

Ecological Niche Modelling Reveals the Peculiarities of Ecological Disjunction Between Two Sympatric Racerunners in Kazakhstan: *Eremias lineolata* (Nikolsky, 1897) and *Eremias scripta* (Strauch, 1867)

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Abstract The ecological-niche models for two sympatric species, *Eremias lineolata* (Nikolsky, 1897) and *Eremias scripta* (Strauch, 1867), reveal evidence of spatial and temporal disjunction in the actual niches of both species. *Eremias lineolata* demonstrates a wide range of adaptations and, at the same time, has a greater need for winter precipitation and minimal temperature than *E. scripta*. Possible explanations for the thermal diversity of both species are provided. Thermal variables (monthly temperatures, monthly solar radiation, etc.) are traditionally important for ectotherm animals. Interestingly, as many as half of the key variables in both species are related to different aspects of environmental water balance (precipitation, air humidity, vapor pressure). There are several ways in which moisture may impact the lizard's life cycle. Soil humidity is related to soil temperature and may be important during winter hibernation. In summer, soil humidity may support successful embryogenesis. Precipitation during the warm months is a key factor in maintaining the moisture content of the soil. In winter, snow cover provides a better thermal balance of the soil's top layers where winter shelters are housed. Ecological niche modeling (ENM) is an interdisciplinary approach combining the geographical, climatic,

ecological, and biological aspects of the wellbeing of species. This interdisciplinary approach lifts biological studies onto a new, integrative level, providing a comprehensive view on species biology and answering the questions that might not be answered if the traditional methods for studying animals were used alone.

Keywords ecology, Kazakhstan, niche modelling, racerunners, species distribution

1. Introduction

Eremias lineolata (Nikolsky, 1897) and *Eremias scripta* (Strauch, 1867) belong to the family Lacertidae and are sympatric psammophilous lizards, though *E. lineolata* may inhabit gravel and clayish deserts, tacyric and even meadow soils. *Eremias scripta* appears to be more strictly limited to aeolian or loose sands with sparse vegetation, where it demonstrates substantially arboreal behavior (Bogdanov, 1960; Brushko, 1995; Chernov, 1959; Said-Aliev, 1979; Shenbrot *et al.*, 1991).

Though not much is known about their thermal biology, both species are believed to be the most thermophilic among the entire genus (Brushko, 1995; Mishagina, 2005). The extremal thermophilic alignment of both species originates from their natural history. The genus *Eremias* sensu Szczerbak is monophyletic (Guo *et al.*, 2011), being endemic to Asia (Szczerbak, 1974; Poyarkov *et al.*, 2014). *Eremias lineolata* and *E. scripta* along with another two psammophilous species (*Eremias intermedia* (Strauch, 1876) and *E. grammica* (Lichtenstein, 1823)), represent a focus on the Turanian sandy desert (Szczerbak, 1971). In contrast to species which are focused on steppe and mountain areas, species of this lineage demonstrate high adaptation to extremely arid and hot

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environments. *Eremias lineolata* and *E. scripta* possess different adaptations which minimize interspecific competition. *Eremias lineolata* has the longest hind legs among the desert *Eremias* species and is the most advanced fast runner and ground dweller, whereas the predominately arboreal and climbing *E. scripta* has maximal relative forelimb length (Ananjeva, 2003). *Eremias lineolata* can however still climb and forage in vegetation (Mishagina, 1992). The available data on the spatial and temporal characteristics of the species indicates that the overlapping of their ecological niches is not significant (Shenbrot *et al.*, 1991). Depending on the specific environment, the temporal disjunction of the niches of the two species may be entirely obscured. In general, *E. lineolata* demonstrates two peaks of daily activity with a more or less pronounced break during the hottest midday hours, whereas the activity of *E. scripta* is single-peaked, and it remains active throughout the day (Brushko, 1995; Mishagina 1992, 2007).

Since the review by Castilla *et al.* (1999), which did not include either *E. lineolata* or *E. scripta* in the list of species with well-studied thermobiology, very little data has become available on the thermal biology of both species. Available data describes the body temperature or ambient temperatures (air or substrate) during the active period (Ananjeva, 1971; Cherlin, 2015; Szczerbak, 1974), and there is no data on winter hibernation or egg incubation. Temperature is not a single resource available for lizards, as moisture conditions, especially for desert species, should be as important as the thermal environment. Recent advances employing geographic-information-systems (GIS) technology have allowed niche-based modeling of species' potential distribution, permitting tests of the geographic predictions of suitable habitats in ways not previously possible (Longley *et al.*, 2005).

The ENM procedure applied in the current study is based on a simple statistical approach (see the description below) that is aimed at revealing the key variables and their particular ranges, using the maximum of the available sets of variables to reveal the possible impact to species' well-being. We consider that the ideal ENM is impossible to develop as we will never have available for analyzing the entire set of variables that outlines the species' existence. For example, it is virtually impossible to obtain spatial and georeferenced data that represent behavioral aspects or to quantize the competition between species in the form of a raster grid. A spatial distribution model (SDM) is not a primary goal of our modeling, as any spatial distribution model, derived from a more or less limited set of input data, will represent the probability of the species' presence within a given area rather than the fact of the species' presence. We do not intend here to discuss the Maxent approach (Phillips *et al.*, 2004, 2006), widely applied to obtain spatial-distribution models. The

problem of the precision of the spatial model and its dependency upon the collinearity of used variables (Synes and Osborne, 2011) is also not a subject of discussion in this paper. The ENM and SDM approaches are based on a different ideology and are discussed in another paper (Malakhov, 2022, in press). There is a good review of Maxent's advantages and limitations (Lissovsky and Dudov, 2020), and of the general issues relating to SDM (Lissovsky *et al.*, 2021). We hope that those readers who may wish to obtain a more detailed view of the problems of ecological and spatial-distribution modelling will become more familiar with the above-mentioned papers. We will only note here that the removal of highly correlated variables from the analysis, being well suited for SDM needs, may result in the misinterpretation of important issues regarding species biology and ecology while carrying out the ENM. In a current paper (see Discussion), we provide a reasoned argument regarding the mean temperature in January as a limiting factor preventing further northward expansion of *E. lineolata*. This conclusion would be impossible if we remove monthly temperatures from the analysis as highly correlated and use only the annual mean temperature in the modelling procedure. The ecological niche modeling approach used in the current study was successfully applied in studying the ecological peculiarities of a diverse range of species (Dujsebayeva and Malakhov, 2017; Malakhov and Islamgulova, 2021).

This study focuses on an extended analysis of the environmental variables related to the Kazakhstan populations of two sympatric species of *Eremias* (the northernmost limit of both species' area), aiming to obtain more insights into species biology regarding the interspecific issues relating to these two sympatric lizards. The second aim is to discuss how and where the niches of both species overlap and which variables provide a niche difference. The species-distribution models were developed as an offshoot of our study. The analysis of the key variables and ranges for both species will provide a better understanding of their biology and adaptations, which facilitate minimal competition between two sympatric lizards of the same genus.

