Abundance dynamics of the Siberian weasel (*Mustela sibirica*) and their determinants on the northeastern periphery of its geographic range (Yakutia, Russia)

Evgenii S. Zakharov*, Valery M. Safronov, Nadezhda N. Zakharova, Roman E. Petrov, Viktoriya V. Filippova, Lena P. Koryakina & Stefan Kruse

ABSTRACT. Long-term changes in the harvesting of the Siberian weasel *Mustela sibirica* in Yakutia indicate a relatively stable population of this species from the end of the 19^{th} century to the beginning of the 21^{st} century. In the 2000s, prolonged depression of water vole and mountain hare populations caused a reduction in Siberian weasel numbers (i.e., abundance), despite the presence of its other prey species: mouse-like rodents and muskrats. The change of the main prey species altered the cyclicity of this predator's population. With the decrease in Siberian weasel abundance, the percentage of young animals diminished (from 85.6% to 60.8%), as did the yield of young animals per mature female (from 11.4 to 5.0); meanwhile, among young animals, the proportion of females went up (to 60.0%), but among adults, there was an increase in the proportion of males (to 69%). Anthropogenic causes of the recent reduction in Siberian weasel abundance are listed. Competition with the sable had an additional negative influence.

How to cite this article: Zakharov E.S., Safronov V.M., Zakharova N.N., Petrov R.E., Filippova V.V., Koryakina L.P., Kruse S. 2022. Abundance dynamics of the Siberian weasel (*Mustela sibirica*) and their determinants on the northeastern periphery of its geographic range (Yakutia, Russia) // Russian J. Theriol. Vol.21. No.2. P.153–161. doi: 10.15298/rusjtheriol.21.2.06

KEY WORDS: Siberian weasel, sable, water vole, muskrat, harvesting, abundance, sex and age structure.

Evgenii S. Zakharov [zevsable@gmail.com], Institute for Biological Problems of Cryolithozone, Siberian Branch of Russian Academy of Sciences, 41 Lenin Avenue, Yakutsk 677980, Russia and M.K. Ammosov North-Eastern Federal University, 48 Kulakovskiy Str., Yakutsk 677013, Russia; Valery M. Safronov [vmsafronov28@gmail.com], Institute for Biological Problems of Cryolithozone, Siberian Branch of Russian Academy of Sciences, 41 Lenin Avenue, Yakutsk 677980, Russia; Nadezhda N. Zakharova, M.K. Ammosov North-Eastern Federal University, 48 Kulakovskiy Str., Yakutsk 677013, Russia; Roman E. Petrov, Institute for Biological Problems of Cryolithozone, Siberian Branch of Russian Academy of Sciences, 41 Lenin Avenue, Yakutsk 677980, Russia and M.K. Ammosov North-Eastern Federal University, 48 Kulakovskiy Str., Yakutsk 677013, Russia; Viktoriya V. Filippova, M.K. Ammosov North-Eastern Federal University, 48 Kulakovskiy Str., Yakutsk 677013, Russia and Institute for Humanities Research and Indigenous Studies of the North, Siberian Branch of Russian Academy of Sciences, 1 Petrovskiy Str., Yakutsk 677027, Russia; Lena P. Koryakina, Arctic State Agrotechnological University, 3 Sergelyakhskoe Rd., Yakutsk 677007, Russia; Stefan Kruse, Alfred Wegener Institute Helmholtz Center for Polar and Marine Research, 14473 Potsdam, Telegrafenberg A45, Germany.

Динамика численности колонка (Mustela sibirica) и детерминирующие факторы на северо-восточной периферии ареала (Якутия, Россия)

Е.С. Захаров*, В.М. Сафронов, Н.Н. Захарова, Р.Е. Петров, В.В. Филиппова, Л.П. Корякина, Ш. Крузе

РЕЗЮМЕ. Многолетние изменения заготовок колонка *Mustela sibirica* в Якутии свидетельствуют об относительно стабильной численности вида с конца 19 до начала 21 века. В 2000-х гг. затяжная депрессия водяной полевки и зайца-беляка вызвала сокращение поголовья колонка, несмотря на наличие других кормов — мышевидных грызунов и ондатры. Смена основных объектов питания изменила цикличность популяции хищника. При снижении численности уменьшился процент молодняка (от 85.6 до 60.8%) и выход молодых на взрослую самку (от 11.4 до 5.0), в прибылой части

^{*} Corresponding author

увеличилась доля самок (60.0%), во взрослой — самцов (67%). Указаны антропогенные предпосылки современного сокращения численности колонка. Дополнительное отрицательное влияние оказала конкуренция с соболем.

КЛЮЧЕВЫЕ СЛОВА: колонок, соболь, водяная полевка, ондатра, заготовки, численность, половозрастная структура.

