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Ecology of sable of North-Western Yakutian native population

Evgenii S. Zakharov* & Valery M. Safronov

ABSTRACT. In 2003–2012, 687 carcasses of aboriginal sables of Zhigansk population represented by the Yenisey subspecies (*Martes zibellina yeniseensis* Ognev, 1925) inhabiting North-Western Yakutia were studied. Skull and body size of native sables were larger and fur colour was lighter as compared to the Vitim subspecies (*M. z. princeps* Birula, 1922) introduced in South-Western Yakutia (Olekma population). Dynamics of the native population is characterized by the prevalence of natural cycles at moderate hunting rates. The portion of juveniles made up 69.3% on average. Among adults 37.0% were 1-year-old animals, 25.1% 2-year-old, and 13.3% 3-year-old sables. Animals aged 4 to 12 years were less numerous (24.6%), especially females (8.5%). Fertility (3.46±0.2) and fecundity (2.77±0.3) rates as well as the number of reproducing females (61.4%), especially at the age of one year (2.9%), were less than in Olekma population. The diet of Zhigansk sables was based on northern red-backed voles (*Myodes rutilus*) (43.7% of studied stomachs), grey red-backed voles (*Craseomys rufocanus*) (43.7%) and root voles (*Alexandromys oeconomus*) (50.2%). Consumption of pikas (*Ochotona* sp.) was increased (up to 31.2%) in separate years. Birds were rarely consumed (1.6%). Plant food mainly consisted of bog bilberry (*Vaccinium uliginosum*) (15.5%). Poorly-nourished sables made up 71.9% of the sample. The number of moderately fat and very fat sables increased with age. Among them, males (30.2%) prevailed over females (25.7%). The relative mass of paranephric fat was lowest in sables aged 1 to 8 years. Sex-related differences in fat index were recorded only in juveniles.
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KEY WORDS: sable, aboriginal population, phenotype, age-sex-related structure, reproduction, fertility, nutrition, fatness.

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Экология соболя нативной популяции северо-запада Якутии

Е.С. Захаров, В.М. Сафронов

РЕЗЮМЕ. В 2003–2012 гг. исследовано 687 тушек соболей енисейского подвида (*Martes zibellina yeniseensis* Ognev, 1925), населяющего северо-запад Якутии. По размерам черепа и тела соболи нативной популяции крупнее, а по окраске меха светлее потомков интродуцированного на юге Якутии витимского подвида (*M. z. princeps* Birula, 1922). Динамика численности характеризуется преобладанием естественной цикличности при умеренном воздействии промысла. На долю молодняка приходилось в среднем 69,3%. Среди взрослых годовики составляли 37,0%, двух- и трехлетки — соответственно 25,1 и 13,3%. Зверьки 4–12 лет немногочисленны (24,6%) особенно самки (8,5%). Потенциальная (3,46±0,2) и реальная плодовитость выше (2,77±0,3), а участие самок в размножении (61,4%), особенно в возрасте 1 года (2,9%), меньше, чем на юго-западе Якутии. Основу питания составляли полевки красная (*Myodes rutilus*) (43,7%), красно-серая (*Craseomys rufocanus*) (43,7%) и экономка (*Alexandromys oeconomus*) (50,2%), в отдельные годы возрастало потребление пищухи (*Ochotona* sp.) (до 31,2%). Птицы поедались редко (1,6%). Из растительных кормов регулярно использовались только ягоды голубики (*Vaccinium uliginosum*) (15,5%). Соболи с низкой упитанностью составляли в среднем 71,9% пробы. Количество средне- и высокоупитанных особей возрастало с увеличением возраста. Среди самцов их было больше (30,2%), чем у самок (25,7%). Наименьший индекс упитанности отмечался у соболей в возрасте 1–8+ лет. Половые различия по индексу жира прослеживались только у сеголеток.

КЛЮЧЕВЫЕ СЛОВА: соболь, автохтонная популяция, фенотип, половая и возрастная структура, репродукция, потенциальная плодовитость, питание, упитанность.