2. Materials and Methods

Occurrence datasets were used to develop ecological niche modeling (ENM) for both species, consisting of 87 points for *E. scripta* and 116 points for *E. lineolata* (Figure 1). The list of points used is given in the Supplementary data for both species. We used our own and colleagues' data as well as literature sources, which are listed in the general list of references. Geographic coordinates were translated to decimal degrees for the GIS applications.

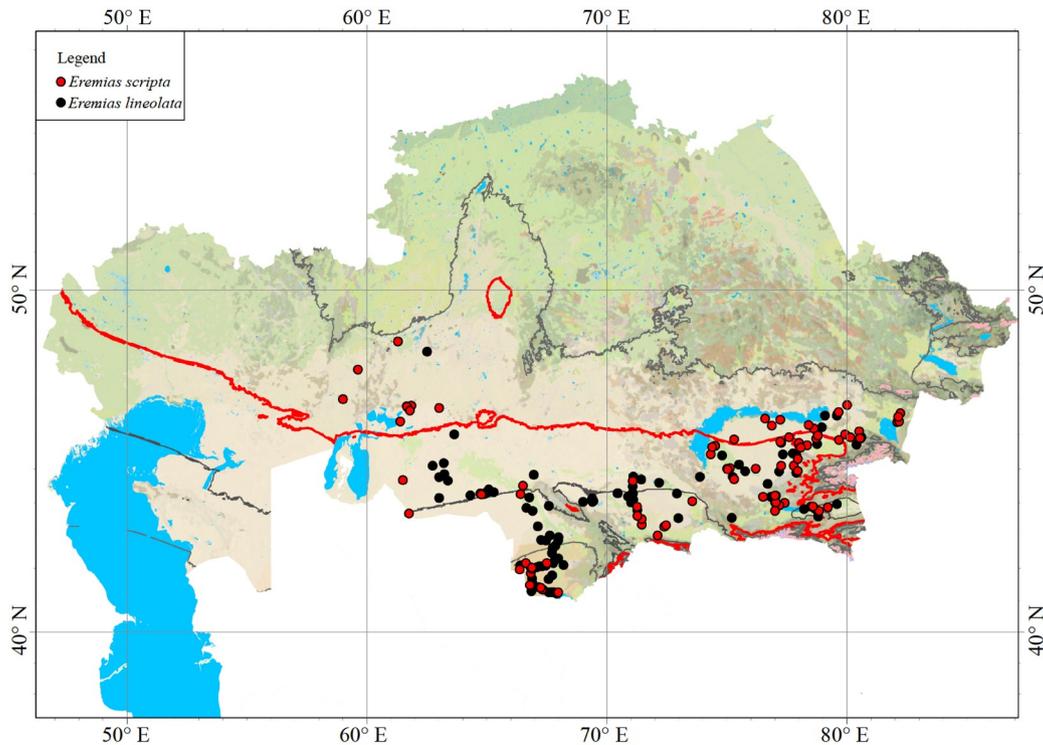


Figure 1 Input data on both species' distribution. Red dots represent known data on *Eremias scripta* in Kazakhstan, black dots resemble data on *E. lineolata*. Red line indicates $-10\text{ }^{\circ}\text{C}$ isotherm of January.

The following climatic datasets were applied in order to develop the current model: WorldClim (monthly temperatures and precipitation, solar radiation, vapor pressure); BioClim (a set of variables derived from WorldClim and meteorological stations—<http://www.worldclim.org>); Global Potential Evapotranspiration (<http://www.cgiar-csi.org/data/globalaridity-and-pet-database>); and the Digital Elevation Model and its derivatives, such as exposition, slope, and curvature, computed with ArcGIS functions. The WorldClim and BioClim datasets and their application in ecological modeling have been well described (Booth *et al.*, 2014; Hijmans *et al.*, 2005; Hutchinson *et al.*, 2009). Global-Pet is an index combining transpiration and evaporation (Allen *et al.*, 1998; UNEP, 1997).

We used the standard tool ESRI ArcGIS 10.8 (<https://www.esri.com/en-us/arcgis/about-arcgis/overview>) in order to make full use of the modeling and statistical capacity of StatSoft Statistica (<http://statsoft.ru/products/>). ArcGIS is a tool for processing geospatial data and producing spatial distribution maps. STATISTICA 12.0 provides the optimal ranges of each variable and, if necessary, a normal-distribution check using the Kolmogorov-Smirnov and Lilliefors tests for normality. It can be hypothesized that variables with normally distributed values have an important influence on the distribution of the species (Beaumont *et al.*, 2005). Variables

that demonstrate skewed distribution may also be relevant, such as those that do not have a negative value, such as solar radiation, and those with values between zero and one, such as vegetation indices. If there is no clear pattern for a variable in the distribution histograms, that variable may be classified as irrelevant. Similarly, where the histogram is normally distributed but is truncated in one or both tails the variable may also be rejected, as these graphs suggest that the species could tolerate other values of this variable not included in the species' climatic envelope. A truncated edge may occur if the distribution records for a species do not cover its entire geographic range (Beaumont *et al.*, 2005).

We use 75% randomly selected points of a given dataset to train the model and outline the optimal range of each variable. The remaining 25% of the ground points serve as a control group to define key variables—this procedure results in tables where key variables and their ranges are listed for each species. Analysis of variables values and key variable recognition is the base for describing the ecological niche and comprehending the meaning of a given variable to the species. To develop a map of spatial distribution, we reclassify the initial raster of each key variable into binary form, where “1” means all original values of the raster that comprise the optimal range of a given variable, and “0” means all original values outside of the variable's optimal range. The map itself results from the “Weighted Sum”

function and represents a new raster with a minimum value equal to “0” and a maximal value equal to the number of key variables for a given species. “Zero” value means an unsuitable environment, and the area of maximal values corresponds to the highest probability of observing a species in nature.

3. Results

Figure 2 shows the species distribution models. Analysis of the key variables (see Supplementary Tables) revealed by the

model indicates that wetness-related variables are at least as important for both species as temperature variables. Of all key variables in *E. scripta*, 40 are temperature-related (i.e., monthly temperatures and solar radiation), and 40 are wetness-related (precipitation, potential evapotranspiration, air humidity, vapor pressure). In *E. lineolata*, the number of wetness-related variables is 45 with 40 variables related to temperature. Further analysis of abiotic variables provides additional clues to support the “moisture” affinity of