Introduction

The Siberian weasel Mustela (Kolonokus) sibirica Pallas, 1773, occurs in Yakutia and is widespread across most parts of Siberia. The northeastern border of its geographic range is located in Yakutia and is bounded by the Arctic Circle in the north and by the western and southern spurs of the Verkhoyansk Ridge in the east. Farther to the south, the Siberian weasel's range reaches the Zeya River basin, where the subspecies M. s. sibirica is replaced by a Far Eastern subspecies M. s. manchurica Brass, 1911, inhabiting the Amur River region and Primorye (e.g., Heptner et al., 1967; Zakharov et al., 2022). The ecology of the Siberian weasel in Yakutia is poorly studied. Only the composition of this predator's diet has been investigated relatively completely, indicating a leading role of food in the dynamics of abundance (i.e., of numbers) of this species (Belyk, 1967; Tavrovsky et al., 1971; Sedalishchev et al., 2015). Siberian weasel reproduction has not been studied. Data on sex/age structure of populations in Yakutia - as well as in Siberia and the Far East as a whole — are fragmentary and have not been replenished with new information for a long time (Korytin, 1963; Voilochnikov, 1977; Sapaev, 1969; Tavrovsky et al., 1971). Meanwhile, the number of Siberian weasels in Yakutia has significantly decreased to date, and more than ever, periodic monitoring of this mammal is needed, as is rational use of this resource and its protection. This article characterizes abundance dynamics and structural/populational parameters of the Siberian weasel, and then their natural and anthropogenic determinants are analyzed.

Material and methods

We studied 74 carcasses of Siberian weasels collected in 2003–2018 in the basin of the middle reaches of the Lena River. To analyze age structure of populations, 187 Siberian weasels' skulls were added to the study population; they were collected in this region during 1950-1980 and are stored at the Institute for Biological Problems of the Cryolithozone, the Siberian Branch of the Russian Academy of Sciences, Yakutsk. The age of the animals (n = 261) was determined from growth layers in the cement of the left upper canine tooth (Klevezal, 2007). Characteristics of harvesting of Siberian weasels' skins were taken from official data of the Territorial Branch of the Federal State Statistics Service for the Republic of Sakha (Yakutia) (Sakha Stat), from the Ministry of Ecology of the Republic of Sakha (Yakutia), and from literary sources (Konstantinov, 1921; Dyakonov, 1990; Zakharov, 1995). Post-harvesting abundance of this species was characterized by means of data on winter route counts (WRCs) from the Hunting Industry Department of the Republic of Sakha (Yakutia).

The collected statistical information was added to an attribute table in the ArcGIS software, which allowed constructing maps of the quantitative distribution of Siberian weasels across Yakutia districts. The addition of GIS layers with administrative territorial, landscape, and hydrographic annotations in ArcGIS online enabled us to determine the modern geographic range of the Siberian weasel.

Statistical calculations were performed in Microsoft Office Excel. An analysis of Siberian weasel abundance cycles was carried out in Python 3.8 software using the SciPy accounting system, version 1.6.2 of 24 March 2021 [https://www.scipy.org/]. For spectral analysis by Welch's method (Welch, 1967), scipy.signal.welch functions were employed [https://docs.scipy.org/doc/ scipy/reference/generated/scipy.signal.welch.html]. A frequency spectrum of population rhythms and characteristics of the cycles (periodicity in years and intensity in units of spectral density) were obtained too. The continuity of the data series served as the criterion for the accuracy of calculations; therefore, cyclicality was determined by means of harvesting volume for 1932–1996 and results on WRCs for 1997–2019.

Results

A general idea about the main fluctuations of Siberian weasel abundance in Yakutia in the 19th–21st centuries can be obtained by looking at long-term changes in the harvesting of fur products from this species (Fig. 1).

Year to year, the volume of harvesting has changed noticeably, probably due in part to organizational and economic factors and natural and climatic aberrations, but overall, this volume closely reflects fluctuations of Siberian weasel abundance, especially during largescale harvesting periods. Almost all published data on the dynamics of Siberian weasel abundance, just as for many other fur species, are based on harvesting statistics (e.g., Laptev, 1958; Ternovsky & Danilov, 1965; Voilochnikov, 1977; Tavrovsky *et al.*, 1971); therefore, the harvesting data discussed below are comparable to those in previous studies.

In the dynamics of harvesting of Siberian weasel skins in Yakutia, several periods stand out. During 1837– 1900, harvesting volume was low (on average 2300, maximum 6000 skins per year), which was also true for the Far East, where separate harvesting of this species

154



Fig. 1. Dynamics of harvesting of Siberian weasel skins in Yakutia during 1837–2012 (according to data from Sakha Stat; Konstantinov, 1921; Dyakonov, 1990; Zakharov, 1995).

was not practiced during this period (Voilochnikov, 1977). At the beginning of the 20th century, the volume of Siberian weasel harvesting began to grow (to the average of 4200, maximum 11200 skins per year) and reached a maximum in 1920–1950. The average volume of purchases was 16200, and the largest one 30800-31600 skins. At the average cull level of ~25% for the Siberian weasels in Eastern Siberian and Far Eastern regions (Shilyaeva & Bakeev, 1982), the maximum abundance of this species in Yakutia during this period could exceed 100000 individuals. In 1960-1990, the harvesting fell to moderate levels (average 7700, maximum 15200 skins per year). In the 21st century, the last peak was noted in 2001 (4940 skins), and then the harvesting diminished to tens of individuals because of a decrease both in this species' abundance and in harvesting volume.