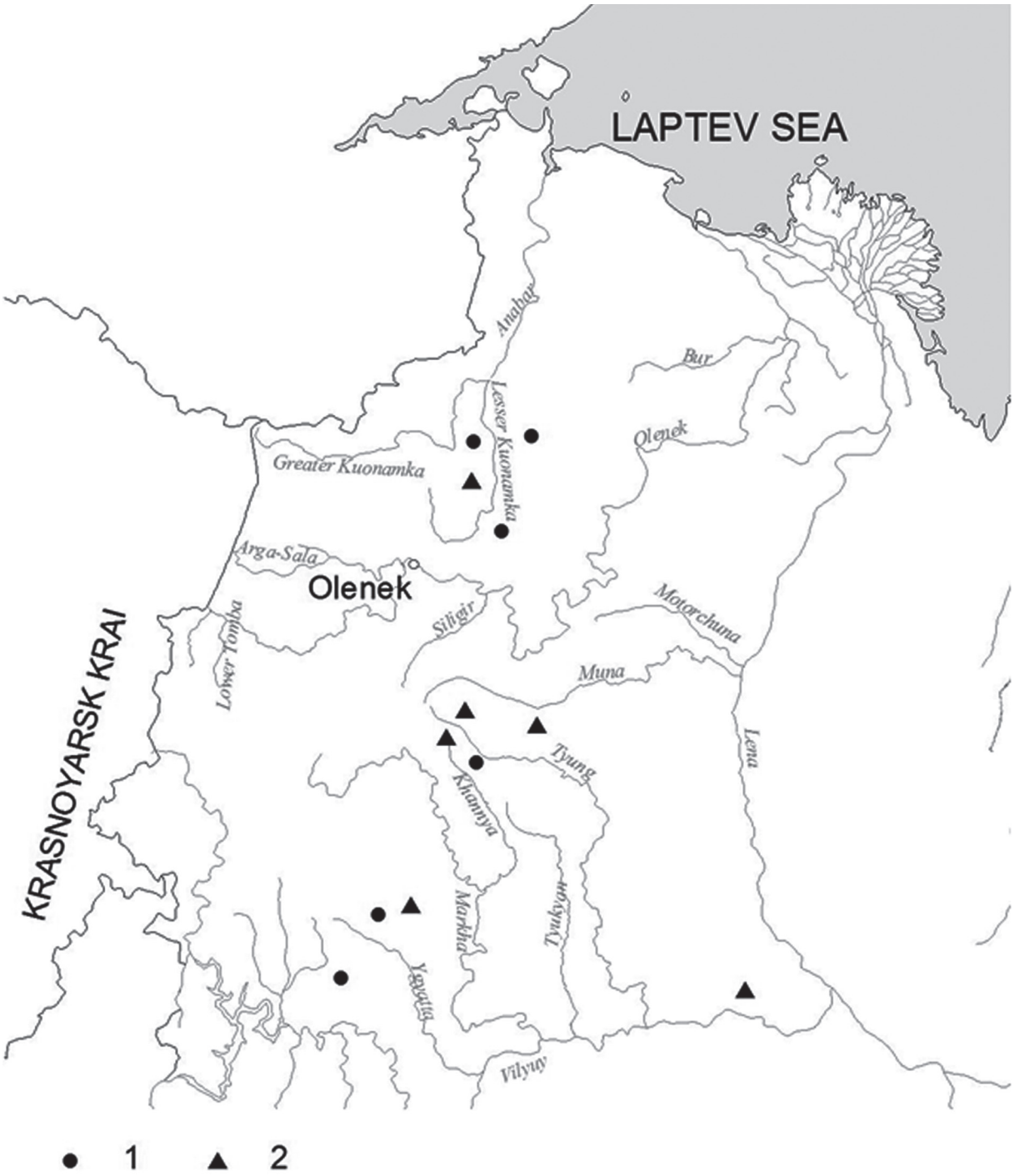

Fig. 1. Study area: 1 — field work sites; 2 — sample collection sites.

Introduction

North-Western Yakutia covers a vast territory bordering with the Lena River in the east, the Vilyuy River in the south, and Laptev Sea in the north. The whole forested area of the region lies within the northern taiga sparse forests subzone inhabited by the light-coloured sable of Yenisey subspecies (*Martes zibellina yenisseensis* Ognev, 1925). In historical and scientific literature, this subspecies is also known as "Zhigansk" or "Olenek-Zhigansk" sable which preserved by the beginning of the 20th century in several limited locations along the Muna, Motorchuna, Birekteh, Arga-Sala, Tyung, and Markha rivers (Romanov, 1938, 1941; Tavrovsky, 1958) (Fig. 1). The modern population of Zhigansk sable originated from remains of these groups.

