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Comparative Assessment of the State of Populations of the Ural Endemic *Lagotis uralensis* Schischk. in the Gradient of Altitudinal Zonality

P. L. Gorchakovskiy and M. G. Khokhlova

Institute of Plant and Animal Ecology, Ural Division, Russian Academy of Sciences,
ul. Vos'mogo Marta 202, Yekaterinburg, 620144 Russia

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Abstract—The endemic species *Lagotis uralensis* is characterized with regard to the stages of ontogeny, population structure and dynamics, and the ways of species adaptation to growing in the form of small isolated populations in high mountains.

Key words: high-mountain plants, the Urals, endemic plants, small populations.

The increasing anthropogenic impact on plant cover often leads to the reduction and disjunction of the ranges of formerly widespread plant species (Gorchakovskiy, 1979). Because of this, conditions providing for the existence of plant species in the form of small isolated populations attract the attention of phytoecologists (Dolan, 1994; Linhart and Premolli, 1994; Ouborg and van Treuren, 1994; Rajzman *et al.*, 1994). In particular, such investigations were performed on some endemic plants of the Ural flora, which have discontinuous ranges and are represented by only a few small populations (Gorchakovskiy, 1997; Gorchakovskiy and Zueva, 1984, 1993; Gorchakovskiy and Stepanova, 1994a, 1994b). From this standpoint, however, of special interest are the plants growing in high mountains: isolation of populations in these areas manifests itself especially clearly because gene exchange between them is severely restricted by the factors controlling the processes of pollination, seed development, and seed distribution (Grasser, 1986). This was the reason behind our choice of the object for this study.

OBJECT, STUDY REGION, AND METHODS

This object was *Lagotis uralensis* Schischk. (Scrophulariaceae), a rare endemic high-mountain species that occurs in a few habitats on the tops of some mountains in the northern and southern Urals (Gorchakovskiy, 1969). As other Ural endemics, it belongs to the most vulnerable species of the aboriginal flora; it was included in the Red Data Book of the Middle Urals (*Krasnaya kniga ...*, 1996). This is a mycotrophic species with vesicular–arbuscular endomycorrhiza, pollinated by insects (Selivanov and Shavkunova, 1973).

Studies were performed in the northern Urals (Denezhkin Kamen' massif, 1492 m a.s.l.), from 1994

to 2000. Altitudinal zonality of the plant cover is well expressed in this region; as elevation increases, the altitudinal belts replace one another in the following order: mountain forests, subgoltsy vegetation, mountain tundras, and cold alpine rock deserts (Gorchakovskiy, 1975, 1989). The upper forest boundary in different parts of the massif lies at elevations of 800–880 m a.s.l.

We studied four local *L. uralensis* populations growing at different elevations in different plant communities (Fig. 1): one population in the subgoltsy belt, and three populations in the mountain tundra belt. They were named according to the site of growth.

(1) Population Kulakovskii-1. The western slope of Kulakovskii Ridge, 850 m a.s.l., a meadow near a creek in an open larch–birch scrub forest (dominants *Larix sibirica* and *Betula tortuosa*). Grass stand had 80% coverage and consisted of *Lagotis uralensis*, *Anemone biarmiensis* (cop.₂), *Polygonum bistorta* (cop.₁), *Allium schoenoprasum*, *Pachypleurum alpinum*, *Geranium albiflorum*, *Valeriana capitata* (sp.–cop.₁), etc.

(2) Population Kulakovskii-2. The top of Kulakovskii Ridge, 900 m a.s.l., dryas–rhacomitrium mountain tundra with bare spots on the soil surface. The herbaceous–dwarf shrub layer had 50% coverage; dominant species included *Dryas octopetala* (cop.₁–cop.₂), *Lagotis uralensis*, *Vaccinium uliginosum*, *Arctous alpina* (cop.₁), *Anemone biarmiensis*, *Gypsophila uralensis*, *Pachypleurum alpinum* (sp.). In the moss layer, *Rhacomitrium lanuginosum* prevailed (cop.₁–cop.₂).