According to the results of WRCs in 1997 and 1998, Siberian weasel abundance was estimated at 23200 and 38900 individuals, respectively; by 2019, the estimated abundance had decreased to 1200 individuals (Fig. 2).

Figure 3 presents a comparison of characteristics of Siberian weasel cycles during 1932–1996 and during 1997–2019 as calculated from the data on harvesting and from WRC results. The validity of comparing such data (obtained by different methods) was shown earlier in an analysis of mountain hare (*Lepus timidus*) cycles (Erdakov & Pereyaslovets, 2020). From the presented graphs, it follows that in the spectra of fluctuations of Siberian weasel abundance, cycles of different periodicity were dominant in the above-mentioned periods. In 1932–1996, in the band of high and medium frequencies, peaks with a periodicity of 11, 7, 4, and 3 years can be distinguished that resemble water vole cyclicity in Siberia, including Yakutia (Erdakov & Litvinov, 2014). In addition, in the region of medium frequencies, the Siberian weasel in Yakutia showed an association with mountain hare cyclicity, which is 11–13 years (Popov, 1977). This finding indicates synchronization of the fluctuations of Siberian weasel abundance by the cycles of the water vole and of the mountain hare: the most important prey species in the period in question.

In 1997-2019, the 4-5-year cycle became the most prominent in the spectrum of Siberian weasel abundance; the 10-13-year cycle was shifted to the second place and toward higher frequencies (Fig. 3B); this change in the population dynamics may be due to altered conditions of feeding. The abundance of water voles and mountain hares declined during this period. The main prey for the Siberian weasel became grey voles (Microtus spp.) and red-backed voles (Myodes spp.), which have characteristic 3-5-year cycles (Prokopyev, 2011; Safronov, 2016); this switch of diet could well have influenced the rhythms of this predator's abundance. Long-periodicity fluctuations of Siberian weasel abundance noted in both periods (22, 23, 65, and 98 years) can be fitted to natural and climatic cycles (Erdakov & Litvinov, 2014). Overall, the presented data support the conclusions of various researchers regarding the tight relation of Siberian weasel abundance with the abundance of water voles and small rodents, and in Yakutia, with mountain hare abundance (e.g., Laptev, 1958; Ternovsky & Danilov, 1965; Heptner et al., 1967; Tavrovsky et al., 1971; Voilochnikov, 1977).





Fig. 2. Changes in Siberian weasel abundance in Yakutia in 1997–2019 (according to data from the Hunting Industry Department of the Republic of Sakha (Yakutia)) (Volkova *et al.*, 2019).



Fig. 3. Frequency spectra of the dynamics of Siberian weasel abundance in Yakutia. A: according to data on the harvesting of skins in 1932–1996; B: based on the results of WRCs in 1997–2019.

The yield of fur products per unit area gives an idea of the Siberian weasel's territorial distribution (Table). The zone of low species density has always included southern, northwestern, and northeastern Yakutia. Levels of the harvesting yield have been the lowest in the northeastern mountainous zone and northwestern zone. In the southern zone, these levels are higher in the Olekminsky and Lensky districts, which include valleys of the Lena and Olekma Rivers with substantial areas of floodplain sites. In the Aldansky, Ust-Maisky, and Neryungri districts — which are located in the Aldan River basin along the eastern border of this species' range — this parameter is low. The zone of this species' medium density is confined to the Vilyui River basin,

156

where the density goes up from the upper to lower reaches of the river.

Siberian weasels are most numerous in the central regions of Yakutia with taiga–alas and floodplain–valley landscapes favorable for this species. According to our calculations, the main habitats of the Siberian weasel are principally confined to floodplains, valleys, and above-floodplain terraces of rivers and streams, shallow valley sites, lakeside biotopes, and edges of alases (92.8% of occurrence). This species occurs much less frequently (7.2%) on vast forested territories.

The modern geographic range of the Siberian weasel is outlined in Fig. 4. Overall, its range in Yakutia between 1941–1964 and 2000–2010 decreased from 1.53 million to 0.79 million km² (by 48.4%). Zones of high productivity of the species have disappeared, and it has become relatively rare almost everywhere.