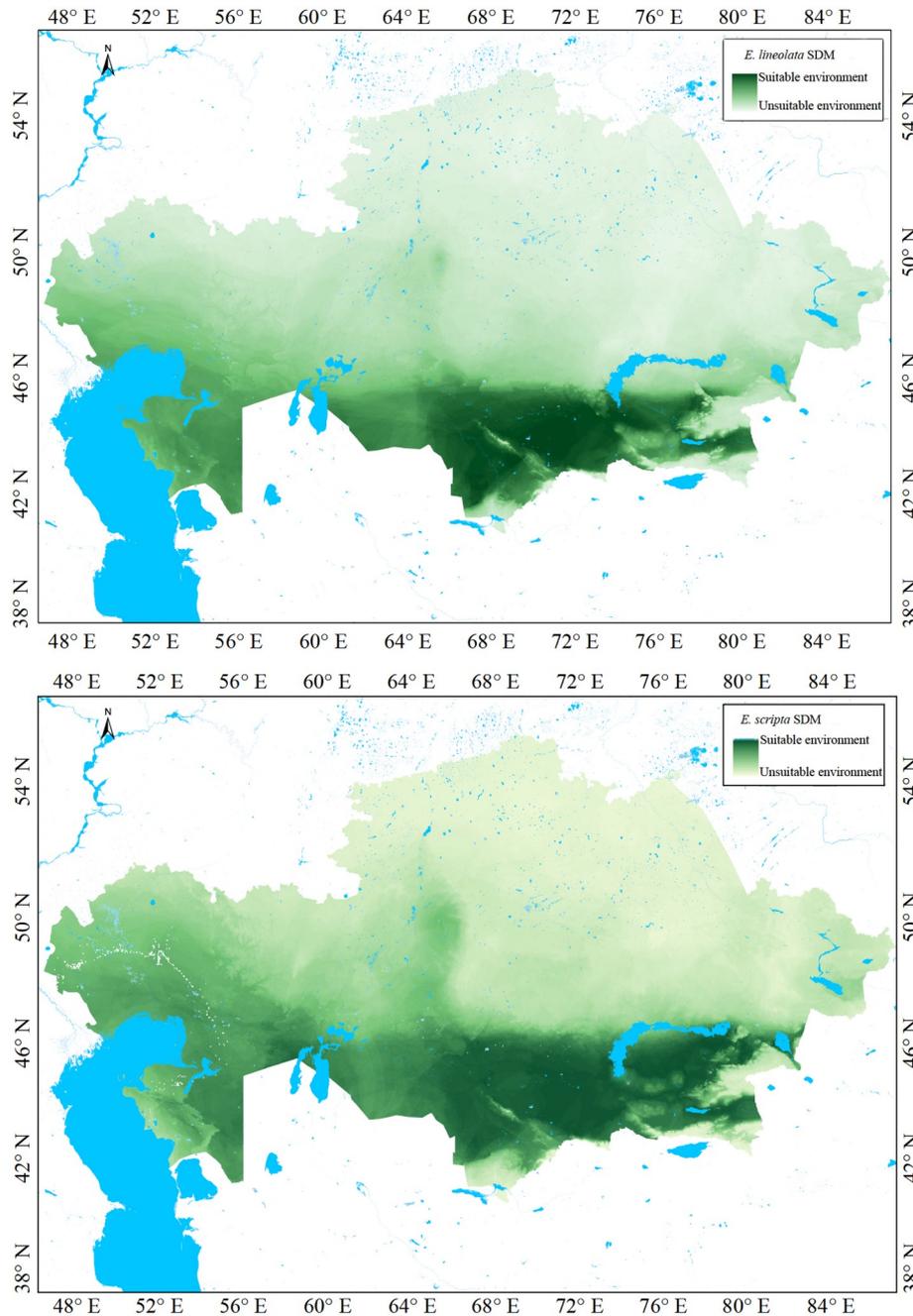


Figure 2 Species distribution model of *Eremias lineolata* (left) and *E. scripta* (right) in Kazakhstan.

E. lineolata. Precipitation during winter, spring, and partially summer-autumn seasons as well as the relative air humidity of the winter and spring months is vital for *E. lineolata*. Evapotranspiration is of particular importance for this species. *Eremias scripta* appears less sensitive to air humidity and maximal temperatures.

The seasonal distribution of key variables (Figure 3) reflects the highly continental environment where both species live.

At least half of the key variables describe winter conditions—the period of hibernation, as well as the autumn and spring months, when the lizards are still inactive.

The high ratio of “cold” variables is a sign of high continentality and those variables represent limiting conditions where species may still survive in a situation where they are unable actively to avoid unfavorable conditions.

4. Discussion

The distribution of ectotherms in general and lizards in part is regulated by ambient environmental temperature. In ectotherms, being able to carry out particular activities such as locomotion, immunity, growth, and even reproduction is greatly affected by body temperature. The mean body temperature of lizards is generally thought primarily to reflect evolutionary relationships rather than ecological associations (Bogert, 1949). Moreover, within-family variations of mean body temperature are significantly lower than those for between-family comparisons (Huey and Pianka, 1977), thus reflecting evolutionary affinities. Sympatric species will evolve mechanisms to minimize infra-specific competition. Niche differentiation is a process by which competing species utilize environmental resources differently, and includes aspects such as activity period, use of space, and

food preferences. Because of its effect on body temperature and thus on function and performance, environmental temperature is one of the most important ecological factors for ectotherm animals and is therefore also considered a vital resource. As ectotherms, sympatric lizards are ideal for investigating temperature-driven niche differentiation and coexistence (Pianka, 1986).

4.1. Spatial distribution model Spatial distribution models of both species demonstrate the optimal ranges of the model in South and South-Eastern Kazakhstan, accordingly to the actual distribution of lizards. The potential area for *E. lineolata* is narrower, especially in the North, which can be explained by the biology of the species. The area to the West of the Aral Sea is defined as quite suitable for both species although there are no documented findings of lizards there. In this case, the substrate is a limiting factor, as a vast area between the Aral Sea and the Caspian Sea is covered with luvic xerosoils and kashtanozems, solonchaks, and solonetz (The Digital Soil Map of the World, 2003) without significant sandy massifs (Figure 4).

The absence of sandy corridors between Central and Western Kazakhstan prevented the expansion of psammophilous species to the West. This barrier renders doubtful the presence of both species in Western Kazakhstan, as documented by some authors (Paraskiv, 1956; Szczerbak, 1974) summarizing data from various collections. These findings were discussed in our previous paper (Dujsebajeva *et al.*, 2017).

4.2. Body temperature in lacertid lizards Lizards living in thermally more variable regions are better able to tolerate low and high temperatures and a broader range of body temperatures (Qu *et al.*, 2011). In general, lacertids possess an

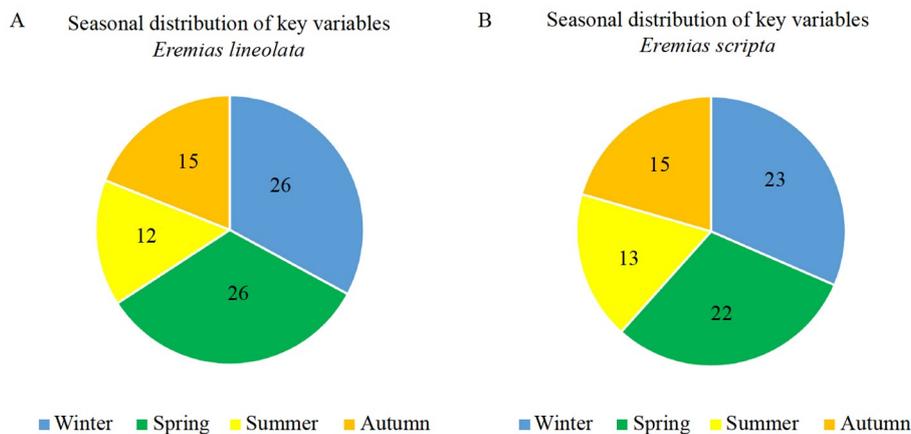


Figure 3 Seasonal distribution of key variables. A: *Eremias lineolata*; B: *E. scripta*.

