 150 m was chosen on the histogram). The largest number of finds of green lizards (143 points, or 39.7%) was made at altitudes from –30 to 120 m, which demonstrates their high-altitude preference in Dagestan. Similar figures are typical for the sand lizard and Caspian green lizards, while 127 points (50.4%) at these marks are known for the second species. Most localities of the three-lined lizard (9 (30%)) are known at altitudes of 1170–1320 m.

When comparing point maps (Fig. 2) with a map of the landscape zones of Dagestan (Fig. 3), we see that the sand lizard and the Caspian green lizard were found in all five zones: lowlands, foothills, frontal ranges, intra-mountain, and high-mountain Dagestan. The largest number of finds of *L. agilis* and *L. strigata* accounts for the third of them and for the first and second of them, respectively; *L. media* was found in the fourth and fifth zones with a quantitative predominance in the highland zone. This corresponds to the analysis of the height distribution of species recording points.

On grid maps (Fig. 4), where the territory of the region is covered by 421 full squares,[3] 150 squares (35.6%) include at least one find of representatives of *Lacerta*. The Caspian green lizard is the most widespread in the region. It is recorded in 117 squares (27.8%) and is a background species; the sand lizard is known in 51 squares (12.1%), and the three-lined lizard is known only in 17 squares (4%) (Table 3). *L. agilis* is characterized by the absence of areas with the maximum number of finds: the largest one (four localities) was noted in the upper reaches of the Kazikumukh Koisu and Hunnikh rivers; for *L. media*, the only red raster was found in the middle course of the Samur River; for *L. strigata*, it was found in the upper reaches of the Sulak River in the area of the Chirkei

[3] ≥50% of which is within the administrative boundaries of Dagestan, covering an area of 50 300 km^2.

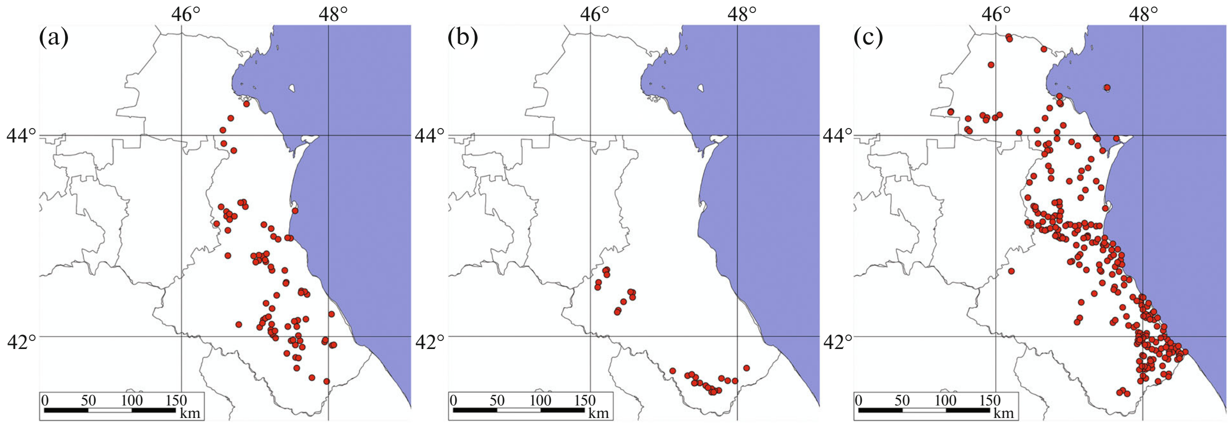

Fig. 2. Maps of points of recording lizards of the genus *Lacerta* in Dagestan: (a) *L. agilis;* (b) *L. media*; and (c) *L. strigata*.