At the same time, the aboriginal sable of South-Western Yakutia was practically exterminated (Tavrovsky *et al.*, 1971). For quick recovery of the population, the sables from the Vitim River basin (*M. z. princeps* Birula, 1922) beyond the territory of Yakutia were introduced to the South-Western Yakutia and became the progenitor of the modern south-western population (cited further as Olekma population) (Fig. 1). With time, the distribution area of introduced sables of South-Western Yakutia expanded northward from the near-Lena region, while Zhigansk sable expanded southwards up to the Vilyuy River, which became the area of hybridization between the two populations (cited further as Vilyuy population) (Zakharov & Safronov, 2012).

Population number and basic ecology of Zhigansk sable was studied in details during the period of population recovery in 1950s (Tavrovsky, 1958). Now population distribution, density, and number of Zhigansk sable have notably changed. The age- and sex-related structure and reproduction character as well as other peculiarities of this sable ecology are still poorly known. The aim of the paper is to fill gaps in available information after long-termed studies conducted by the authors.

Some data on Zhigansk sable ecology have been reported in conferences proceedings (Zakharov, 2005, 2008) and published here in full for the first time.

Materials and methods

The material was collected from 2003 to 2012 within the basic hunting region of Zhigansk sable distribution range that covers basins of the Tyukyan, Khannya, Tyung, Bolshaya, and Malaya Kuonamka rivers (Fig. 2). Population size was assessed by the methods of true and indirect censuses (Gusev, 1966; Vershinin, 1976).

The true census method means the estimation of the number of animals within study plots. The plots, each about 20 km^2 in size, were set out in most typical habitats. The sables were counted along parallel or circular routes. The true census results were supplemented by indirect census estimation conducted along linear routes. The animals numbers, evaluated using indirect census were counted according to the formula by A.N. Formozov (1932) corrected by V.I. Malyshev and S.D. Pereleshin (Gusev, 1966). An average distance covered by a sable per day was taken as a route width.

Age- and sex-related population structure was estimated on the basis of study of 687 sable carcasses, provided by hunters. This estimate was compared with estimations of Olekma (n=436) and Vilyuy (n=489) populations.

The age of animals was estimated in two steps. First, adult specimens were distinguished from juveniles based on craniological characteristics and value of relative width of canine root canal (less than 41% for males and less than 34% for females) (Timofeyev & Nadeyev, 1955; Smirnov, 1960; Shadrina, 1988). At the second step, individual age was estimated by means of counting annual increment layers number on histological sections of teeth (Klevezal, 2007).

Reproduction was characterized by fertility and fecundity rates. Fertility was expressed as a number of yellow bodies counted on histological sections of ovaries (Zaleker, 1950). Fecundity was estimated by counting the number of blastocytes in uterine horns (Tumanov, 1988).

Annual mortality was estimated as difference in relative number of animals in preceding and following age groups.

For diet characteristics, we analyzed the content of 247 stomachs and 329 feces. Consumption rates of various food types were estimated on the basis of occurrence of the particular type in all samples and expressed in percent. Fatness index was estimated as ratio (g/kg) of mass of fat surrounding kidneys to skinless carcass mass (Shvartz *et al.*, 1968). Morphometric measurements were conducted for specimens of age 2+. This helped us to reduce the effect of age variation (Zakharov, 2012).

Sable hunting rates (a number of animals hunted per year) were calculated on the basis of data provided by the Game Department of the Republic of Sakha (Yakutia) for the period of 1969–2010. Fur colour variation was taken from the reports of the Fur Company "Sakhabult" for the period of 1994–2005. The skins (n=22340) were sorted into four colour categories in accordance to All-Union State Standard 27571-87. K.M. Eremeyeva's scale was used (1952) for fur colour description. The darkest fur (black) is attributed to category I (4 points), dark brown fur is category II (3 points), chestnut brown fur colour is attributed to category III (2 points), and all light colours are combined in category IV (1 point). The colour index was calculated as an arithmetic mean of points for each population. Basic statistics were calculated using MS Excel Analysis ToolPak and STATISTICA 8.0. Between-sample one-dimensional differences were estimated using Student's t-test.