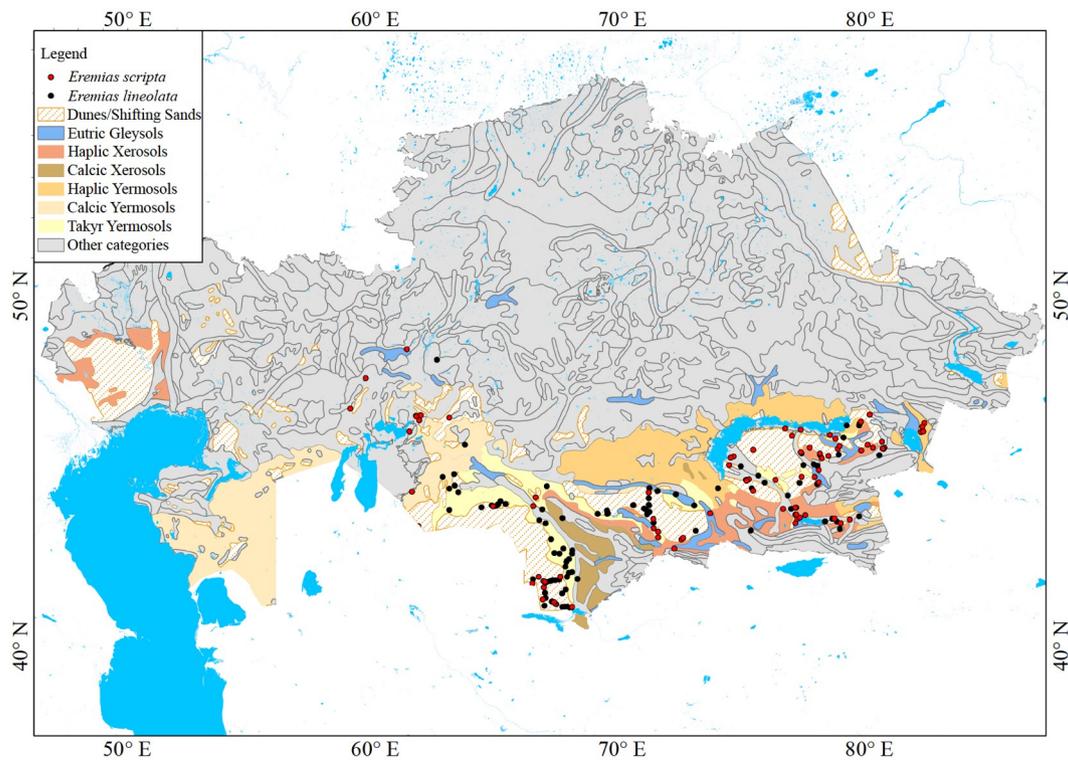


Figure 4 Soil map (based on FAO World Soil Map) shows the spatial distribution of soil types preferable by both *Eremias* species. Note the absence of suitable soils between Aral and Caspian Seas.

active body temperature at 32–38 °C, with a critical maximum temperature (CT_{max}), when the animal becomes immobile, of about 44 °C and a critical minimum temperature (CT_{min}) of about 3.5 ± 2.2 °C (Clusella-Trullas *et al.*, 2014). Although we did not find direct evidence of body temperature during wintering, it may be supposed that the wintering temperature is close to CT_{min} and will not reach negative values. Selected body temperature (T_{sel}) is the optimal range that an animal reaches by means of thermoregulatory behavior which permits the best performance in terms of locomotor and digestive activities. The mechanisms of body temperature regulation are different in sympatric species. Wang *et al.* (2019) provided an example of differentiated T_{sel} in open-ground species (*Phrynocephalus przewalskii* (Strauch, 1876)) and those occupying shaded and cooler habitats (*Eremias argus* Peters, 1869; *E. multiocellata* Günther, 1872). The T_{sel} of open-ground animals varies between 34 °C and 39 °C and the T_{sel} of both *Eremias* species varies between 33–37 °C. The active body temperature in *E. scripta* is close to 40 °C (Cherlin, 2015). The active body temperature range of the rapid racerunner *E. velox* (Pallas, 1771) is 38–41 °C (Cherlin and Chikin, 1991). The desert psammophilous *E. grammica* has a wider range of 36–42 °C (Cherlin and Muzychenko, 1983). Cherlin (2019) discussed the ecological disjunction of two *Eremias* species (*E.*

intermedia and *E. lineolata*), noting that the extended plasticity of *E. lineolata* results in behavioral reactions within this species. *E. lineolata* can use shrubs to avoid overheating from the substrate and have higher active body temperature values. The range of active body temperature in *E. lineolata* is 34–41 °C, whereas in *E. intermedia* it falls between 33–39 °C. More thermophilous and diverse in behavior, *E. lineolata* has more possibility of utilizing thermal resources than *E. intermedia*. It seems very important that the optimal locomotor body temperature is higher than the optimal digestive body temperature (van Damme *et al.*, 1991), and the range of optimal digestive temperature has a broader thermal breadth. Another important aspect one should consider prior to discussing thermal prerequisites of a given lizard species is that of the lower body temperatures in juveniles (Tang *et al.*, 2013; Xu and Ji, 2006). Moreover, the juveniles of *Eremias brencleyi* Günther, 1872 and *E. multiocellata* have a narrower range of active body temperatures than adults (Tang *et al.*, 2013; Xu and Ji, 2006). There are no significant differences in the thermal ranges of active animals. Variations in active body temperature have a rather behavioral nature and do not directly regulate the distribution of a species. Critical body temperatures appear to be important when describing the spatial distribution of lizards. However, this problem has yet to be studied in detail.

4.3. Incubation temperature Another important factor in regulating or limiting the distribution of ectotherm species is incubation. This stage is the most vulnerable in the entire life cycle, as embryos cannot take action to avoid environmental changes. There exists a specific optimal range of incubation temperatures. Hatchlings from eggs incubated at moderate temperatures are generally larger, have better functional performance, and grow faster than those which experience extremely low and high incubation temperatures (Du *et al.*, 2013). We could not find direct data on incubation temperature relating to *E. lineolata* and *E. scripta*. For other lacertids (*Podarcis muralis* (Laurenti, 1768)), the optimal incubation temperature is 24–28 °C (van Damme *et al.*, 1992). Hao *et al.* (2006) postulated decreased locomotor activity of *E. argus* hatchlings incubated under high temperatures and concluded that the range of temperatures that provide the best-quality hatchlings is 24–27 °C. Similar ranges are known for lizards of the *Phrynocephalus* genus (Tang *et al.*, 2012), with an optimal incubation temperature of about 30 °C.