(3) Population Sharp. The depression between the Sharpinskaya peaks, 1160 m a.s.l., herbaceous–moss mountain tundra. Composition of the herbaceous–dwarf shrub layer (40–50% coverage): *Festuca ovina* ssp. *ruprechtii*, *Carex bigelowii* ssp. *arctisibirica* (cop.₁–cop.₂),

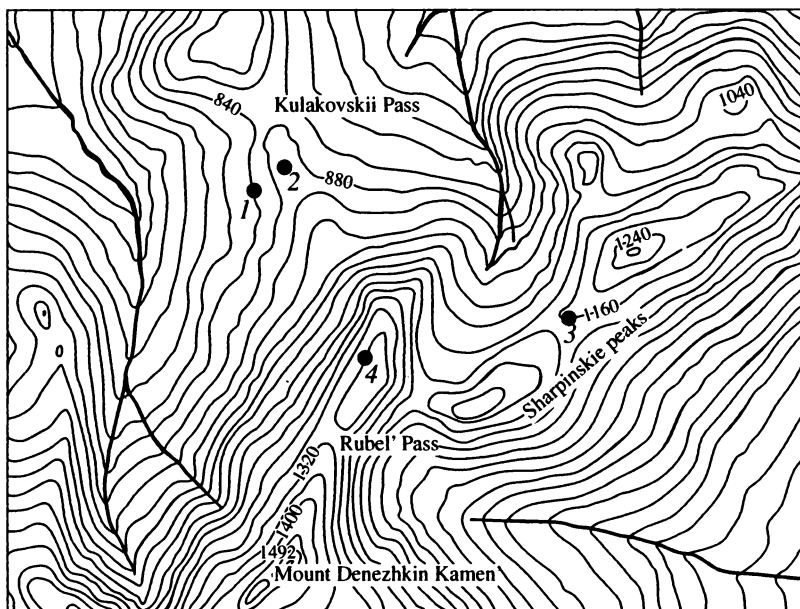


Fig. 1. Sites of local populations of *Lagotis uralensis*: (1) Kulakovskii-1, (2) Kulakovskii-2, (3) Sharp, (4) Rubel'.

Lagotis uralensis (cop.₁), *Pachypleurum alpinum*, *Cerastium krylovii*, *Polygonum bistorta*, *Empetrum hermaphroditum*, *Thalictrum alpinum*, *Hieracium alpinum* (sp.), etc. In the moss layer (60% coverage), *Aulacomnium turgidum* prevailed (cop.₂).

(4) Population Rubel'. Rubel' Pass, 1320 m a.s.l., sedge–aulacomnium mountain tundra. In the shrub layer, *Salix reticulata* prevailed (cop.₁). The herbaceous–dwarf shrub layer (60% coverage) with the prevalence of *Carex bigelowii* ssp. *ruprechtii* (cop.₂–cop.₃), *Lagotis uralensis* (cop.₁), *Pachypleurum alpinum*, *Anemone biarmiensis*, *Luzula frigida* (sp.), etc. In the moss–lichen layer (50% coverage), *Aulacomnium turgidum* prevailed (cop.₂).

SOME ANATOMICAL AND MORPHOLOGICAL FEATURES AND ONTOGENETIC (AGE) STATES

Innovation buds in *L. uralensis* are open (Mineeva, 1986). They are subdivided into two types: vegetative buds containing only the rudiments of stem and leaves and buds of a mixed type, with the rudiments of both vegetative and generative organs. The rudiments of internodes, leaves, inflorescence, and flowers are clearly distinguished in a mixed-type bud.

Only vegetative buds appear in the pregenerative period of ontogeny, and both generative and mixed buds appear in the generative period. A vegetative bud gives rise to a shortened shoot with one or several relatively large leaves.