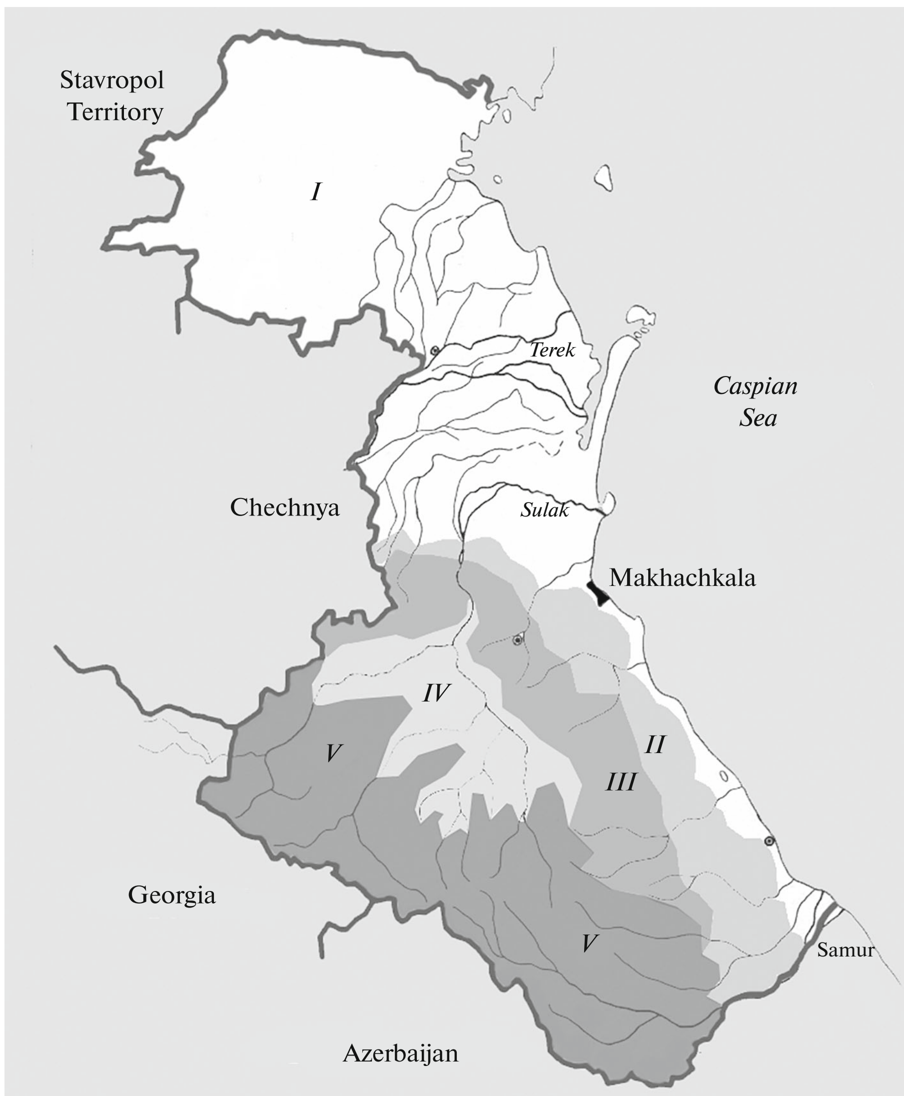

Fig. 3. Map of the landscape zones of Dagestan: *I,* lowlands; *II,* foothills; *III,* frontal ranges; *IV,* intra-mountain areas; *V,* highlands (according to Fedina, 1963; from the study by Mazanaeva and Tuniyev, 2011, with changes).

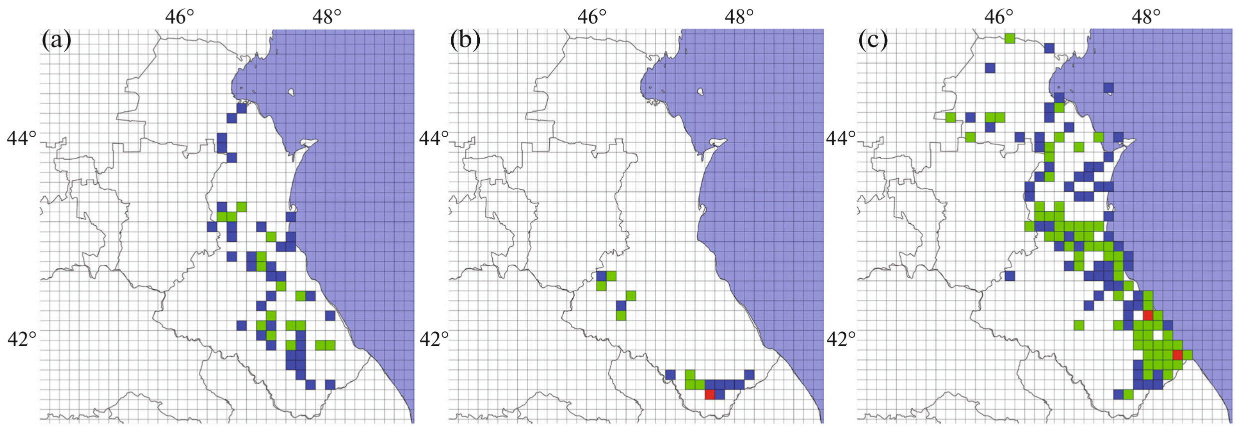

Fig. 4. Maps of the distribution of the number of points of recording lizards of the genus *Lacerta* using the grid (raster) method for dividing the territory of Dagestan: (a) *L. agilis;* (b) *L. media;* (c) *L. strigata*. The color shading indicates the number of recording points in a standard 15 × 15 km square: white, 0; blue, 1; green, 1–5; red, 5–10.

reservoir and in the coastal zone of the Caspian Sea in the lower reaches of the Ulluchay River.

On the resulting map of species abundance (Fig. 5), the maximum indicator was noted only for one (0.2%) square located in the valley of the Kurakh River—a small arid basin with vegetation of the Mediterranean type; there were 116 squares (27.6%) with the presence of one species and 33 squares (7.8%) with the presence of two species. "Empty" squares with zero values are concentrated mainly in the northern part of the region in the Terek-Kuma lowland and in the southwestern part in the area of high-altitude watershed ridges and plateaus. Most likely, this reflects the real absence of lizard populations there due to the unsuitability of the territory: the lowlands are characterized by insufficient moisture (the driest part of the republic) and very hot summers (the highest average annual temperatures), and the highlands are characterized by a sharply continental climate with cold winters and cool summers (the lowest mean annual temperatures).

When modeling the distribution of the species using the MaxEnt program, good results were obtained for the performance of the potential distribution model (AUC index = 0.98–0.99). Based on these data, the maps reliably characterize the features of the distribution of the studied species and allow us to give our comments and additions together with new material.

The most significant contribution to the construction of the models (≥10%) of the modern ranges of all three species was made by the minimum temperature of the coldest month (Bio 6), the amount of precipitation of the driest month (Bio 14), and the amount of precipitation of the coldest season (Bio 19) (Table 4). The total contribution of these factors to the formation of the model reaches 76.2%. For *L. agilis* and *L. media*, the dominant predictors included the annual temperature range (Bio 7); for *L. media* alone, they included the seasonality of precipitation (Bio 15). Thus, in the presence of a significant number of common indicators, each species demonstrated an individual set of parameters that dominated in the construction of the model under the conditions of the northeastern Caucasus. Noteworthy is the lack of influence of the height of the terrain on the construction of the maps.

On the obtained GIS maps (Fig. 6), the highest prevalence, i.e., the proportion of the area in which we expect the presence of the species, was noted for the Caspian green lizard. The sand lizard is slightly inferior to it in this indicator, while the number of its actual finds is 3.2 times less. Differences were revealed

Table 3. Distribution of the number of finds of lizards of the genus *Lacerta* using the grid (raster) method for dividing the territory of Dagestan

Species	Number of squares (%) with finds of lizards			
	white (0 points)	blue (1 point)	green (1–5 points)	red (5–10 points)
L. agilis	370 (87.9)	35 (8.3)	16 (3.8)	0
L. media	404 (96)	9 (2.1)	7 (1.7)	1 (0.2)
L. strigata	304 (72.2)	52 (12.3)	63 (15)	2 (0.5)