In 1950–1980, underyearlings accounted for $85.6 \pm 2.6\%$ (n = 187) of harvested Siberian weasels. Males were slightly more numerous $(55.1 \pm 3.6\%, p < 0.05)$ than females. Male predominance among young animals (56.3%) almost disappeared among adult animals (51.8%). The proportion of young animals among males (87.4%) was almost the same as that among females (83.3%), suggesting that the rates of renewal of age composition are similar between the sexes. In general, the sex ratio in this population was close to 1:1. On average, there were 11.4 juveniles per adult female. This is greater than the average fertility of the Siberian weasel (6.2 \pm 0.5) but is within the limits of its fertility variability (2 to 12) (Ternovsky & Ternovskaya, 1994).

In 2003–2018, with a decrease in Siberian weasel abundance, the proportion of young animals declined to $60.8 \pm 3.1\%$ (n = 74, p <0.01). Percentages of males $(51.3 \pm 5.8\%)$ and females $(48.7 \pm 5.8\%)$ were almost equal, with slight predominance of males. In this context, among young animals, females were clearly more numerous (60.0%), and at older ages, the same was true for males (69.0%). Among females, the proportion of young animals (75%) was three times greater than the number of adults (25%). Among males, the numbers of young (52.6%) and adult animals (47.4%) differed less. If we ignore possible sex and age biases of the harvesting, these data indicate more frequent births of female kits and growing mortality of females with age during the period of the decline in Siberian weasel abundance in the 2000s. The average number of underyearlings per adult female diminished to 5.

Among adult Siberian weasels (the group older than 1 year of age) sampled in 1978–1988 and 2000–2010, the vast majority were 1+ years (i.e., 1 year and several months) of age (81.5% and 72.5%, respectively), and the proportion of

Districts	Average yield of skins per 100 km ²		
	years 1941–1964	years 1978–1988	years 2000–2010
South (Aldan and Prilensk) zone			
Aldansky	0.554	0.003	0.002
Ust-Maisky	0.458	0.128	0.044
Neryungri	0.177	0.001	0.0003
Olekminsky	1.341	0.156	0.051
Lensky	1.456	0.068	0.016
Western (Vilyui) zone			
Mirninsky	0.024	0.005	0.001
Suntarsky	1.694	2.227	0.509
Verkhne-Vilyuisky	0.187	0.060	0.042
Nyurba	1.583	0.963	0.470
Vilyuisky	2.079	0.888	0.314
Kobyaysky (left bank part)	1.562	0.563	0.166
Central zone			
Tattinsky	0.951	1.237	0.547
Amginsky	3.583	0.997	0.312
Ust-Aldansky	2.634	2.630	0.440
Churapchinsky	2.683	1.733	0.482
Megino-Kangalassky	5.056	6.259	0.399
Namsky	8.507	4.645	0.828
Gorny	0.921	0.453	0.025
Khangalassky	3.962	2.372	0.921
Yakutsk	4.281	2.920	0.713
Northwestern (Oleneko-Zhiganskaya) zone			
Oleneksky	0.0002	0.001	0.0001
Zhigansky	0.026	0.026	0.001
Northeastern (mountainous) zone			
Tomponsky	0.122	0.120	0.055
Eveno-Bytantaysky	0.359	_	_
Verkhoyansk	_	0.0002	0.001
Oymyakonsky	0.0002	_	_

Table. The yield of Siberian weasel skins in different ecologicalgeographic zones and administrative districts of Yakutia.

animals 2+ years old was 14.8% and 17.2%, respectively. Individuals 3+ years of age constituted 3.7% and 10.3%, respectively. Animals 4+ years of age were not found in our study population. In the Far East, the life span of the Siberian weasel can reach 4+ years, and the proportion of adults among the harvested animals is 33.9% on average (Voilochnikov, 1977), which is greater than that in Yakutia (21.5% in our study population; n = 261). In captivity (in a cage), this species can live to 8.8 years (An Age..., 2021), presumably owing to lower stress on the energy balance as compared to natural habitats.



Fig. 4. The geographic range and quantitative distribution of the Siberian weasel in 1978–1988 and 2000–2010 (yield of skins from 100 km²).

In our total Yakutian study population, young animals represented 78.5%. In a highly productive population in the Far East (up to 69–90 individuals per 1000 ha), the proportion of young animals in various years has been 50% to 88%, on average 66.1% (Voilochnikov, 1977). In the southern Amur River region, during years of elevated abundance of Siberian weasels, there were 12.5 young animals per adult female, whereas during a decline of abundance, this number was 8.7 (Sapaev, 1969). In our dataset, as noted above, these parameters averaged 11.4 and 5.0, respectively. According to these data, Siberian weasels while colonizing Yakutia preserved their wide range of potential fecundity, which allows them to quickly increase their abundance when conditions are favorable, as confirmed by reports of a sharp increase in Siberian weasel harvesting during periods of mass reproduction of the water vole or mountain hare (Tavrovsky *et al.*, 1971).