In late summer, plants in the generative period of ontogeny form the apical vegetative bud; in addition, one or several lateral buds (both vegetative and mixed-type) are formed. In the next year, the apical bud gives

rise to a short monopodial shoot with several (up to four) relatively large leaves, and a mixed-type lateral bud produces a long floral shoot with several small sessile leaves and an inflorescence. Vegetative lateral buds usually remain dormant but sometimes give rise to a short second-order vegetative shoot.

Long generative shoots are annual. They function during only one growing season and die off after fruiting. The stem of the short vegetative shoot remains viable and overwinters, being protected from cold by the petioles of dead leaves, moss, and in some cases the upper soil layer. Innovation buds appear in leaf axils of the monopodial shoot in the zone of its annual increment, and additional roots are formed in the lower, perennially growing part of the stem. The additional roots draw this perennial part of stem into the soil, so that it gradually goes under the surface and is transformed into an epigeogenic rhizome. Such a drawing action of additional roots was previously observed in other plant species (Serebryakov and Serebryakova, 1965; Khokhryakov, 1976; Mikhailovskaya, 1981).

In *L. uralensis* ontogeny, the following age states can be distinguished: plantlets, juvenile plants, immature, virginal, young generative, middle-aged generative, old generative, subsenile, and senile plants (Fig. 2).

Plantlets (pl) are small plants 1.5–2 cm in height that have a hypocotyl; two narrow lanceolate cotyledons; and a tap root with one or two lateral rootlets, which penetrates the soil to a depth of 3.5–4 cm. The tap root sometimes has a spiral form, which probably aids in driving the plant into the soil (Ignat'eva, 1967). The cotyledons function during one growing period; by its end, the apical bud is formed.



Fig. 2. Age states of *Lagotis uralensis*: (pl) plantlet, (j) juvenile, (im) immature, (v) virginal, (g₁) young generative, (g₂) middle-aged generative, (g₃) old generative, (ss) subsenile, and (s) senile plants; (mr) main root, (lr) lateral root, (ar) additional root, (rh) rhizome.

Juvenile (j) individuals. In the beginning of the second growing period, the apical bud produces a short vegetative shoot with one entire leaf, which has a glabrous lanceolate blade and a relatively long stalk. The plants remain in this age state for 3–5 years; their height varies from 3 to 8 cm. The tap root gradually dies off, and a rhizome begins to form. Well-developed juvenile individuals have a short (0.5 cm) rootstock 0.1–0.2 cm in diameter with several (up to 5–6) additional roots.

Immature (im) individuals are 6–12 cm high and have one leaf. The leaf blade is elliptical or ovate, with a slightly crenate margin; the leafstalk is long, with a relatively wide sheath at the base. The apical vegetative bud with 3–4 leaf rudiments is formed by the end of each growing season, but only one leaf emerges. The rootstock is thin (0.4–0.5 cm in diameter) and short (0.5–2 cm), with 8–10 additional roots.

Virginal (v) individuals are larger (7–17 cm in height) and usually have two leaves. Leaf blades are lanceolate or ovate, with slightly crenate margins. The rhizome is 1.5–4 cm long, 0.5–0.8 cm in diameter, with 12–16 additional roots. The sheaths of dead leaves begin to envelop the growth cone.

Young generative (g₁) individuals have a short vegetative monopodial shoot usually bearing two basal

leaves. These leaves have elongated oval blades with weakly crenate margins and begin to form a kind of rosette. One generative shoot is 14–22 cm long, with several sessile leaflets on the stem and one terminal spicate inflorescence. The latter is 3–5 cm long and consists of 10–30 flowers. The rhizome is vertical, up to 3 cm in length and 0.7 cm in diameter.