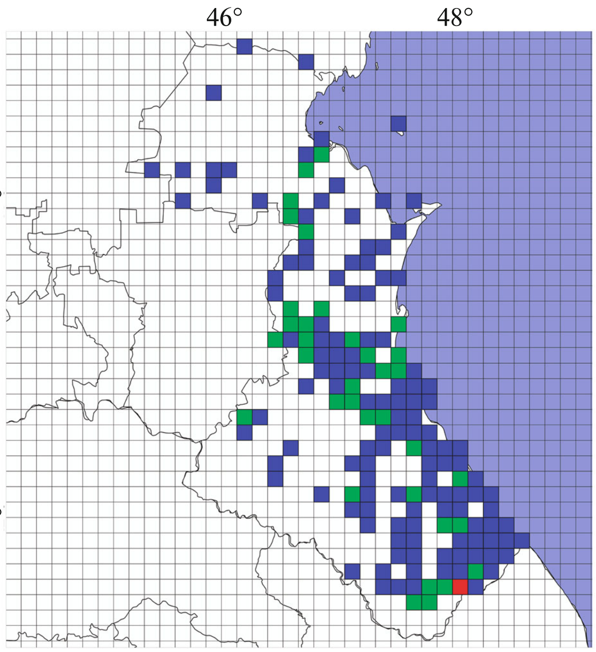

Fig. 5. Maps of the distribution of the number of lizard species of the genus *Lacerta* using the grid (raster) method for dividing the territory of Dagestan. Color shading indicates the number of species marked in a standard 15 × 15 km square: white, 0 species; blue, 1; green, 2; red, 3.

in the location of the territories that are most suitable for them, which can be designated as the core areas: for *L. strigata*, these are lowlands and foothills; for *L. agilis*, these are foothills and frontal ridges.

The overlap of ecological (ecological–climatic) niches in our study is minimal for the three-lined lizard with all species studied (Table 5), with which it is sympatric in single localities according to field studies. The maximum overlap was noted for the sand lizard and Caspian green lizard (0.52/0.78) living together over a large area of the region (Roytberg, 1994).

DISCUSSION

Despite significant altitude marks, none of these three species in Dagestan reaches the limit of its distribution known in the Caucasus: *L. agilis* ≈ 2730 m in the area of the Ardagan Pass in Turkey (Tuniyev et al., 2014), *L. media* ≈ 2700 m in the vicinity of Mount Ag-yurt in the Nakhchivan Autonomous Republic of Azerbaijan (Kuzmin, 1981), and *L. strigata* ≈ 2100 m on Mount Ara (=Araler, Arailer) in Armenia (ZISP no. 20216).

In contrast to Transcaucasia (Rudik, 1986), in the North Caucasus the joint habitation of all three species of green lizards was previously unknown. During field research in the valley of the Kurakh River on July 28, 2003, we identified a zone of their sympatry: the Caspian green lizard (2–3 ind./200 m of the survey route) was found between the village of Kurakh and the village of Kukaz in the area where sibljak forms dense thickets along the northern slopes closer to the river valley. The three-lined lizard (1–4 ind./500 m of the survey route) was found between the village of Kukaz and the village of Kurakh on the northern slopes with sparse sibljak and tragacanth, as well as in the section of the gorge between the village of Kurakh and the village of Huta with mountain–steppe vegetation; the sand lizard was noted on the slope with mountain–meadow vegetation of this part of the gorge (1 ind./500 m). Taking into account the high scientific value of the designated territory, we recommend expanding the boundaries of Kasumkentskii State Nature Reserve in the southwesterly direction, which will contribute to the preservation of the saurofauna of this region.

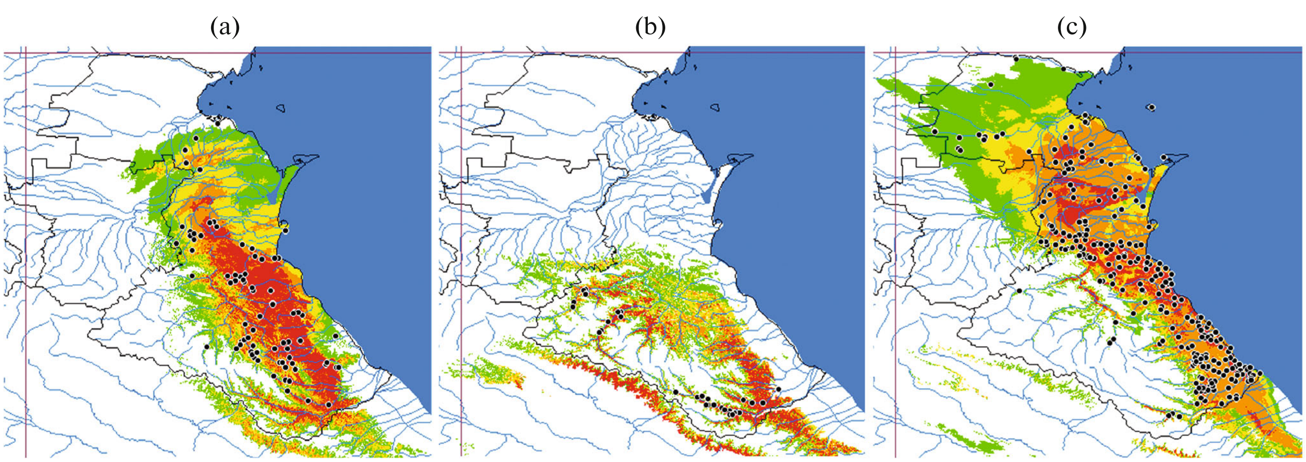

Fig. 6. Maps of predicted areas of geographical distribution of lizards (SDM-maps) of the genus *Lacerta* on the territory of Dagestan, which were built using the MaxEnt v program. 3.4.1: (a) *L. agilis;* (b) *L. media;* (c) *L. strigata*. Color shading indicates the areas of likely distribution (habitat suitability) with high (100–80%; red), medium (80–60%; orange), low (60–40%; yellow), and extremely low (40–20%; green color) probability of recording; black dots mark places of finds.

Table 4. Significance of the involved bioclimatic parameters (%) in the construction of distribution models (habitat suitability) of lizards of the genus *Lacerta* on the territory of Dagestan

Parameter	Abbreviation	Species					
		L. agilis		*L. media*		*L. strigata*	
		contribution	permutation	contribution	permutation	contribution	permutation
Temperature mean diurnal range (monthly average, min–max)	BIO 2	5.6	26.2	5.1	43.8	8.2	33
Minimum temperature of coldest month (×10, °C)	BIO 6	11.1	0.5	11.9	2.4	39.3	41.1
Temperature annual range (BIO 5-BIO 6) (×10, °C)	BIO 7	32.1	33.5	29.4	37.5	8.7	0.1
Mean temperature of wettest quarter of the year (×10, °C)	BIO 8	1.9	0	6.1	0.2	0.8	0.1
Mean temperature of warmest quarter of the year (×10, °C)	BIO 10	0.1	0	2.9	0.1	1.7	0
Precipitation of driest month, mm	BIO 14	11.8	0.1	11.8	0	16.9	5
Precipitation seasonality (coefficient of variation)	BIO 15	1.7	0.6	19.6	2.8	4.4	0.7
Precipitation of coldest quarter of the year, mm	BIO 19	35.7	39.1	13.2	13.2	20	20

* The gray color indicates the values of the leading parameters, the contribution of which exceeds 10%.