Discussion

According to the analysis of stomach contents in 1950–1960, the staple food of the Siberian weasel in Yakutia consisted of mouse-like rodents (52.4% of ingested animals), water voles (13.7%), mountain hares (17.8%), and, to a lesser extent, muskrats (5.0%) (Belyk, 1967). The Siberian weasel is connected most tightly with the water vole. Their ranges, quantitative distributions

across the territory, and long-term fluctuations of harvesting of skins have matched (Tavrovsky *et al.*, 1971). The water vole plays an important role in the Siberian weasel's diet and abundance dynamics in the Volga-Kama region and Western Siberia (Bakeev, 1977; Polyakov, 1977; Ternovsky, 1977). High importance of the mountain hare for the Siberian weasel's diet has been registered only in Yakutia, where the mountain hare's abundance has been estimated at millions (Tavrovsky *et al.*, 1971). During peak years, the prevalence of hares in Siberian weasels' stomachs reached 50% (Tavrovsky *et al.*, 1971).

The trophic relationship of the Siberian weasel with medium-size and large rodents and lagomorphs was detected in many parts of the geographic range, where, in addition to the above species, the Siberian weasel often hunts Daurian pika, Altai pika, Altai zokor, large jerboa, chipmunk, and squirrel (Heptner *et al.*, 1967; Voilochnikov, 1977). Scavenging the prey of large predators and commensalism are characteristic of the Siberian weasel in the Far East and Western Siberia (Voilochnikov, 1977; Ternovsky & Ternovskaya, 1994). Furthermore, we can clearly see the Siberian weasel's need for quick satiation with voluminous food that does not require much time and effort to find.

One water vole fulfills the Siberian weasel's daily nutritional needs (100-120 g, 20-40% of body weight), and it stops hunting (Heptner et al., 1967; Ternovsky, 1977), whereas the capture of a mountain hare provides even more food. The principle of economizing energy metabolism is clearly manifested in the behavior of Siberian weasels in widely differing parts of its range. In the coldest time of winter, the Siberian weasel sharply reduces its above-snow activity and can "lie" under the snow for long periods in diverse parts of its range (Laptev, 1958; Sysoev, 1960; Heptner et al., 1967; Polyakov, 1977; Voilochnikov, 1977; Gaidar, 1990), consistently with ecological and physiological features of this species. According to research on gas exchange in the Siberian weasel, it has a well-pronounced metabolic type of thermoregulation associated with high energy expenditures, which it compensates under winter conditions by the consumption of relatively large animals and by a decrease in activity (Safronov, 2002).

The current climate warming is favorable for the Siberian weasel. The average January air temperature in Yakutia has increased by 7°C over the past 100 years (Gavrilova, 2009), and spring-associated phenomena have shifted to earlier dates; hence, an increase in the reproduction and abundance of the Siberian weasel could be expected. In actuality, this increase has not occurred, pointing to a decisive influence of other factors.

In recent decades, the profile of the Siberian weasel's prey animals in central Yakutia has changed considerably due to long-term depression of water vole abundance. In 1950–1970, its density reached 120 individuals per ha (Solomonov, 1980); later, it almost disappeared owing to chemical treatment of hayfields and long dry periods (Prokopiev, 2011). To some extent, this decline was worsened by the competitive relationship with the

muskrat, which naturalized in 1939–1959 (Sedalishchev *et al.*, 2015; Chibyev, 2020). The deficit of the water vole in the diet of the Siberian weasel was aggravated by a drop of mountain hare abundance. Long-term mass culling of hares via driven hunts across large areas has resulted in the "collapse" of the hare population in Central Yakutia and prevented its characteristic periodic spikes of abundance (according to harvesting data: up to 800-fold, and according to counts: up to 1.0–3.4 individuals per ha) (Tavrovsky *et al.*, 1971). The remaining part of the population seemed to lose its former cyclicity. The last, albeit minor, increase in abundance has remained minimal.

In the 1990s, in comparison with 1950–1960, the prevalence of water voles in the diet of Siberian weasels diminished to 2.7%, and that of mountain hares to 8.9%. Muskrats, as before, constituted a small proportion of the Siberian weasel's food (2.7%). The consumption of mouse-like rodents (80.1%) — and among them, of grey (41.0%) and forest voles (26.8%) — went up (Mordosov, 1997).

In the 2000s, the prevalence of water voles (as a percentage of all ingested animals) in the diet of the Siberian weasel changed little (3.3-3.8%), while the prevalence of the mountain hare declined (1.2-1.9%). Mouse-like rodents (47.3–59.2%), including grey voles (22.2–24.2%) and forest voles (11.7–16.9%), were eaten less, but the overall level of their consumption was high. Consumption of muskrats increased 10–14-fold (to 28.3–38.2% prevalence) (Sedalishchev *et al.*, 2015), and the total proportion of large prey animals (34.0–42.7%) rose to the level of 1950–1960 (37.8%).