Middle-aged generative (g₂) individuals have a more or less developed rosette consisting of three to four glabrous ovate leaves with slightly crenate or smooth margins. Leaf stalks have wide enveloping sheaths at the base. One or two (rarely, three) floral shoots vary in length from 19 to 40 cm. The leaves on a floral shoot are sessile and small; their arrangement is alternate in the lower part of the stem and opposite in the upper part. Inflorescences are spicate, 6–12 cm long; each consists of 70 to 200 flowers. In this age state, the rhizome sinks into the soil to the maximum depth: the growth cone with innovation buds is 3–10 cm below the surface. The rhizome is vertical or slightly curved, up to 7 cm in length and 1 cm in diameter, and has a well-developed system of 30–60 branching additional roots; it is enveloped in dead leaf sheaths and petioles.

In old generative (g₃) individuals, a short vegetative shoot has one or two oval leaves with crenate margins.

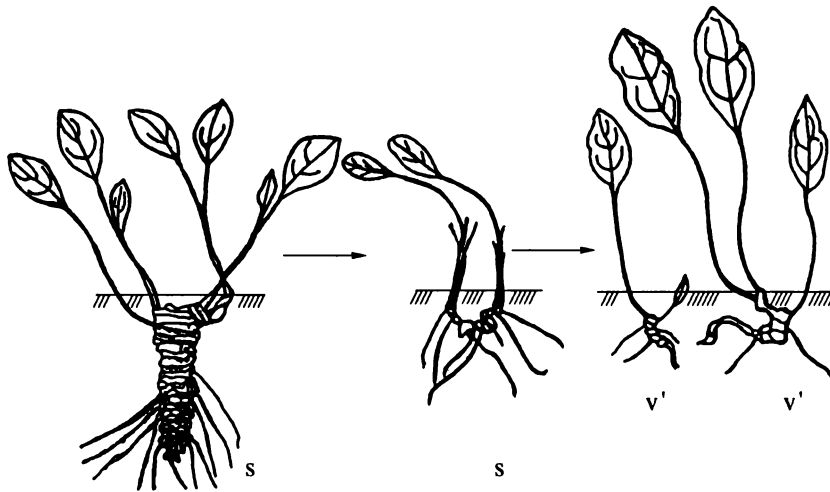


Fig. 3. Vegetative reproduction of *Lagotis uralensis* by particulation of senile (s) individuals; v' are separated particulae (individuals of vegetative origin).

One generative shoot is 16–29 cm long, with a short (3–5 cm) spicate inflorescence consisting of 50–70 flowers, some of which are underdeveloped. The rhizome is strong, but its lower part dies off. The number of additional roots decreases to 10–26.

Subsenile individuals (ss) have a short vegetative shoot with two (rarely, three) oval or ovate leaves wrapped in feltlike remains of dead leafstalks. The plants do not form floral shoots. The lower part of the rhizome is dead and decomposed; additional roots concentrate in the upper part of rhizome.

Senile (s) individuals have only one leaf with an oval blade; its size is significantly smaller than those in subsenile plants. The rhizome is decomposed except in the upper part; additional roots are few (five to seven).

In rare cases, subsenile and senile plants display vegetative reproduction by particulation: the rhizome separates into fragments, and lateral buds in the latter produce vegetative shoots (Fig. 3). The resulting individuals live for several years and approach the virginal age state. They play an auxiliary role in the life of a population, which consists in retaining the population range and protecting it from invasion by competing species until the emergence of new individuals entering the generative state in the seed progeny.

POPULATION STRUCTURE AND DYNAMICS

The duration of the total life cycle of *L. uralensis* varies from 35 to 73 years, judging from the traces of internodes remaining on the rhizomes. The maximum individual life span in populations proved to increase with elevation: 49 years in Kulakovskii-1 vs. 73 years in Rubel'.

Figure 4 shows the age structure and dynamics of four *L. uralensis* populations over the observation period. It is seen that Kulakovskii-1 is a middle-aged

population with some signs of rejuvenation. Its age spectrum has a peak corresponding to middle-aged generative individuals, but the proportions of juvenile, immature, and virginal individuals in some years are also relatively large.