According to GIS-maps, the middle and upper reaches of the Avar Koisu River (with the Karakoisu and Kazikumukh Koisu tributaries) and the Andi Koisu River can be recognized as a promising territory for searching for similar territories. Thus, populations of *L. media* and *L. strigata* were found in the vicinity of the village of Botlikh on July 3, 2002, and the high cenotic diversity of this area (broad-leaved forests, meadow steppes, subalpine meadows) (Abdulaev et al., 2011) suggests that *L. agilis* also lives here. It is significant that during the herpetogeographic zoning of the republic this territory was assigned to the Intramountain District of limestone Dagestan—the most original division within the entire Greater Caucasus, which is of significant scientific and environmental value (Mazanaeva and Tuniyev, 2011).

Speaking about the predictive role of GIS maps, we note that at the first stage of modeling we did not have information about the finds of the sand lizard in the valley of the Kurakh River, but this territory was included in the area with the maximum suitability for the species.

An unresolved issue is the habitation of the sand lizard in the valley of the Samur River: for the lower reaches of this river, the species was given in the publication by Khonyakina (1970), Szczerbak et al. (1976), and Roytberg et al. (2000); moreover, in the second study the locality was given with a reference to the data of Khonyakina, and the third one referred to the article by Bannikov (1954), which, in fact, gives no indications of the exact places of observation of lizards. Samples of the species from this territory are absent in all collections that are known to us. On the obtained GIS map, the Samur delta was not included in the number of favorable territories, but high suitability was revealed in the middle and upper reaches of this river, in the valleys of the Akhtychay and Usukhchay rivers, as well as in the adjacent territory of Azerbaijan from the upper and middle reaches of the Kusarchay River to the Velvelichay River. This territory has already been included in the range of the sand lizard (Szczerbak et al., 1976), but without reliable confirmation of this: unfortunately, the cadastre in the

Table 5. Values of the ecological niche identity test—the Schoener's index and the standardized Hellinger's distance (D/I) in a pairwise comparison of lizard species of the genus *Lacerta* inhabiting the territory of Dagestan

Species	*L. agilis*	*L. media*
L. agilis	–	–
L. media	0.41/0.66	–
L. strigata	0.52/0.78	0.30/0.57

monograph *The Sand Lizard* was compiled with numerous errors. New finds of *L. agilis* are also expected in the lower reaches of the Terek River, in the valley of the Avar Koisu and Andi Koisu Rivers.

The ZMMU collection (no. 2014) contains a sample of *L. agilis* made by B.A. Krasavtsev in the village of Tushilovka in the Kizlyarskii district on June 25, 1932. At present, the species has not been found there (field studies on May 24, 2006, and June 18, 2010), and on the GIS map (SDM) this point, which is the northernmost point in the range of *L. a. boemica*, fell out of the suitable area. We can assume the extinction of this population located in the pessimum zone at the border of the range.

The Caspian green lizard can be detected with a high probability in the valley of the Avar Koisu and Andi Koisu rivers, which was also noted for the sand lizard; in this case, the GIS map indicates the likely routes of penetration of these species into the intramountain and high-mountain zones. In addition, it is necessary to search for lizards in the valley of the Samur River above the village of Akhty. A detailed analysis of the distribution model of *L. media* was given by us earlier (Doronin et al., 2018).

The intensive development of GIS and their introduction into zoology again raises one of the key questions—what determines the boundary of the species range? Following the approach of modern ecological niche researchers (see Hargreaves et al., 2014; Lee-Yaw et al., 2016), the choice must be made between two main responses—the restriction of expansion due to isolation barriers or the deterioration of habitat conditions, including climatic ones. In our case, based on the data obtained, in particular, the absence of dependence of the model construction on heights, preference must be given to the second option.

The temporal (historical) factor cannot be ignored either. The most illustrative example is *L. media*: according to our unpublished data, populations from the territory of Dagestan, the appearance of which is attributed to the final stage of the phylogeny of the species and is dated about one million years ago (Lower Pleistocene), are included on its phylogenetic tree in the Transcaucasian–East Anatolian subclade, and the divergence within it is dated at less than 200 ka (Middle Pleistocene) (Ahmadzadeh et al., 2013a; Sagonas et al., 2014). It is possible that this species, having penetrated from Transcaucasia into the territory of Dagestan, did not have time to spread in the North Caucasus, although favorable climatic conditions for it were identified in the adjacent territory of Chechnya and in the region of the Caucasian Mineralnye Vody (Doronin et al., 2018). On the other hand, the previously existing North Caucasian populations could have disappeared from the enclaves during the last glacial maximum about 22000 years ago, after which *L. media* did not manage to restore its former range.

In the future, it is necessary to compare the MaxEnt models of lizard ranges built only on the basis of points from the territory of Dagestan with the models covering the Caucasus, or the entire area of their distribution. This will allow us to highlight in more detail the regional features of the populations we studied, to assess the sensitivity of GIS to changes in the analyzed volume of primary data like the localities, as was already done when modeling the range of the bog turtle (*Emys orbicularis* (Linnaeus 1758)) (Duysebaeva et al., 2019). Here we can expect differences in niche overlap rates for green lizards in different parts of the ranges. At the same time, if they live in different climatic conditions, then it is obvious that the indicator of the similarity of the ecological niches of populations of the same species may have a low value, but this does not yet indicate their ecological and climatic divergence, since they can live in different environments due to ecological plasticity (see Zink, 2015).

ACKNOWLEDGMENTS

The authors are grateful to E.A. Golynsky, S.N. Litvinchuk, and E.A. Pavlov for valuable advice and assistance in this work.