Air and soil temperatures are correlated reasonably closely in a temperate continental environment (Shulgin, 1967; Zheng *et al.*, 1993), and predicted soil temperatures are reasonably accurate for simulating biological processes (Zheng *et al.*, 1993). Various local and regional models for estimating soil temperature at different depths have been developed. Park *et al.* (2020) attempted to develop a model to predict soil temperature by analyzing the air temperature and soil-water content in a cold environment. Ahmad and Rasul (2008) proposed different regressions in order to estimate the soil temperature of warm continental environments at a given season of the year and for a particular soil depth. Islam *et al.* (2015) have produced a somewhat generalized and simplified

model for predicting continental soil temperature. Since we did not find similar research on air and soil temperature correlations for the Kazakhstan desert, we used the simplified approach of Islam *et al.* (2015) to provide a rough estimate of soil temperature throughout the entire year for both species. ENM provides species-specific values of air temperatures so that it is possible to calculate soil temperature using the existing regression equations (Tables 1 and 2).

Supposing the lower limit of successful incubation in our species to be around 19–20 °C, we may obtain appropriate periods for both species based on soil-temperature estimation. Both species deposit their egg clutches at depths of up to 10 cm (Paraskiv, 1956). If egg clutches are laid at a depth of 5 cm and under the stress of minimal summer temperatures, embryogenesis in *E. lineolata* is possible during all of the summer months. In *E. scripta*, by contrast, embryogenesis meets with relatively acceptable conditions only in July. Eggs of both species that are laid more deeply (10 cm) during a cool summer may develop throughout all the summer months. However, the temperature of *E. scripta* eggs is still near the lower edge of the acceptable range. *Eremias lineolata* appears better adapted for successful reproduction. It is also known (Bogdanov and Sudarev, 1989) that the reproductive period of sandy lizards starts later and continues longer than that of solid-soil inhabitants. Again, *E. lineolata*, associated with a wide range of soils, demonstrates relatively higher plasticity and a more comprehensive “corridor of possibility” for successful reproduction in terms of both the thermal and physical properties of the soil. The first author of the current paper documented the absence of *E. scripta* in some years in the same (*sensu lato*) area, where the species was found in other years. Knowing the adaptive narrowness and physical limits of *E. scripta* reproduction, as revealed by ENM, it is possible to

Table 1 Monthly soil temperatures by *E. lineolata* model. Temperatures acceptable for embryogenesis (see text below) are given in bold.

	Averaged min air temperature (°C)	Tsoil_10 cm (°C)	Tsoil_5 cm (°C)	Averaged mean air temperature (°C)	Tsoil_10 cm (°C)	Tsoil_5 cm (°C)	Averaged max air temperature (°C)	Tsoil_10 cm (°C)	Tsoil_5 cm (°C)
December	-6.5	0.751	-2.04	-3.65	3.1507	0.525	2.2	8.0764	5.79
January	-9.9	-2.1118	-5.1	-5.35	1.7193	-1.005	-0.7	5.6346	3.18
February	-8.5	-0.933	-3.84	-3.65	3.1507	0.525	1.35	7.3607	5.025
March	-1.5	4.961	2.46	3.7	9.3394	7.14	8.9	13.7178	11.82
April	6.85	11.9917	9.975	12.85	17.0437	15.375	18.9	22.1378	20.82
May	12.45	16.7069	15.015	19.05	22.2641	20.955	25.55	27.7371	26.805
June	17	20.538	19.11	23.85	26.3057	25.275	30.75	32.1155	31.485
July	19.3	22.4746	21.18	26.25	28.3265	27.435	33.35	34.3047	33.825
August	16.9	20.4538	19.02	24.35	26.7267	25.725	31.75	32.9575	32.385
September	11.25	15.6965	13.935	18.8	22.0536	20.73	26.4	28.4528	27.57
October	4.3	9.8446	7.68	11	15.486	13.71	17.7	21.1274	19.74
November	4.7505	2.235	4.7505	3.5	9.171	6.96	8.65	13.5073	11.595

Table 2 Monthly Soil temperatures by *E. scripta* model. Temperatures acceptable for embryogenesis (see text below) are given in bold.

	Averaged min air temperature (°C)	Tsoil_10 cm (°C)	Tsoil_5 cm (°C)	Averaged mean air temperature (°C)	Tsoil_10 cm (°C)	Tsoil_5 cm (°C)	Averaged max air temperature (°C)	Tsoil_10 cm (°C)	Tsoil_5 cm (°C)
December	-7.95	-0.4699	-3.345	-3.65	3.1507	0.525	0.65	6.7713	4.395
January	-11.85	-3.7537	-6.855	-7.1	0.2458	-2.58	-2.45	4.1611	1.605
February	-10.25	-2.4065	-5.415	-5.25	1.8035	-0.915	-0.25	6.0135	3.585
March	-2.65	3.9927	1.425	2.5	8.329	6.06	7.6	12.6232	10.65
April	5.75	11.0655	8.985	12.2	16.4964	14.79	18.75	22.0115	20.685
May	11.5	15.907	14.16	18.65	21.9273	20.595	25.5	27.695	26.76
June	16.2	19.8644	18.39	23.6	26.0952	25.05	30.75	32.1155	31.485
July	18.4	21.7168	20.37	25.9	28.0318	27.12	33.3	34.2626	33.78
August	16	19.696	18.21	24	26.432	25.41	31.7	32.9154	32.34
September	10.45	15.0229	13.215	18.4	21.7168	20.37	26.3	28.3686	27.48
October	3.2	8.9184	6.69	10.2	14.8124	12.99	16.8	20.3696	18.93
November	-3	3.698	1.11	2.3	8.1606	5.88	7.5	12.539	10.56

hypothesize that the cooling events during the previous summer resulted in the mass death of egg clutches and reduced population density. Repeated cold summers over several years may result in total devastation of the local population as the life expectancy of *Eremias* may appear well be too short to overcome the consequences of the cooling effect.

4.4. Hibernation Winter hibernation is a stage of high risk since animals are immobile and can only withstand environmental fluctuations by means of the organism's physiological capacity (which appears to be species-specific). Having no direct evidence of the wintering conditions of *Eremias*, we expect its body temperature in winter to be close to the CTmin where the animal is immobile but still alive. A list of key variables for both species encompasses minimal and mean monthly winter-month temperatures (see Supplementary Tables). A rough estimate of the mean temperature of the soil at a depth of 10 cm (Tables 1 and 2) gives a temperature for winter shelter of around 0–3 °C. This range is similar to the CTmin of lizards, so the modeling data confirmed our suggestion regarding the similarity of CTmin and wintering body temperature. Of course, it is possible to expect a variety of local fluctuations in soil temperatures during the winter. Factors that may regulate the soil temperature in a given location include, among others, the mechanical components of the soil, the presence of snow cover in a particular year, soil moisture and the microrelief. Such fluctuations are difficult to take into account when designing a model. However, we may conclude from our model that minimal winter monthly temperatures may appear as a limiting factor. In contrast, mean monthly temperatures describe the existing preferences of both species and fit well

with our knowledge of the physiology of lizards as discussed here. Analyzing the temperature gradients, it is possible to conclude that *E. lineolata*'s distribution is virtually limited by a January isotherm of -10 °C as there are only a few known finds of this species to the north of this isotherm (Figure 1).