The depression of the abundance of water voles and mountain hares, and especially of the former, was the main reason for the decline of Siberian weasel abundance in Yakutia in the 2000s. With a deficit of these prey animals, which allow the Siberian weasel to reduce its locomotor activity in cold weather, this species cannot maintain a positive energy balance for long, and its abundance goes down even in the presence of other nutritionally important animals such as mouse-like rodents and muskrats. The substitutive role of the muskrat in Yakutia turned out to be insufficient due to difficulties with catching and limited availability relative to the population size of the predator in question. Small rodents were eaten constantly but did not fully compensate for the lack of large prey. Big expenditures of energy on the searching for such prey at extremely low temperatures are not always compensated by sufficient amounts of ingested grey and forest voles, which overwinter with a body weight of 15-25 g (Safronov, 1983). All these factors undoubtedly have had a negative effect on the course of the Siberian weasel's rut (which begins at the end of March [still under winter conditions]) and on the fertility and pregnancy of females; the latter problem manifested itself e.g. as the aforementioned decrease in the offspring yield. Besides, the change in the profile of prey animals during the 2000s restructured the cycles of Siberian weasel abundance (see Fig. 3), which at

a turning point, could reduce the resistance of the population to adverse factors.

The sable is among influential competitors of the Siberian weasel. The negative influence of the sable on the geographic range and abundance of the Siberian weasel was first noted in 1960–1970 in south Yakutia (Revin, 1989) and in 1980–1990 in central Yakutia (Mordosov, 1997). A negative impact of the sable on Siberian weasel populations has been observed in Western and Eastern Siberia (Timofeev & Nadeev, 1955; Voilochnikov, 1977; Polyakov, 1977). Among contents of sables' stomachs (n = 2820) analyzed by us, remains of a Siberian weasel were found only in one stomach, from the Vilyui River basin (Zakharov *et al.*, 2016). There are no data on the diet of the sable in spring and summer, when it can predate Siberian weasel offspring.

It is known that in its main habitats, the sable pursues and attacks the Siberian weasel (and eats it when starving), but in rarely visited areas, the sable is not aggressive towards it (Voilochnikov, 1977). In Yakutia, according to our findings, with an increase in sable abundance in recent decades (to 220000-270000 individuals), the area devoid of sable has substantially shrunk. In southern Yakutia, the Siberian weasel, being harassed by neighboring sables, was displaced from forest habitats and then from its native floodplain sites as early as 1960–1970 (Revin, 1989). A similar situation was observed by us in 1970-1980 on the widest plot of the Lena River floodplain downstream of the Vilyui River mouth (up to 45 km) containing many large and small islands, channels, oxbow lakes, and lakes densely populated by Siberian weasels (up to 5.9 individuals per 1000 ha, on average 3.8). Here, in the early 1980s, sable began to colonize large islands covered by forest, thereby displacing the Siberian weasel to a low floodplain where the conditions offered less protection and were less favorable in terms of food. According to WRC data in February-March 2010, 67 sable tracks were found in this area along a 194 km route but only 10 Siberian weasel tracks. Thus, the constraining influence of the sable on the Siberian weasel population can be considerable even without direct extermination of the latter.

The sable-free period in the 19th and 20th centuries includes the greatest rise of Siberian weasel harvesting in 1920–1950 (to 31600 skins per year). The oppressive effect of the sable on Siberian weasels began with the recovery of the sable's abundance in 1960–1970 (see Fig. 1). In the latest decades, the impoverishment of food resources has played a decisive role in the decline of Siberian weasel abundance, and the sable had an additional negative influence.

Conclusion

In long-term dynamics of harvesting of Siberian weasels' skins in Yakutia, there are several clear-cut periods having different levels of harvesting. Especially noteworthy is the decline in the harvesting during the 2000s. Taken together with official WRC data, this observation indicates a profound reduction in Siberian weasel abundance in recent decades. The main reason for this decline is long-term depression of the abundance of the water vole and mountain hare, especially of the former. This situation was exacerbated by a disruptive influence of shifts in the profile of prey animals on the cycles of Siberian weasel abundance. An adaptive adjustment of this predator to the cyclicity of small rodents, which became its leading food source, apparently was not instantaneous and temporarily weakened the Siberian weasel's resistance to adverse factors.

Judging by the curve of long-term harvesting, the current decline of Siberian weasel abundance is unprecedented. Among multiple reasons for this phenomenon in Yakutia, there are consequences of human economic activity: chemical treatment of hayfields across large areas, efforts to exterminate the water vole, excessive culling of the mountain hare via hunting, and uncontrolled post-introduction growth of sable populations.

The period of a decrease in Siberian weasel abundance in Yakutia featured a decline of the proportion of young animals, a decrease in the number of kits per adult female, predominance of males among adult animals, a rise of the percentage of females among young animals, and a strong decline of this percentage in older groups, compensated by a higher percentage of newborn females. The relatively high yield of young animals in 1950–1980 shows that in the north of its geographic range, the Siberian weasel has retained elevated reproductive potential and the ability to sharply raise its abundance under favorable conditions, which is typical for species with a wide range (Shvarts, 1980). Competition with the sable is an additional contributing factor for the decline of Siberian weasel abundance in this region.