FUNDING

This study was carried out within the framework of a State Assignment of the Institute of Zoology, Russian Academy of Sciences (St. Petersburg), project no. AAAA-A19-119020590095-9, and with the financial support from the Russian Science Foundation, project no. 22-24-00079.

COMPLIANCE WITH ETHICAL STANDARDS

Conflict of interest. The authors declare that they have no conflicts of interest.

Statement on the welfare of animals. All applicable international, national, and/or institutional guidelines for the care and use of animals were followed.

AUTHOR CONTRIBUTIONS

The authors made an equal contribution to the writing of this article.

REFERENCES

Abdulaev, K.A., Ataev, Z.V., and Bratkov, V.V., *Sovremennye landshafty Gornogo Dagestana* (Modern Landscapes of Mountainous Dagestan), Makhachkala: Dagestan. Gos. Pedagog. Univ., 2011.

Ahmadzadeh, F., Flecks, M., Carretero, M.A., Böhme, W., Ilgaz, C., Engler, J.O., Harris, D.J., Üzüm, N., and Rödder, D., Rapid lizard radiation lacking niche conservatism: ecological diversification within a complex landscape, *J. Biogeogr.*, 2013, vol. 40, no. 9, pp. 1807–1818.

Ahmadzadeh, F., Flecks, M., Rödder, D., Böhme, W., Ilgaz, C., Harris, D.J., Engler, J.O., Üzüm, N., and Carretero, M.A., Multiple dispersal out of Anatolia: biogeography and evolution of oriental green lizards, *Biol. J. Linn. Soc.*, 2013a, vol. 110, no. 2, pp. 398–408.

Ananjeva, N.B., Doronin, I.V., and Mazanaeva, L.F., VII Congress of the Nikolsky Herpetological Society under the Russian Academy of Sciences, *Izv. Vyssh. Uchebn. Zaved., Povolzh. Reg., Estestv. Nauki*, 2019, no. 1 (25), pp. 5–11.

Balashov, Yu.S., *Parazitizm kleshchei i nasekomykh na nazemnykh pozvonochnykh* (Parasitism of Ticks and Insects on Terrestrial Vertebrates), St. Petersburg: Nauka, 2009.

Bannikov, A.G., Materials on the biology of amphibians and reptiles of Southern Dagestan, *Uch. Zap. Mosk. Gor. Pedagog. Inst. im. V.P. Potemkina*, 1954, vol. 28, pp. 75–88.

Bischoff, W., Zur verbreitung und systematik der zauneidechse, *Lacerta agilis* Linnaeus, 1758, *Mertensiella*, 1988, no. 1, pp. 11–30.

Borkin, L.J. and Litvinchuk, S.N., Amphibians of the Palearctic: taxonomic composition, *Proceedings of the Zoological Institute RAS*, 2013, vol. 317, no. 4, pp. 494–541.

Busby, J.R., BIOCLIM—a bioclimate analysis and prediction system, *Plant Prot. Q.*, 1991, vol. 6, pp. 8–9.

Butaeva, F.G., Komarov, Yu.E., and Lotiev, K.Yu., Introduction, in *Krasnaya kniga Respubliki Yuzhnaya Osetiya* (Red Data Book of the Republic of South Ossetia), Kabulov, A.Z., Ed., Nalchik: Izd. M. i V. Kotlyarovykh (OOO Poligrafservis i T), 2017, pp. 8–11.

Claudia, A., Franke, F., Bleidorn, C., Bernhard, D., and Schlegel, M., Phylogenetic analysis of the *Lacerta agilis* subspecies complex, *Syst. Biodiversity*, 2014, vol. 12, no. 1, pp. 43–54.

Darevsky, I.S., *Lacerta media* Lantz et Cyren, 1920, in *Krasnaya kniga Rossiiskoi Federatsii (zhivotnye)* (Red Data Book of the Russian Federation (Animals)), Danilov-Danil'yan, V.I. et al., Eds., Moscow: AST-Astrel', 2001, pp. 333–334.

Doronin, I.V., Ananjeva, N.B., Barabanov, A.V., Milto, K.D., and Khairutdinov, I.Z., On the type specimens of amphibians and reptiles from the collection of Eduard Eichwald, in *Materialy yubileinoi otchetnoi nauchnoi sessii, posvyashchennoi 185-letiyu Zoologicheskogo Instituta RAN. Sankt-Peterburg, Rossiya 13–16 noyabrya 2017* (Proceedings of the Anniversary Scientific Session Dedicated to the 185th Anniversary of the Zoological Institute, Russian Academy of Sciences, St. Petersburg, Russia, November 13–16, 2017), St. Petersburg: Zool. Inst. Ross. Akad. Nauk, 2017, pp. 77–80.

Doronin, I.V., Mazanaeva, L.F., and Doronina, M.A., The use of GIS-modeling for the analysis of the distribution of three-lined lizard, *Lacerta media* Lantz et Cyren, 1920, in the territory of Dagestan (Russia), *Proceedings of the Zoological Institute RAS*, 2018, vol. 322, no. 4, pp. 463–480.

Duisebaeva, T.N., Doronin, I.V., Malakhov, D.V., Kukushkin, O.V., and Bakiev, A.G., GIS analysis of the distribution and habitat conditions of *Emys orbicularis orbicularis* (Testudines, Emydidae): methodological aspects, *Izv. Vyssh. Uchebn. Zaved., Povolzh. Reg., Estestv. Nauki*, 2019, no. 1 (25), pp. 28–40.

Eichwald, E., *Reise auf dem Caspischen Meere und in den Caukasus. Unternommen in den Jahren 1825–1826. Erster band*, Stuttgart: Verlag der J.G. Gotta'schen Buchhandlung, 1834.

Elith, J., Quantitative methods for modeling species habitat: comparative performance and an application to Australian plants, in *Quantitative Methods for Conservation Biology*, New York: Springer, 2002, pp. 39–58.

Elith, J., Phillips, S.J., Hastie, T., Dudik, M., Chee, Y.E., and Yates, C.J., A statistical explanation of MaxEnt for ecologists, *Diversity Distrib.*, 2011, vol. 17, no. 1, pp. 43–57.

Fedina, A.E., The main patterns of landscape differentiation of mountainous Dagestan and their influence on the economic use of the territory, in *Voprosy landshaftovedeniya* (Problems of Landscape Science), Alma-Ata: Akad. Nauk KazSSR, 1963, pp. 5–96.