As shown by the ENM (Table 1), an air temperature of -10 °C is the lowest acceptable winter temperature for *E. lineolata*. An air temperature of -10 °C means the shelter temperature in the shelter is (-5) to (-2), depending on the depth of the shelter. However, the question of actual body temperature during winter hibernation still requires experimental support. Table 3 shows the differences in the optimal range for selected variables. Variables listed in the table, except for the Aridity Index, are key for both species, so a direct comparison is permissible.

The aridity index, calculated as a ratio of mean annual precipitation and mean annual potential evapotranspiration, is a measure of precipitation availability (UNEP 1997). Higher index values represent more humid conditions. The index range can be divided into the following classes: Hyper Arid < 0.01; Arid 0.03–0.2; Semi-Arid 0.2–0.5, Dry sub-humid 0.5–0.65, Humid > 0.65 (UNEP 1997). Following this classification, both *Eremias* species inhabit arid to semi-arid areas.

Eremias lineolata requires slightly higher values for its annual temperature range. The difference is mainly concerned with the lower limit, which is almost 3 °C higher than for *E. scripta* (see Min temperature of the coldest month and Mean temperature of the coldest quarter). The mean temperature of the driest quarter is almost the same. Interestingly, the lower value of the minimal temperature in July is almost 2 °C higher in *E. lineolata*. Precipitation during the winter and spring months in *E. lineolata* is markedly higher. It may be explained

by the thickness of the snow cover required to maintain the temperature of the winter shelter for the winter months. Optimal spring vegetation may be related to the optimal energy cost of foraging.

Analysis of the distribution of both species within the Köppen-Geiger climatic zonation (Kottek *et al.*, 2006) reveals quite an interesting pattern of climatic adaptations of both species in Kazakhstan (Table 4).

More than half of the localities for *E. scripta* are associated with an Arid/Steppe/Cold zone (BSk). As many as 39% of the occurrence points for *E. lineolata* also fall into BSk. Four *Eremias* species (*E. lineolata*, *E. scripta*, *E. grammica*, and *E. intermedia*) compose the Turanian sandy-desert focus of genus diversification, in contrast to the Steppe focus (*E. arguta* and *E. velox*) (Szczerbak, 1971). Populations from Kazakhstan form the northernmost frontier of the entire desert group, spreading almost to the steppe zone (Figure 5). At the same time, areas of the steppe species are partially (*E. arguta*) or almost entirely (*E. velox*) overlapping known areas of the desert species discussed here (Szczerbak, 1974).

Hence, it is a good idea to provide a complex ecological analysis of both desert and steppe groups encompassing all the available data on the distribution and abiotic variables available. Such an analysis may provide valuable information on the evolution of the genus and the radiation and ecological traits of *Eremias* species. Considering such a variety of thermal reactions and traits within even a single genus, it appears

reasonable to analyze the set of thermal variables and its correlation to other (wetness) data rather than focus on a single variable.

4.5. Important variable sets The study of variable values by key dataset and the study of selected variables may result in significant observations and conclusions. In our case, the analysis of species-specific temperature requirements (Figure 6) provides additional evidence of extended thermal sensitivity in relation to *E. lineolata*. Graphs have been produced with averaged values for the optimal range of each variable.

The graphs show that *E. lineolata* has a greater requirement for minimal monthly temperatures throughout the entire year and monthly winter precipitation. What could be the reason for such a difference in thermal and precipitation requirements in sympatric species of the same genus? The higher demand by *E. lineolata* for winter precipitation has a simple explanation. We have found that the northern border of *E. lineolata* is almost coterminus with the January isotherm of -10°C , so the species is less resistant to low temperatures than *E. scripta*. Thicker snow cover provides more stable soil temperature, so *E. lineolata* has better chance of surviving hibernation if the soil is covered with snow. Thermal difference appears to have more complicated nature. The impact of winter temperatures as a limiting factor of the survival of the species is clear. Why do lizards have different requirements during the warm season? The maximum air

Table 3 The optimal ranges of some ENM variables describing the general climate prerequisites of *Eremias lineolata* and *E. scripta*.

Variable	<i>Eremias lineolata</i>	<i>Eremias scripta</i>
Aridity Index	0.1197–0.3078	0.1497–0.3069
Annual mean temperature ($^{\circ}\text{C}$)	7.8–14.4	6.2–14.0
Min temperature of the coldest month ($^{\circ}\text{C}$)	(–15.1)–(–4.8)	(–17.9)–(–5.8)
Mean temperature of the coldest quarter ($^{\circ}\text{C}$)	(–8.7)–1.1	(–10.9)–1.0
Mean temperature of the driest quarter ($^{\circ}\text{C}$)	20.8–25.4	19.6–25.4
Minimal temperature, July ($^{\circ}\text{C}$)	17.5–21.1	15.9–20.9
Solar radiation, July ($\text{kJ}/\text{m}^2\text{day}^{-1}$)	24 200–27 268	21 278–24 485
Annual Precipitation (mm)	136–313	147–302
Precipitation of the wettest month (mm)	20–48	18–44
Precipitation of the wettest quarter (mm)	50–129	48–102
Precipitation of the coldest quarter (mm)	42–105	36–89

Table 4 Distribution of known finds within Köppen-Geiger zones in Kazakhstan.

Climate	<i>E lineolata</i>	%	<i>E scripta</i>	%
BWk (Arid/Desert/Cold)	32	27.82609	15	17.44186
BSk (Arid/Steppe/Cold)	46	39.13043	45	51.16279
Dsa (Cold/Dry_summer/Hot_Summer)	27	23.47826	10	11.62791
Dfa (Cold/Without_dry_season/Hot-Summer)	11	9.565217	17	19.76744
Total number of occurrence points	116	100	87	100