Results

There were no differences revealed in weight for Zhigansk and Vilyuy sables. At the same time, body lengths of males (450.9±1.7 mm, n=38) and females (415.5±1.9 mm, n=19) of Vilyuy sables were greater than those of Zhigansk sables (446.4±1.5 mm, n=72, $p<0.05$ and 409.3±2.1 mm, n=36, $p<0.05$ respectively). Animals of both populations were significantly larger as compared to Olekma sables (442.5±1.7 mm, n=47 $p<0.01$ for males; 401.0±2.2 mm, n=32 $p<0.01$ for females).

Zhigansk males (84.3±0.2 mm, n=52) and females (76.6±0.4 mm, n=37) were similar to Vilyuy sables (84.0±0.3 mm, n=38 and 76.2±0.5 mm, n=11 respectively) in condilobasal length of skull. As compared to Olekma specimens, this parameter was significantly larger in males (83.3±0.3 mm, n=25, $p<0.01$), while females did not differ significantly (76.1±0.9 mm, n=10).

Fig. 2. Remaining distribution area of aboriginal sables and sites of reintroduction: 1 — sites of sable reintroduction in 1948–1961; 2 — remaining home range of aboriginal sables in mid1930-s; 3 — modern distribution area of aboriginal sables in North-Western Yakutia.

Table. Proportion of sables with various fur colour in North-West Yakutia in 1946–2005.

Years	Colour categories, %			
	I	II	III	IV
1946–1948 (Eremeyeva, 1952)	29.3		70.7	
1951–1956 (Tavrovsky, 1958)	1.6	8.7	31.5	58.2
1960–1964 (Tavrovsky, 1971)	2.0	10.2	37.6	50.2
1994–2005 (our data)	0.5	4.8	19.3	75.4

The portion of dark-coloured (categories I and II) Zhigansk sables made up about one third of the population in 1946–1948, 10.3–12.2% in 1950–60s, and 5.3% in 1995–2005 (Table). Fur colour index in Zhigansk sables hunted in 1994–2005 varied from 1.3±0.01 to 1.74±0.01, being 1.34±0.1 in average. Phenotypically close sables of the Vilyuy population had a similar average fur colour index value (1.24±0.03, n=34237). Olekma sables displayed darker fur coloration (1.73±0.04, n=56392, $p<0.01$).

Population dynamics of Zhigansk sable featured the prevalence of natural cyclic fluctuations. Due to light

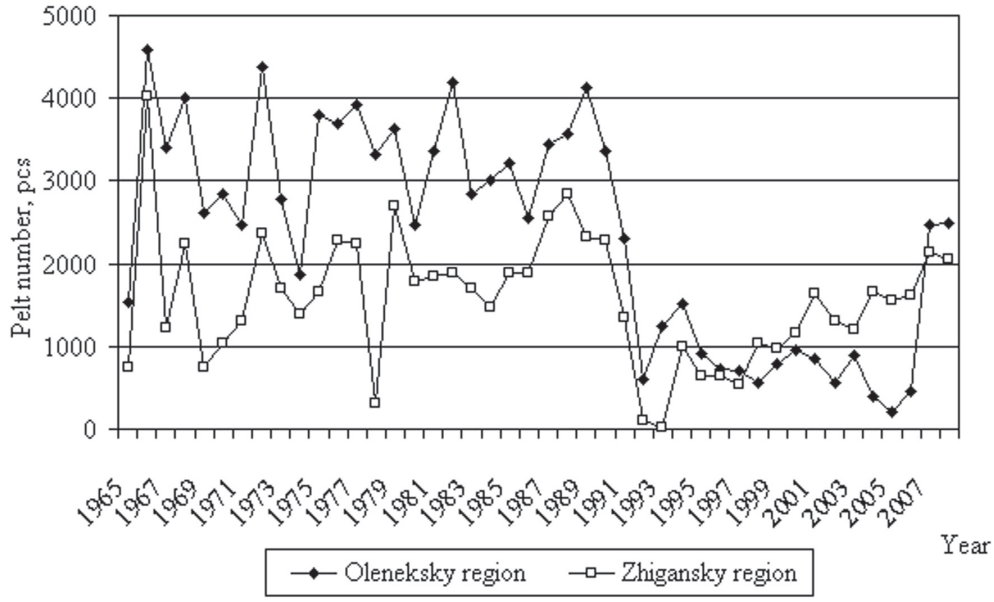

Fig. 3. Sable hunting rates in main regions of North-Western Yakutia in 1969–2010.