Ficetola, G.F., Falaschi, M., Bonardi, A., Padoa-Schioppa, E., and Sindaco, R., Biogeographical structure and endemism pattern in reptiles of the Western Palearctic, *Prog. Phys. Geogr.*, 2018, vol. 42, no. 2, pp. 220–236.

Gurlev, I.A., *Prirodnye zony Dagestana* (Natural Zones of Dagestan), Makhachkala: Daguchpedgiz, 1972.

Hargreaves, A.L., Samis, K.E., and Eckert, C.G., Are species' range limits simply niche limits writ large? A review of transplant experiments beyond the range, *Am. Nat.*, 2014, vol. 183, no. 2, pp. 157–173.

Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G., and Jarvis, A., Very high resolution interpolated climate surfaces for global land areas, *Int. J. Climatol.*, 2005, vol. 25, pp. 1965–1978.

Honegger, R.E., *Threatened Amphibians and Reptiles in Europe*, suppl. vol. of *Hanbuch der Reptilien und Amphibien Europas*, Wiesbaden: Akademische Verlagsgesellschaft, 1981.

Kafash, A., Ashrafi, S., Ohler, A., and Schmidt, B.R., Environmental predictors for the distribution of the Caspian green lizard, *Lacerta strigata* Eichwald, 1831, along elevational gradients of the Elburz Mountains in northern Iran, *Turk. J. Zool.*, 2019, vol. 43, pp. 106–113.

Kalyabina-Hauf, S.A. and Ananjeva, N.B., Phylogeography and intraspecies structure of wide distributed sand lizard, *Lacerta agilis* L., 1758 (Lacertidae, Sauria, Reptilia) (case study of mitochondrial cytochrom *b*), *Proc. Zool. Inst. Russ. Acad. Sci.*, St. Petersburg, 2004, vol. 302.

Khonyakina, Z.P., Materials on the biology of the sand lizard of Dagestan, in *Issledovaniya po zoologii i parazitologii v Dagestane. Sbornik nauchnykh soobshchenii kafedry zoologii Dagestanskogo gosudarstvennogo universiteta* (Studies in Zoology and Parasitology in Dagestan. Collection of Scientific Reports of the Department of Zoology of the Dagestan State University), Makhachkala, 1970, pp. 88–93.

Khonyakina, Z.P., Caspian Green Striped and Three-lined lizards of Dagestan, in *Issledovaniya po zoologii i parazitologii v Dagestane. Sbornik nauchnykh soobshchenii kafedry zoologii Dagestanskogo gosudarstvennogo universiteta* (Studies in Zoology and Parasitology in Dagestan. Collection of Scientific Reports of the Department of Zoology of the Dagestan State University), Makhachkala, 1972, pp. 150–159.

Kidov, A.A., Kovrina, E.G., Timoshina, A.L., and Matushkina, K.A., Host–parasite relationships of the *Ixodes* tick (*Ixodes ricinus* L.) and the Terek lizard (*Lacerta boemica* S.) in North Ossetia, *Izv. Timiryazevsk. S-kh. Akad.*, 2016, no. 5, pp. 81–90.

Kireev, V.A., Amphibians and reptiles of Kalmykia, *Cand. Sci. (Biol.) Dissertation*, Kiev, 1981.

Koblik, E.A., Lappo, E.G., Red'kin, Ya.A., Tomkovich, P.S., and Kalyakin, M.V., Applied imaging of ranges is a weak link in Russian ornithology, *Zool. Zh.*, 2011, vol. 90, no. 7, pp. 835–845.

Kornilios, P., Thanou, E., Lymberakis, P., Ilgaz, Ç., Kumlutaş, Y., and Leaché, A., A phylogenomic resolution for the taxonomy of Aegean green lizards, *Zool. Scr.*, 2019, vol. 49, no. 1, pp. 14–27.

Krasovsky, D.B., Materials for the knowledge of the fauna of terrestrial vertebrates of the Rutul canton of the Dagestan ASSR, *Izv. 2-go Sev.-Kavkazsk. Pedagog. Inst.*, 1932, vol. 9, pp. 185–218.

Kuzmin, S.L., On the ecology of lizards in the Nakhchivan Autonomous Soviet Socialist Republic, *Pyataya Vsesoyuznaya gerpetologicheskaya konferentsiya "Voprosy gerpetologii," Avtoreferaty dokladov, Ashkhabad, 22–24 sentyabrya 1981 g.* (Fifth All-Union Herpetological Conference. Issues of herpetology, Ashkhabad, September 22–24, 1981, Abstracts of Papers), Leningrad: Nauka, Leningr. Otd., 1981, pp. 78–79.

Lee-Yaw, J.A., Kharouba, H.M., Bontrager, M., Mahony, C., Csergo, A.M., Noreen, A.M.E., Li, Q., Schuster, R., and Angert, A.L., A synthesis of transplant experiments and ecological niche models suggests that range limits are often niche limits, *Ecol. Lett.*, 2016, vol. 19, pp. 710–722.

Lisovsky, A.A., Dudov, S.V., and Obolenskaya, E.V., Advantages and limitations of application of the species distribution modeling methods. 1. A general approach, *Zh. Obshch. Biol.*, 2020, vol. 81, no. 2, pp. 123–134.

Marzahn, E., Mayer, W., Joger, U., Ilgaz, Ç., Jablonski, D., Kindler, C., Kumlutaş, Y., Nistri, A., Schneeweiss, N., Vamberger, M., Žagar, A., and Fritz, U., Phylogeography of the lacerta viridis complex: mitochondrial and nuclear markers provide taxonomic insights, *J. Zool. Syst. Evol. Res.*, 2016, vol. 54, no. 2, pp. 85–105.

Mazanaeva, L.F. and Askenderov, A.D., Landscape-zonal distribution of amphibians and reptiles in the intramountain Dagestan, *Vestn. Dagestan. Nauchn. Tsentra*, 2014, no. 54, pp. 53–58.

Mazanaeva, L.F. and Askenderov, A.D., On the distribution and ecology of the *Lacerta media* Lantz et Cyren, 1920 (Reptilia: Sauria: Lacertidae) in Dagestan, *Vestn. S.-Peterburg. Univ., Ser. 3: Biol.*, 2016, no. 3, pp. 93–99.