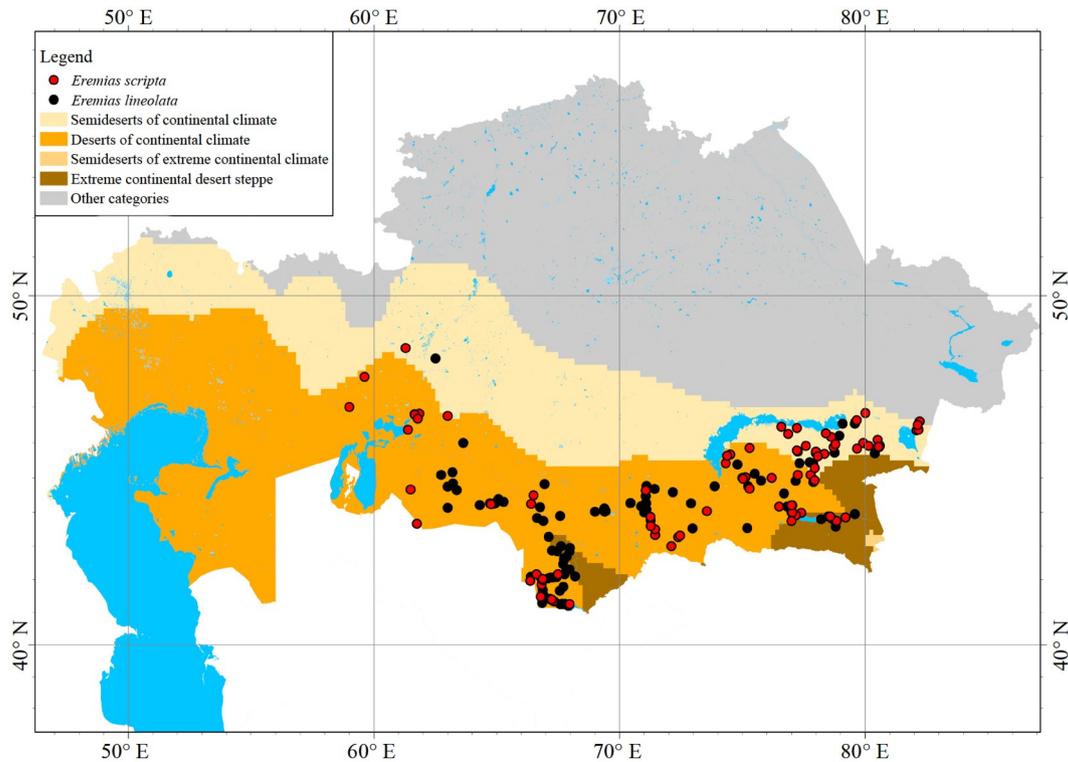


Figure 5 Distribution of studied species within major ecological divisions.

temperature ($\sim 33^\circ\text{C}$) is a limiting factor, as it defines the substrate temperature up to 60°C (Brushko, 1995). It has been shown (Ananjeva, 2003) that this temperature is the upper allowable limit for *E. lineolata*. The substrate temperature preferred by this species is $38\text{--}41^\circ\text{C}$ (Szczerbak, 1974). The higher requirements of *E. lineolata* seem, at first glance, not entirely justified in comparison with the arboreal *E. scripta*. In the hot months, *E. lineolata* has two peaks of daytime activity (Brushko, 1995; Mishagina, 2005), avoiding high temperatures, while *E. scripta* remains active all day (Brushko, 1995; Cherlin, 2015). During midday, *E. scripta* remains in the relative shade of shrubs, which offer lower ambient temperatures. The seeming contradiction regarding the higher requirements of *E. lineolata* in terms of minimum temperatures can be explained as follows. Presuming that lizards belonging to the same genus tend to have similar, but not necessarily identical, mean body-temperature preferences, even though they live in different habitats or climatic regions (Bogert, 1949), it can be hypothesized that the different requirements in this case reflect evolutionary adaptations of species with different lifestyles. *E. lineolata* is predominantly a ground-dweller that only through external pressures and for a brief period moves to an arboreal lifestyle. It is known (Xu *et al.*, 2001) that increase in sprint speed with increase in body temperature up to its optimal upper limit in *E. brenchleyi* and

the length of continuous locomotion is longer when the body temperature is higher. Bi *et al.* (2015) demonstrated decrease in locomotor performance in *E. multiocellata* with increasing vegetation cover and the appearance of branch barriers. This means that the absolute speed of arboreal species is less than that of ground-dwellers, as well as the absolute length of a single trail between two stops. Another study (Bennett *et al.*, 1984; Nagy *et al.*, 1984) demonstrated a significant difference in energy consumption between the active predator *Eremias lugubris* (*Heliobolus lugubris* (Smith, 1838)) and the sit-and-wait hunter *E. lineocellata* (*Pedioplanis lineocellata* (Dumeril, Bibron, 1839)), with intensity of metabolism in *E. lugubris* almost five times greater. Of the two species, *E. scripta*, with shorter trails and having lesser relative speed, spent less energy when foraging in shady arboreal environments compared with open-ground *E. lineolata*. Thus, the higher energy requirements of *E. lineolata* become well established. In addition, if we consider temperature not so much as a limiting factor but as an environmental resource (Magnuson *et al.*, 1979), then species will compete for the resource rather than tolerate it. In the case of our two species, maximal temperature is a physiological barrier to species well-being when the only way to withstand the extreme values is to avoid them. However, mean temperature appears as a subject of utilization along with other resources, such as food and

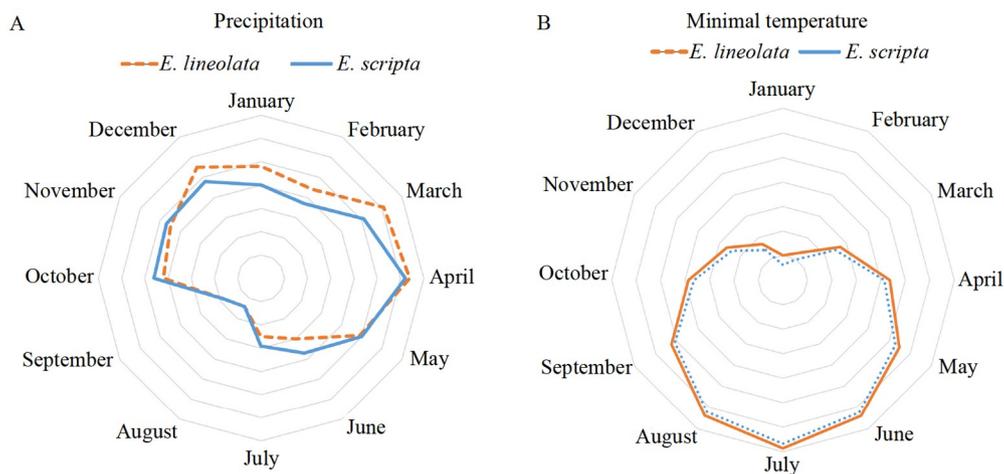


Figure 6 Yearly dynamics of monthly precipitation (A) and minimal temperature (B) values for *Eremias lineolata* and *E. scripta*.

moisture. The optimal body temperature in lizards, being of importance for sprint speed and endurance, is important in another significant way, since digestive performance is far more sensitive to body temperature than locomotor performance (Angiletta *et al.*, 2002; Luo *et al.*, 2006). From this point, the lower boundary of optimal mean temperatures, when the animal is passive, should provide optimal digestive conditions rather than locomotor performance.