fur colour, low density and remoteness of its distribution range, it was hunted to a lesser extent as compared to populations of dark-coloured sable. In 1980s, hunting rates in north-western regions averaged 5.3 thousand skins per year against 7.8 thousand in the Lena-Olekma Interfluve in South-Western Yakutia. In early and mid 1990s, hunting rates in the north-west reduced sharply (0.7–2.0 thousand skins per year) due to restructurization of hunting economy and refocusing on reindeer hunting which was more profitable under new economic conditions. In the second half of 2000s, sable hunting rates increased (3.3–4.6 thousands) after population growth and fur price rise, which is clearly depicted on the diagram (Fig. 3).

In April 2003, we recorded the highest post-hunting density in the southern part of the region along the upper streams of the Tyukyan and Markha rivers (1.6–2.4 individuals, 2.1 ind./1000 ha on average). This was much higher as it had been believed before: 0.6–0.7 ind./1000 ha (Tavrovsky, 1958). By 2004, pre-hunting population size of Zhigansk sable constituted 23–25 thousand individuals (Safronov *et al*., 2006). According to the data provided by the Game Department of the Republic of Sakha (Yakutia), in 2012, the sable number increased up to 26–29 thousand.

Analysis of the data of 2003–2010 years showed the relative part of juveniles varied from year to year from 51.9±9.6 to 85.1±3.8% (Fig. 4). Of the total eight-year sample in average, juveniles constituted 69.3±1.8%.

Adult population was mainly represented by 1- (37.0±3.3%), 2- (25.1±3.0), and 3-year-old (13.3±2.3%) sables; elder age groups (24.6%) were less numerous due to heavy mortality, especially in females (Fig. 5). Average mortality in male juveniles reached 81.6%, while in females — 85.5%. During the second year of life, mortality decreased, comprising 45.7% for females and 20.9% for males. Increased elimination of females (61.0%), as compared to males (45.0%), was observed in each age group. Though early mortality of females being in reproductive age was recorded in all sable populations (Bolshakov & Kubantsev, 1984), this phenomenon is clearly pronounced in Yakutia. In Zhigansk population, only 19.2% of sable males and 7.0% of females survived from the birth to the age of 3–7 years. In Vilyuy population, 10.3% of males and 5.0% of females survived. In Olekma population, where living conditions are not so harsh, differences in survival rates between males and females are not so big, comprising 14.5 and 11.3% respectively.

Sex ratio among young specimens in Zhigansk and Viluy populations was near 1:1 with some prevalence of females (51.3±2.3%). On the contrary, in Olekma population, the males (52.4±2.8) insignificantly predominated over females (47.6±2.8%). Among adult specimens, males prevailed throughout the whole range. In Zhigansk population, portion of males constituted 62.6±3.3% ($p<0.01$), while in Vilyuy population this number was 74.4±3.8% ($p<0.01$). In Olekma population, as it was expected from lesser female mortality, male prevalence was not so strong (57.1±4.5, $p<0.03$).

The portion of reproductive females in samples varied from 12.5 to 55.5% in different years, averaging 35.4% (n=79). One-year-old females in Zhigansk sable showed weak participation in reproduction (2.9%) as compared to those from Vilyuy population (13.6%), and even more to Olekma animals (31.3%). At the age of 2 years, the number of reproducing females increased to 57.9%, reached the maximum level at the age of 5–7