Mazanaeva, L.F. and Orlova, V.F., *Lacerta media* Lantz et Cyrén, 1920, in *Krasnaya kniga Respubliki Dagestan* (Red Data Book of the Republic of Dagestan), Abdurakhmanov, G.M., Ed.-in-Chief, Makhachkala, 2009, pp. 382–383.

Mazanaeva, L.F. and Orlova, V.F., Taxonomic and ecological diversity of lizards of Dagestan, in *Gornye ekosistemy i ikh komponenty: Materialy V Vseros. konferentsii s mezhdunarodnym uchastiem, posvyashchennoi 25-letiyu nauchnoi shkoly chl.-korr. RAN A.K. Tembotova i 20-letiyu Instituta ekologii gornykh territorii im. A.K. Tembotova KBNTs RAN* ("Mountain Ecosystems and Their Components," Proceedings of the V All-Russian Conference with International Participation Dedicated to the 25th Anniversary of the Scientific School of Correspodning Member of the Russian Academy of Sciences A.K. Tembotov and the 20th Anniversary of the Tembotov Institute of Ecology of Mountain Territories, KBNTs RAS), Nalchik, 2014, pp. 74–75.

Mazanaeva, L.F. and Tuniyev, B.S., Zoogeographical analysis of the Dagestan herpetofauna, *Current Studies in Herpetology*, 2011, vol. 11, nos. 1/2, pp. 55–76.

Ostrovskikh, S.V., *Lacerta strigata* Eichwald, 1831, in *Krasnaya kniga Krasnodarskogo kraya. Zhivotnye* (Red Data Book of the Krasnodar Territory. Animals), Zamotailov, A.S., Lokhman, Yu.V., and Vol'fov, B.I., Eds., Krasnodar: Adm. Krasnodar. Kraya, 2017, pp. 493–494.

Peel, M.C., Finlayson, B.L., and McMahon, T.A., Updated world map of the Koppen–Geiger climate classification, *Hydrol. Earth Syst. Sci.*, 2007, vol. 11, pp. 1633–1644.

Petrosyan, V., Osipov, F., Bobrov, V., Dergunova, N., Nazarenko, E., Omelchenko, A., Danielyan, F., and Arakelyan, M., Analysis of geographical distribution of the parthenogenetic rock lizard *Darevskia armeniaca* and its parental species (*D. mixta, D. valentini*) based on ecological modeling, *Salamandra*, 2019, vol. 55, no. 3, pp. 173–190.

Petrosyan, V., Osipov, F., Bobrov, V., Dergunova, N., Omelchenko, A., Varshavskiy, A., Danielyan, F., and Arakelyan, M., Species distribution models and niche partitioning among unisexual *Darevskia dahli* and its parental bisexual (*D. portschinskii, D. mixta*) rock lizards in the Caucasus, *Mathematics*, 2020, vol. 8, no. 1329, pp. 1–21.

Phillips, S.J. and Dudik, M., Modeling of species distributions with Maxent: new extensions and a comprehensive evaluation, *Ecography*, 2008, vol. 31, no. 2, pp. 161–175.

Roytberg, E.S. A comparative study of intra- and interpopulation variation in two sympatric lizards, *Lacerta agilis boemica* and *L. strigata* in Daghestan, *Russian Journal of Herpetology*, 1994, vol. 1, no. 1, pp. 77–85.

Roitberg, E.S., Mazanaeva, L.F., Ilyina, E.V., and Orlova, V.F., Die Echsen Dagestans (Nordkaukasus, Russland): Artenliste und aktuelle Verbreitungsdaten (Reptilia: Sauria: Gekkonidae, Agamidae, Anguidae, Scincidae et Lacertidae), *Faunistische Abhandlungen, Staatliches Museum für Tierkunde Dresden*, 2000, vol. 22, no. 8, pp. 97–118.

Rudik, A.M., Record of a striped lizard (*Lacerta strigata* Eichwald) on the Black Sea coast of the Caucasus, in *Gerpetologicheskie issledovaniya na Kavkaze* (Herpetological Research in the Caucasus), Leningrad: Zool. Inst. Akad. Nauk SSSR, 1986, pp. 187–188.

Sagonas, K., Poulakakis, N., Lymberakis, P., Parmakelis, A., Pafilis, P., and Valakos, E.D., Molecular systematics and historical biogeography of the green lizards (*Lacerta*) in Greece: insights from mitochondrial and nuclear DNA, *Mol. Phylogenet. Evol.*, 2014, vol. 76, pp. 144–154.

Scheldeman, X. and van Zonneveld, M., *Training Manual on Spatrial Analysis of Plant Diversity and Distribution*, Rome: Bioversity International, 2010.

Szczerbak, N.N., *Zemnovodnye i presmykayushchiesya Kryma (Herpetologia Taurica)*, Kiev: Naukova Dumka, 1966.

Szczerbak, N.N., Ostashko, N.G., Darevsky, I.S., Baranov, A.S., Andrushko, A.M., Vedmederya, V.I., Garanin, V.I., Ishchenko, V.G., Lukina, G.P., Okulova, N.M., Rashkevich, N.A., Tertyshnikov, M.F., Toporkov, L.Ya., Khonyakina, Z.P., Shvetsov, Yu.G., and Shcherban', M.I., Range, chapter 1 in *Prytkaya yashcheritsa. Monograficheskoe opisanie vida* (The Sand Lizard. Monographic Description of the Species), Yablokov, A.V., Ed., Moscow: Nauka, 1976, pp. 9–52.

Shibanov, N.V., Materials on the reptile fauna of Dagestan, in *Sbornik Trudov Gosudarstvennogo Zoologicheskogo muzeya (pri MGU)* (Proceedings of the State Zoological Museum under Moscow State University), 1935, vol. 2, pp. 63–68.

Sillero, N., Campos, J., Bonardi, A., Corti, C., Creemers, R., Crochet, P.-A., Crnobrnja Isailović, J., Denoël, M., Ficetola, G.F., Gonçalves, J., Kuzmin, S., Lymberakis, P., de Pous, P., Rodríguez, A., Sindaco, R., Speybroeck, J., Toxopeus, B., Vieites, D.R., and Vences, M., Updated distribution and biogeography of amphibians and reptiles of europe, *Amphibia–Reptilia*, 2014, vol. 35, pp. 1–31.