Kulakovskii-2 is a young population with three peaks in its age spectrum: the first two correspond to juvenile and virginal (sometimes, to juvenile and immature) individuals, and the third, lower peak corresponds to middle-aged generative individuals. Annual changes were mainly observed in the young fraction of the population.

Sharp is a young population with two peaks in its age spectrum. One peak corresponds to immature individuals; the other, lower peak, to middle-aged generative individuals. No significant changes in age structure were revealed during the period of study.

Population Rubel' is closer to a middle age: one peak in its age spectrum corresponds to virginal individuals; the other peak, to middle-aged individuals. Annual changes in this population occurred mainly in the fraction of juvenile individuals.

According to Rabotnov (1950), all these populations can be characterized as normal, i.e., independent of the input of disseminules from the outside. Therefore, the emergence of young individuals and their maturation, aging, and dying off proceed relatively smoothly, without sharp changes and serious disturbances. This largely depends on the long duration of plant ontogeny. Most of the age spectra have two peaks; i.e., they are bimodal according to Zaugol'nova (1976). Their right part, which corresponds to the generative period, remained fairly stable during the observation period, whereas the left part, which characterizes the young fraction of the population, was subject to significant annual changes. The dynamics of age spectra in their left part reflects the fact that young plants are more

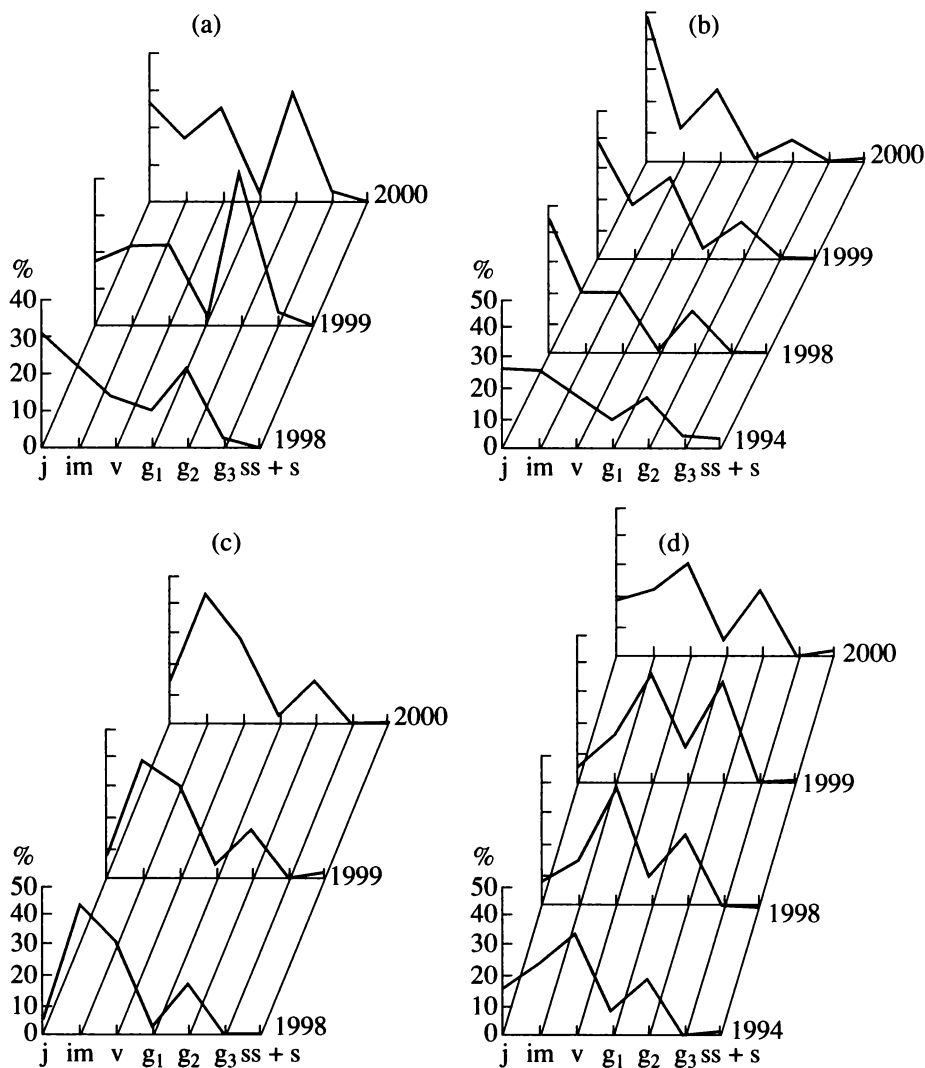


Fig. 4. Age structure of local *Lagotis uralensis* populations and its annual dynamics: (a) Kulakovskii-1, (b) Kulakovskii-2, (c) Sharp, (d) Rubel'.

dependent on meteorological conditions in individual years and pass through the early stages of ontogeny more rapidly. It is noteworthy that all the populations have sufficient numbers of virginal individuals, which continuously replenish the generative fraction.

Annual changes in the generative part of the age spectrum occur because individuals undergo transition from one age state to another and, moreover, bloom and fruit not annually but at intervals of one or two years (in some cases, up to four years), forming only vegetative shoots in these periods. Blooming can be interrupted because of both unfavorable weather and the deficiency of plastic substances necessary for the formation of generative organs. The frequency and durations of pauses in blooming increase along the altitudinal gradient. However, as the generative period in the life of *L. uralensis* lasts for several decades, pauses in blooming in some individuals do not disturb the continuous