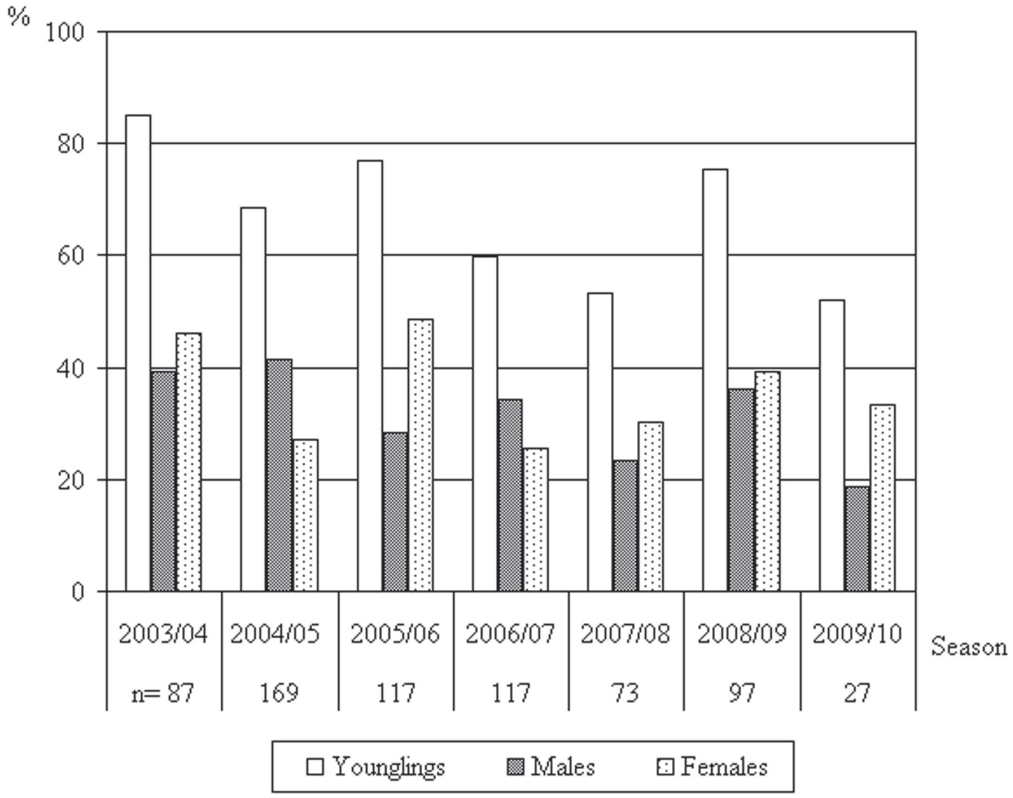

Fig. 4. Relative amount of juveniles among total amount of sables hunted in 2003–2010.

years (100%), and then reduced at the age of 9–12 years (90%) at age limit of 13–14 years in wild (Sokolov, 1979). The reproductive core was comprised by 2–5-year-old females (45.6% of all reproducing females) with the prevalence of 2-year-old animals (24.1%). On average, 61.4% of females at the age of 2+ contributed to reproduction in Zhigansk population, 64.0% in Vilyuy population, and 74.3% in Olekma population. This reflects the tendency to decrease the number of reproducing females northwards.

Fertility indices were on average 3.46±0.20 that was higher as compared to the same index in 1950-1960 (3.0±0.09, $p<0.05$; Tavrovsky *et al.*, 1971). Fecundity was on average 2.77±0.31 which was by 19.9% less than fertility. In Vilyuy population, this parameter (2.26±0.39) was less than fertility by 28.0% (3.14±0.26, n=22, $p<0.05$). Under relatively favourable conditions, the difference between fertility (2.97±0.15) and fecundity (2.54±0.3) in Olekma population was less pronounced (14.5%).

The animal food (94.3%) prevailed over plants (15.3%) in the diet of Zhigansk sable. The food composition was rather diverse. Along with northern red-backed vole (*Myodes rutilus*) (43.7% of occurrence on average), it also included grey red-backed vole (*Craseomys rufocanus*) (43.7%) and root vole (*Alexandromys oeconomus*) (50.2%). In juvenile animals (n=112) 37.5% stomachs contained root voles and 29.5% red-backed voles, while adult sables (n=60) showed an opposite ratio, 25.0% and 48.3% correspondingly.

In some years, consumption of pikas (*Ochotona* sp.) increased. From autumn 2005 to spring 2008, pikas were recorded in 16.9–31.2% of the studied stomachs. In winter 2006–2007, it was consumed as often (26.7%) as *Myodes*, *Craseomys*, and *Alexandromys* species (23.3–26.7% each). However, as for the whole period of study, pikas were observed in 5.6% of samples. Wood lemming (*Myopus schisticolor*) was also quite regular food item (3.3% on average). Additional food sources included shrews (*Sorex* spp.) (1.2%), squirrels (*Sciurus vulgaris*), flying squirrels (*Pteromys volans*), muskrats (*Ondatra zibethicus*), and mountain hares (*Lepus timidus*) (0.2% each). The fragments of ermine *Mustela erminea* were recorded in three stomachs (0.5%).