4.6. Moisture Humidity is the main key factor for any arid ecosystem (Odum, 1986). The plains are more or less extensive land areas with almost uniform or poorly dissected relief and relatively weak development of valleys (Edelshtein, 1947). In the arid plains with their almost flat surfaces, uniform abundant incoming solar radiation, and intensive outgoing evaporation, the humidity of the habitat will strongly depend on the precipitation. Wetness-related or moisture-related key variables are as crucial as temperature-related variables. We will not discuss each variable separately, as there is very limited data on the impact of soil moisture or air humidity on lizards in general and in particular the two species discussed here. In other words, there is a lack of comparable experimental and field data to begin a detailed discussion on every single variable. Bearing in mind that the models revealed as many as half of the key variables (40 for *E. scripta* and 45 for *E. lineolata*) related to humidity (see Supplementary Tables), we will attempt to speculate on the possible impact of those variables on desert lizards.

After solar radiation and air temperature, soil moisture is one of the factors that regulates soil temperature. Shulgin (1967) noted that daily temperature fluctuations are significantly narrower in wet soils than in dry, and the difference between the temperatures of soil layers is not

significant for wet soils. In addition, snow cover (winter precipitation, which is a key variable for both species) prevents soil cooling during the winter months. Analyzing the seasonal dynamics of moisture content at different depths of a single sandy dune (Tomashevskiy, 1931), it is possible to conclude (Figure 7) that the dynamics of wetness fluctuations in the upper layer have a wider range compared to the deeper layers, especially in the summer months. The surface sand layer, where wetness fluctuations are significant, houses the shelters of adult and juvenile animals and egg clutches. The importance of soil moisture is thus evident, although experimental observations are needed to justify the precise impact of soil wetness on lizards.

Several studies of embryogenesis in different lizard species have provided evidence for moisture's importance on embryo development in general and the quality of hatchlings. Xu *et al.* (2005) documented much bigger final eggs in wetter substrates than those incubated in a drier environment. Tang *et al.* (2012) concluded that there is faster growth for embryos incubated in moist conditions. Marco *et al.* (2004) found dry eggs produce smaller hatchlings and reduced egg survival. Sun *et al.* (2014) related the cognitive function of hatchlings to the increased level of oxygen. The oxygen level dissolved in the egg substance depends on the egg temperature – the lower the temperature, the greater the oxygen content. Finally, all other things being equal, wetter soils possess a lower temperature and smaller temperature fluctuations and, thus a stable and relatively high oxygen level in the egg. Additionally, there is an indication (with no details on the amount of precipitation required, however) that summer or even autumn rains may trigger the development of follicles. Rains in June can trigger the re-development of follicles in females that have already

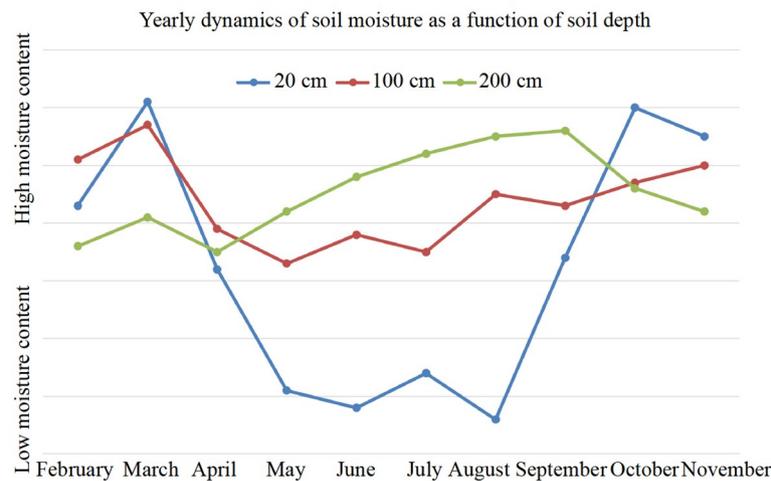


Figure 7 Yearly dynamics of the moisture content at different depths of sand dune.

completed breeding (Bogdanov and Sudarev, 1989). Another aspect of moisture impact, though poorly studied so far, may be related to the water homeostasis of adults (Litvinov *et al.*, 2014; Sannolo *et al.*, 2018). The water loss in different lizard species may differ significantly, and though our knowledge of the transpiration in reptiles is relatively insufficient, the relation of water loss to ambient temperature and wetness is undoubtedly clear. The number of wetness-related variables revealed as key variables is significant for both species studied, so the importance of humidity is rather an objective phenomenon than the modeling error. It may be hoped that future experiments will provide more details. One more impact of wetness may rely upon the dietary opportunities of lizards. Optimal wetness leads to an increase in the biomass of arthropods inhabiting plant litters, whereas increased aridity means their disappearance and a dietary shift to open-ground arthropods (Mishagina, 2005). In terms of species energetics, the growth of aridity means an increase in the animals' energy cost as regards foraging, as the lizard must run further to catch open-ground prey.

5. Conclusions

Our study provided important ideas regarding the evolutionary traits and possible ecological affinities of two *Eremias* – *E. lineolata* and *E. scripta*. The ENM developed provides evidence of wider adaptations of *E. lineolata* that demonstrate more diverse reactions and requirements than *E. scripta*. Lizards with a broader tolerance range occupy warmer habitats (Tang *et al.*, 2013), and we have demonstrated that *E. lineolata* has a higher requirement for winter precipitation and minimal temperature. Minimal temperature is a limiting factor, outlining the northern border of the specific area and

snow cover is a factor stabilizing the soil temperatures during hibernation. Along with conclusions fitting the existing knowledge on both species, the ENM raises fundamental questions on the possible impact of moisture on different stages of the lizard's life cycle and these will require additional experiments and measurements.

Another output of this paper concerns the methodological basis of biological studies. A single approach may not be effective when studying living nature. There are many examples of divergence in several aspects of thermal physiology in multiple taxonomic scales. Different traits have different heritability and rates of macro and microevolutionary change (Bodensteiner *et al.*, 2021). Ecological and morphological analyses raise important questions concerning the organization of biological communities (Ricklefs *et al.*, 1981). Morphological approaches offer the advantages of sampling large numbers of species assemblages unambiguously and measuring the evolutionary diversification that underlies community structure more precisely than an ecological approach. If ecological and morphological measurements can be intercorrelated, they will offer a much more complete description of communities and provide a stronger phenomenological basis for ecological theory formation and testing. Applying different instruments is an excellent way to clarify some existing questions or to open up new and otherwise unreachable lines of study. ENM is the instrument that utilizes the advantages of the morphological, ecological, and geospatial approaches within a single framework. One of the problems confronting adherents of natural selection lies in the difficulties encountered in explaining the evolution of complex mechanisms, many

parts of which would seemingly have to have evolved separately and yet be of little value to the animal until each is integrated and functioning within the organism as a whole. In our opinion, biologically based ENM is the instrument which possesses the capacity to account for multiple interrelations and interactions of environmental, physiological, and geographical parameters and thus to provide new and extended knowledge on seemingly familiar natural phenomena.

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