Sukhov, G.F., Review of the lizards of subgenus *Lacerta* (Sauria) found in the USSR, in *Sbornik rabot po sistematike, zoogeografii i ekologii* (A Collection of Papers on the Taxonomy, Zoogeography and Ecology), *Proceedings of the Zoological Institute of the Academy of Sciences of the USSR*, 1948, vol. 7, no. 3, pp. 101–117.

Tertyshnikov, M.F., Shchepot'ev, N.V., Rashkevich, N.A., Strel'tsov, A.B., Bulakhov, V.L., Konstantinova, N.F., and Zharkova, V.K., Movement and migration, chapter 9 in *Prytkaya yashcheritsy. Monograficheskoe opisanie vida* (The Sand Lizard. Monographic Description of the Species), Moscow: Nauka, 1976, pp. 246–251.

Troidl, A. and Troidl, S., *Lacertidae. Eidechsen Porträt, Ausgabe Nr. 1*, Text & Bild, Fürth, 2000.

Troidl, A. and Troidl, S., *Lacertidae. Eidechsen Porträt, Ausgabe Nr. 2*, Text & Bild, Fürth, 2001.

Tuniyev, B.S. and Lotiev, K.Yu., *Lacerta agilis* Linnaeus, 1758, in *Krasnaya kniga Respubliki Yuzhnaya Osetiya* (Red Data Book of the Republic of South Ossetia), Kabulov, A.Z., Ed., Nalchik: Izd. M. i V. Kotlyarovykh (OOO Poligrafservis i T), 2017, pp. 225–226.

Tuniyev, B.S. and Lotiev, K.Yu., *Lacerta media* Lantz et Cyren, 1920, in *Krasnaya kniga Respubliki Yuzhnaya Osetiya* (Red Data Book of the Republic of South Ossetia), Kabulov, A.Z., Ed., Nalchik: Izd. M. i V. Kotlyarovykh (OOO Poligrafservis i T), 2017a, pp. 226–227.

Tuniyev, B.S. and Ostrovskikh, S.V., *Lacerta media* Lantz et Cyren, 1920, in *Krasnaya kniga Krasnodarskogo kraya. Zhivotnye* (Red Data Book of the Krasnodar Territory. Animals), Zamotailov, A.S., Lokhman, Yu.V., and Vol'fov, B.I., Eds., Krasnodar: Adm. Krasnodar. Kraya, 2017, pp. 492–493.

Tuniyev, B.S. and Tuniyev, S.B., *Lacerta agilis* grusinica Peters, 1960, in *Krasnaya kniga Krasnodarskogo kraya. Zhivotnye* (Red Data Book of the Krasnodar Territory. Animals), Zamotailov, A.S., Lokhman, Yu.V., and Vol'fov, B.I., Eds., Krasnodar: Adm. Krasnodar. Kraya, 2017, pp. 490–491.

Tuniyev, S.B. and Tuniyev, B.S., *Lacerta agilis mzymtensis* (Tuniyev S. et Tuniyev B., 2008), in *Krasnaya kniga Krasnodarskogo kraya. Zhivotnye* (Red Data Book of the Krasnodar Territory. Animals), Zamotailov, A.S., Lokhman, Yu.V., and Vol'fov, B.I., Eds., Krasnodar: Adm. Krasnodar. Kraya, 2017a, pp. 491–492

Tuniyev, B.S., Tuniyev, S.B., Avdzhi, A., and Ilgaz, Ch., Herpetological research in eastern and northeastern Turkey, *Sovrem. Gerpetol.*, 2014, vol. 14, nos. 1/2, pp. 44–53.

Uetz, P., Cherikh, S., Shea, G., Ineich, I., Campbell, P.D., Doronin, I.V., Rosado, J., Wynn, A., Tighe, K.A., Mcdiarmid, R., Lee, J.L., Köhler, G., Ellis, R., Doughty, P., Raxworthy, C.J., Scheinberg, L., Resetar, A., Sabaj, M., Schneider, G., Franzen, M., Glaw, F., Böhme, W., Schweiger, S., Gemel, R., Couper, P., Amey, A., Dondorp, E., Ofer, G., Meiri, S., and Wallach, V., A global catalog of primary reptile type specimens, *Zootaxa*, 2019, vol. 4695, no. 5, pp. 438–450.

Vences, M., Brown, J.L., Lathrop, A., Rosa, G.M., Cameron, A., Crottini, A., Dolch, R., Edmonds, D., Freeman, K.L.M., Glaw, F., Grismer, L.L., Litvinchuk, S., Milne, M.G., Moore, M., Solofo, J.F., Noël, J., Nguyen, T.Q., Ohler, A., Randrianantoandro, C., Raselimanana, A.P., van Leeuwen, P., Wogan, G.O.U., Ziegler, T., Andreone, F., and Murphy, R.W., Tracing a toad invasion: lack of mitochondrial DNA variation, haplotype origins, and potential distribution of introduced *Duttaphrynus melanostictus* in Madagascar, *Amphibia–Reptilia*, 2017, vol. 38, no. 2, pp. 197–207.

Voronov, A.G., Drozdov, N.N., Krivolutsky, D.A., and Myalo, E.G., *Biogeografiya s osnovami ekologii* (Biogeography with the Basics of Ecology), Moscow: Mosk. Univ., Vyschaya Shkola, 2002.

Warren, D.L., Glor, R.E., and Turelli, M., ENMTools: a toolbox for comparative studies of environmental niche models, *Ecography*, 2010, vol. 33, pp. 607–611.

Zamotailov, A.S., Lokhman, Yu.V., Vol'fov, B.I., et al., Introduction, in *Krasnaya kniga Krasnodarskogo kraya. Zhivotnye* (Red Data Book of the Krasnodar Territory. Animals), Zamotailov, A.S., Lokhman, Yu.V., and Vol'fov, B.I., Eds., Krasnodar: Adm. Krasnodar. Kraya, 2017, pp. 9–18.

Zink, R.M., Genetics, morphology, and ecological niche modeling do not support the subspecies status of the endangered southwestern willow flycatcher (*Empidonax traillii extimus*), *Condor*, 2015, vol. 117, no. 1, pp. 76–86.

Translated by L. Solovyova