process of fruiting and seed reproduction in the population as a whole.

ECOLOGICAL OPTIMUM OF THE SPECIES

The ecological optimum for *L. uralensis* can be estimated from a series of parameters, namely, the average individual phytomass, population density, and the proportions of blooming and young plants. Their values are rated on a three-grade scale, and the sum of grades is used as an integrated index for determining the ecological optimum. The results of such estimation for the four populations, based on the data obtained in 1999, are shown in the table. It is seen that the sum of grades is maximum in the subgoltsy belt and gradually decreases with elevation. This is evidence that the ecological optimum for *L. uralensis* is in the subgoltsy belt. Indeed, conditions for *L. uralensis* growth in this zone are most favorable; this especially concerns the

Some parameters of *Lagotis uralensis* populations

Population	Average individual phytomass		Population density		Proportion of blooming plants		Proportion of young plants (pl, j, im)		Sum of grades
	g	grade	ind./m ²	grade	%	grade	%	grade	
Kulakovskii-1	2.1	3	39.9	3	17.8	3	37.6	2	11
Kulakovskii-2	1.55	2	5.1	1	5.9	2	59	3	8
Sharp	1	1	18.8	2	6.6	2	46.5	3	8
Rubel'	0.98	1	14.8	2	17.6	3	18.6	1	7

areas near the brooks, where the water flowing from the upper part of the mountain massif ensures sufficient soil moistening and air temperature changes less sharply.

DISCUSSION

Lagotis uralensis is a monopodially growing half-rossette polycarpic herbaceous plant with a short rhizome; it is classified as hemicryptophyte and mesophyte with some signs of hygromorphism.

Similarly to other high-mountain and arctic plants, *L. uralensis* has open buds. In the course of evolution, bud scales have undergone reverse metamorphosis into primordial green leaves, which open immediately after air temperature rises above zero. Thus, the period of photosynthetic activity begins earlier and its duration increases. The innovation buds in *L. uralensis* are protected from low temperatures by dead leaves, mosses, and the upper soil layer, rather than by special bud scales. The results of studies performed by Serebryakov (1961, 1962, 1964) showed that the proportion of flowering plants with open buds increases upon transition from the taiga forest belt to the mountain tundra belt.