ACKNOWLEDGMENTS. The study was conducted within the framework of a state assignment from the Ministry of Science and Higher Education of the Russian Federation within the project "Populations and communities of animals of aquatic and terrestrial ecosystems in the cryolithozone of the eastern sector of the Russian Arctic and Subarctic: diversity, structure, and stability under natural and anthropogenic impacts" (No. 0297-2021-0044, EGISU R&D No. 121020500194-9) and by the project part of a state assignment in the field of scientific research from the Ministry of Science and Higher Education of the Russian Federation on topic FSRG-2020-0019 "Bio- and chemo-diversity of ecosystems, evolution, and genetic features of bioindicators in Eastern Siberia as well as the development of technologies for effective use of renewable plant resources" 2020-2022. This study has been supported by the ERC consolidator grant Glacial Legacy to Ulrike Herzschuh (No. 772852). The manuscript was translated into English and certified by shevchuk-editing.com.

References

AnAge: Database of Animal Ageing and Longevity. Availabe at https://genomics.senescence.info/species/query. php?search=mustela+sibirica. Accessed on 17 October 2021.

- Bakeev Yu.N. 1977. [Siberian weasel. Middle Volga basin, Ural and adjacent part of Western Siberia] // Nasimovich A.A. (ed.). Kolonok, Gornostay, Vydra. Moscow: Nauka. P.17–31 [in Russian].
- Belyk V.I. 1967. [Materials on winter nutrition of the Yakutian water weasel]//Trudy VNIIZHP. No.21. P.48–53 [in Russian].
- Chibyev V.Yu. 2020. [On the ecology of the water vole (*Arvicola terrestris* L.) in the example of the middle reaches of the Lena River] // Priroda Vnutrennei Azii. Vol.1. No.14. P.112–120 [in Russian].
- Dyakonov A.L. 1990. [Fur Trade in Yakutia at the End of the 18th-mid-19th Centuries]. Yakutsk: YANTS SO AN SSSR. 144 p. [in Russian].
- Erdakov L.N. & Litvinov Yu.N. 2014. [The cyclicity of the long-term variation of the abundance in the populations of the water vole (*Arvicola terrestris* L.)] // Izvestiya Irkutskogo Gosudarstvennogo Universiteta. Seriya Biologiya i Ekologiya. No.8. P.40–48 [in Russian].
- Erdakov L.N. & Pereyaslovets V.M. 2020. [Cyclicity of the long-term dynamics of the number of the snow hare] // Vestnik Severo-Vostochnogo Federalnogo Universiteta im. M.K. Ammosova. Vol.1. No.75. P.5–16 [in Russian].
- Gaidar I.S. 1990. [Distribution, abundance and economic use of the weasel in South Baraba] // Evsikov E.I. (ed.). Resursy Zhivotnogo Mira Sibiri. Okhotnich'ye-Promyslovyye Zveri i Ptitsy. Novosibirsk: Nauka. P.173–176 [in Russian].
- Gavrilova M.K. 2009. [Climate change (air temperature and precipitation) on the territory of Yakutia and the possibility of its impact on agriculture] // Nauka i Obrazovaniye. No.3. P.48–54 [in Russian].
- Heptner V.G., Naumov N.P., Yurgenson P.B., Sludsky A.A., Chirkova A.G., Bannikov A.G. 1967. [Mammals of the Soviet Union. Vol.2. Sea Cows and Carnivores]. Moscow: Vysshaya Shkola. 1002 p. [in Russian].
- Klevezal G.A. 2007. [Principles and Methods for Determining the Age of Mammals]. Moscow: KMK Scientific Press. 288 p. [in Russian].
- Konstantinov M. 1921. [Fur Trade in the Yakutsk Territory]. Irkutsk: Gosizdat, Irkutskoye otdeleniye. 94 p. [in Russian].
- Korytin S.A. 1963. [On the Siberian weasel hunting] // Ratsionalizatsiya Okhotnich'yego Promysla. No.1. P.66–70 [in Russian].
- Laptev I.P. 1958. [Mammals of the Taiga Zone of Western Siberia]. Tomsk: Izdatel'stvo Tomskogo Universiteta. 285 p. [in Russian].
- Mordosov I.I. 1997. [Mammals of the Taiga Part of Western Yakutia]. Yakutsk: Izdatel'stvo SVFU. 214 p. [in Russian].
- Polyakov E.F. 1977. [Siberian weasel. Southeast of Western Siberia] // Nasimovich A.A. (ed.). Kolonok, Gornostay, Vydra. Moscow: Nauka. P.31–44 [in Russian].
- Popov M.V. 1977. [Key to Mammals of Yakutia]. Novosibirsk: Nauka. 424 p. [in Russian].
- Prokopiev N.P. 2011. [Herbivorous Mammals of Alas Ecosystems]. Yakutsk: Izdatel'stvo SVFU. 221 p. [in Russian].
- Revin Yu.V. 1989. [Mammals of South Yakutia]. Novosibirsk: Nauka. 320 p. [in Russian].
- Safronov V.M. 1983. [Winter Ecology of Forest Voles in Central Yakutia]. Novosibirsk: Nauka. 158 p. [in Russian].
- Safronov V.M. 2002. [Ecological and physiological features of mustelids in winter conditions of Yakutia] // Labutin Yu.V. (ed.). Nazemnyye Pozvonochnyye Yakutii: Ekologiya,

Rasprostraneniye, Chislennost'. Yakutsk: YF SO RAN. P.50–67 [in Russian].