Birds were quite rarely consumed in our study (1.6%), though as it is known from literature their portion in sable's diet may increase in some years (27.9%; Tavrovsky & Shitarev, 1957). The most numerous were willow (*Lagopus lagopus*) and rock (L. *mutus*) ptarmigans congregating abundantly during their autumn migrations.

Fish remains in stomachs (3.3%) were presented mainly by hunters' bait. As for plant food, only bog bilberry (*Vaccinium uliginosum*) (15.1%) was consumed regularly.

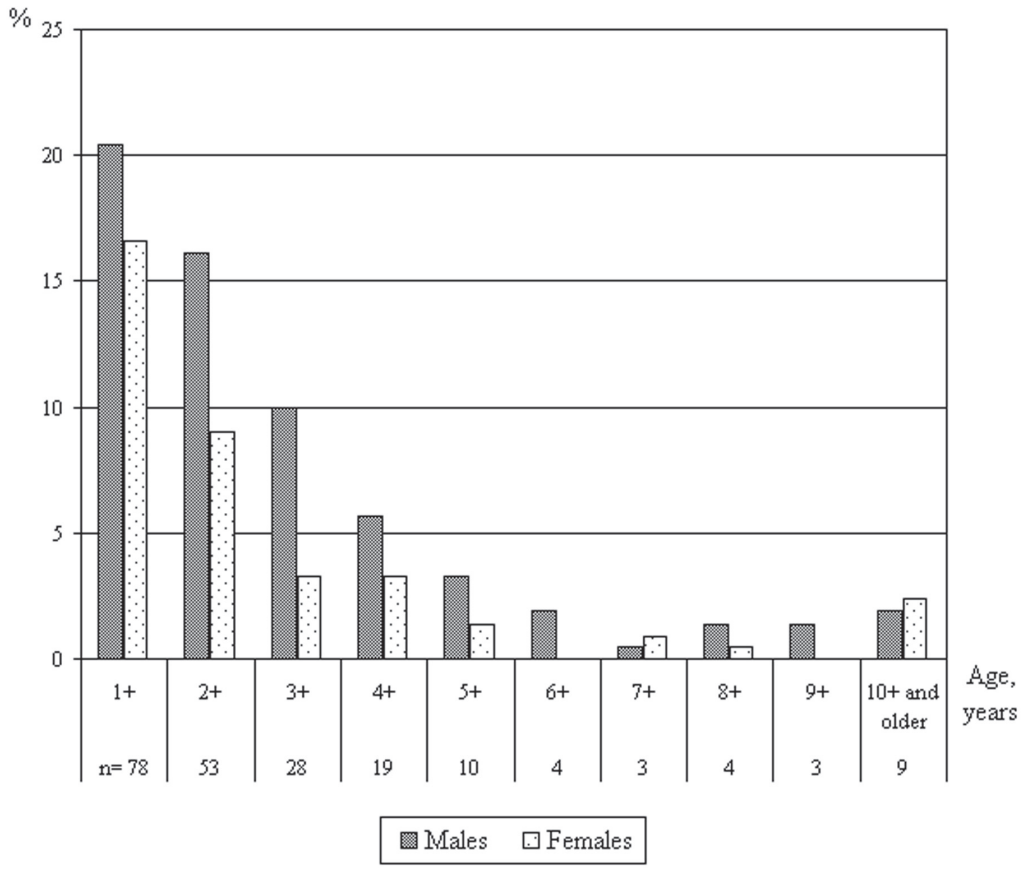

Fig. 5. Age distribution in adult animals in 2003–2010.

The portion of sables with low fat content in Zhigansk population (71.9%) was about two times larger than in Olekma population (39.9%). In Vilyuysk population such sables constituted 67.1%.

A number of animals with medium and high fat content increased with age: 24.2±2.0% in juveniles, 34.1±4.2% in 1–2-year-old specimens, and 45.6±6.0% ($p<0.01$) in 3–8-year-old animals. The portion of such fat animals was larger among males (30.2%) than among females (25.7%). However, annual variations of this parameter (14.6–54.4 and 9.4–53.1% respectively) were synchronous in both sexes.