The preliminary formation of flower and inflorescence rudiments in *L. uralensis* innovation buds is the result of species adaptation to growing in high mountains, as it provides for accelerated blooming and fruiting under conditions of a short growing period. This feature is typical of many other plants growing in the mountain and arctic tundras. Thus, according to Serebryakov (1952), 80–90% of flowering plants in the forest and mountain tundra belts of the Khibiny Mountains in the Kola Peninsula and all flowering plants in the arctic tundras of the Taimyr Peninsula have flowers and inflorescences developing from the rudiments preliminary formed in innovation buds.

The generative individuals of *L. uralensis* do not always bloom every year; in some cases, only the vegetative part of the shoot grows for one or several years prior to blooming and fruiting. Pauses in blooming are explained by unfavorable weather conditions in the growing seasons when the innovation buds are formed.

Lagotis uralensis belongs to the plant species that exist in the form of small isolated populations. Isolation

is conditioned by several factors restricting gene exchange between local populations. The main factor is the mosaic distribution of this species. It is found in some higher mountain massifs with treeless peaks and well-expressed subgoltsy and mountain tundra belts, and its habitats are often remote from each other. For example, the group of populations in the southern Urals is approximately 550 km away from the nearest *L. uralensis* habitats in the northern Urals. In the latter region, where the greater part of the *L. uralensis* range is located, separate habitats are found in large mountain massifs (Konzhakovskii Kamen', Denezhkin Kamen', Yalping-N'er, Oika-Chakhl', Chistop, etc.). Intermontane depressions are covered with forests, which are an insurmountable barrier to the spread of this species. Moreover, there usually are several local populations of *L. uralensis* within each mountain massif. They are separated not only by physical barriers (mountains, hills, and valleys) but also by phytocenotic (dense dark coniferous forests in which this species cannot grow) and phenological barriers (differences in the dates of blooming and fruiting between local populations growing in different altitudinal belts). Additionally, isolation of populations may depend on the pattern of distribution and insufficient number of insect pollinators.

In the course of evolution, *L. uralensis* developed some adaptations to the existence in the form of small isolated populations under severe high-mountain conditions with unstable weather and a short growing period. In particular, unfavorable factors include cold spells, sometimes with snowfall, which cause flower damage; early frosts in the end of summer, which do not allow the seeds to ripen; and steady rains and strong winds, which interfere with pollination by insects. The evolution of this species proceeded via an increase in the number of flowers in the inflorescence (up to 200) and in the duration of the total life cycle (to approximately 70 years), with the plants remaining in the generative state for up to 20–30 years in the course of ontogeny. This increases the probability of successful seed reproduction, especially in more favorable years.

CONCLUSION

The range of *L. uralensis* in the Pleistocene was apparently much broader than today: the upper bound-

ary of species distribution was at lower elevations, and this created favorable conditions for its dispersal over many mountains of the northern Urals and expansion to the southern Urals. Changes of the climate and the plant cover in the Holocene resulted in the fragmentation of the species range and the formation of small isolated populations in different mountain massifs and, within the same massif, in different biotopes and altitudinal belts; in the latter case, the populations proved to be separated by various barriers (physical, phytoecenic, and phenological).

Although the ecological optimum for *Lagotis uralensis* is in the subgoltsy belt, this species can live at higher elevations, in the mountain tundra belt, where it successfully reproduces and is a natural component of various plant communities.

Observations performed in typical *L. uralensis* habitats in these two belts provided evidence for wavelike changes in the age structure of its populations. Their age spectra are mostly bimodal, with the peaks corresponding to the fractions of young and middle-aged plants. However, it is noteworthy that the generative part of the spectrum in all populations remained relatively stable throughout the period of observations. To some extent, this is explained by the fact that the plants remain in the generative state for a long time, although pauses in blooming and fruiting occur in some individuals. This provides for the continuity of seed reproduction and the enrichment of populations with young individuals. Therefore, the populations of *L. uralensis*, notwithstanding their small size, occupy a relatively stable position in the natural undisturbed plant cover of the Ural high mountains.

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