- Safronov V.M. 2016. [Population dynamics of forest voles in the basin of the middle Lena] // Printsipy Ekologii. Vol.5. No.3. P.143 [in Russian].
- Sapaev V.M. 1969. [Sex and age structure of field samples from the weasel] // Sbornik Nauchno-tekhnicheskoy Informatsii (Okhota, Pushnina i Dich'). Vol.27. P.3–5 [in Russian].
- Schwartz S.S. 1980. [Ecological Patterns of Evolution]. Moscow: Nauka. 278 p. [in Russian].
- Sedalishchev V.T., Okhlopkov I.M. & Odnokurtsev V.A. 2015. [To the ecology of the weasel (*Mustela sibiricus* Pall., 1773) in Yakutia]// Izvestiya Samarskogo Nauchnogo Tsentra Rossiiskoi Akademii Nauk. Vol.17. No.4(5). P.867–874 [in Russian].
- Shilyaeva L.M. & Bakeev N.N. 1982. [Resources of the main species of fur-bearing animals in the USSR and their use] // Bibikov D.I. & Grakov N.N. (ed.). Promyslovaya Teriologiya. Moscow: Nauka. P.5–27 [in Russian].
- Solomonov N.G. 1980. [Ecology of the Water Vole in Yakutia]. Novosibirsk: Nauka. 136 p. [in Russian].
- Sysoev V.P. 1960. [Hunting in the Far Eastern Taiga]. Khabarovsk: Knizhnoye Izdatel'stvo. 200 p. [in Russian].
- Tavrovsky V.A., Egorov O.V., Krivosheev V.G., Popov M.V. & Labutin Yu.V. 1971. [Mammals of Yakutia]. Moscow: Nauka. 660 p. [in Russian].
- Ternovsky D.V. & Danilov O.N. 1965. [Materials on the biology of mustelids (Mustelidae) in the foci of mass reproduction of the water rat] // Maksimov A.A. (ed.). Zhivotnyi Mir Baraby. Novosibirsk: Nauka. P.78–112 [in Russian].
- Ternovsky D.V. & Ternovskaya Yu.G. 1994. [Ecology of Mustelidae]. Novosibirsk: Nauka. 223 p. [in Russian].
- Ternovsky D.V. 1977. [Biology of Mustelidae]. Novosibirsk: Nauka. 280 p. [in Russian].
- Timofeev V.V. & Nadeev V.N. 1955. [Sable]. Moscow: Izdatel'stvo Tekhnicheskoy i Ekonomicheskoy Literatury po Voprosam Zagotovok. 404 p. [in Russian].
- Voilochnikov A.T. 1977. [Siberian weasel. Cisbaikalia and Transbaikalia. Far East] // Nasimovich A.A. (ed.). Kolonok, Gornostay, Vydra. Moscow: Nauka. P.44–70 [in Russian].
- Volkova L.S, Olesova A.I. & Kychkina I.I. 2020. [State Report on the State and Protection of the Environments of Republic of Sakha (Yakutia) in 2019]. Available from https://minpriroda.sakha.gov.ru/uploads/ckfinder/ userfiles/2021/04/13/files/%D0%93%D0%94%20-2019. pdf 678 p. [in Russian].
- Welch P. 1967. The use of the fast Fourier transform for the estimation of power spectra: A method based on time averaging over short, modified periodograms // IEEE Transactions on Audio and Electroacoustics. Vol.15. P.70–73.
- Zakharov E.S., Safronov V.M. & Pavlova A.I. 2016. [Winter feeding of sable (*Martes zibellina* L.) in Yakutia] // Dostizheniya Nauki i Tekhniki APK. Vol.30. No.11. P.82–86 [in Russian].
- Zakharov E.S., Safronov V.M., Zakharova N.N., Pestryakova L.A., Koryakina L.P., Kruse S. & Bochkarev N.A. 2022. Morphogenetic features of the Siberian weasel (*Mustela sibirica* Pall.) on the northeastern edge of its areal (Middle Lena Basin, Yakutia) // Biology Bulletin. Vol.49. No.6. P.626–635.
- Zakharov V.P. 1995. [Fur Trade and Trade in Yakutia (Late XIX–Early XX Centuries)]. Novosibirsk: Nauka. 137 p. [in Russian].