Increase of the number of fat animals was recorded during the winters of 2005–2006, 2006–2007 and 2007–2008 (27.7, 53.8 and 39.7% respectively) together with sharply increased consumption of pikas as it was mentioned above (Fig. 6). During other winters ill-nourished animals prevailed (77.8–85.3%).

The relative mass of paranephric fat averaged 1.04± 0.05 g/kg (n=168). From year to year, it varied (from 0.65±0.06 to 1.36±0.5 g/kg) synchronously with the number of fat animals in the sample. At the largest portion of well-nourished sables during the winters of 2005–2008 (Fig. 6), fat index was minimal (Fig. 7). During the same winters, the absolute mass of kidney fat was also less (471.1–669.9 mg) as compared to sables hunted in 2003–2005 and 2008–2010 (845.3–1175 mg), while the body mass was higher (722.4 on average as against 706.9 g), which is especially true for males (825.4 g against 797.4 g). This negative correlation determined the reduced fat index values.

No sex-related differences in fat index were observed among adult sables (0.87±0.08 g/kg for males and 0.94±0.1 g/kg for females). Male juveniles displayed larger relative mass of paranephric fat (1.33±0.12 g/kg, n=57) as compared to females of the same age (0.87±0.06 g/kg, n=40, $p<0.01$). The average relative mass in juveniles was 1.14±0.08 g/kg. It was reduced in animals aged 1–8 years up to 0.86±0.05 g/kg, and increased in older specimens of 9+ years old up to 1.34±0.5 g/kg (Fig. 8).

Discussion

As V.A. Tavrovsky (1958) summarized, the vast territory from the Lena through the Yenisey rivers, north of N 61°, was inhabited by genetically homogenous sables that most likely correspond to the "Zhigansk" subspecies. By present, the southern border of its distribution range has shifted northwards up to N 65°. The right bank and partly the left bank of the

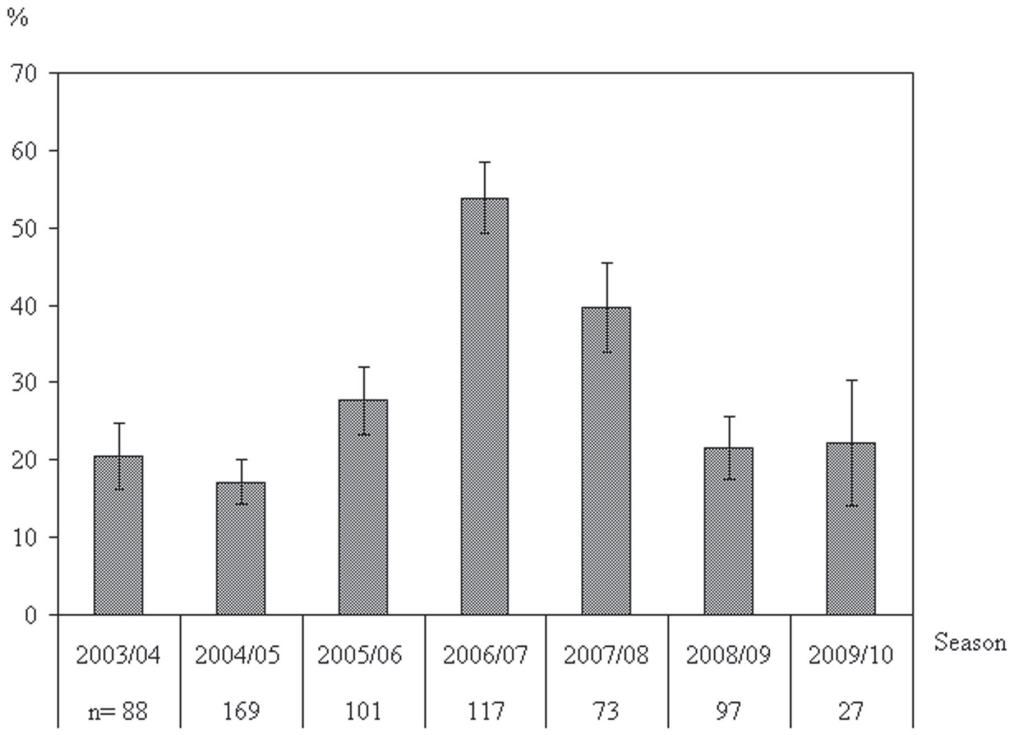

Fig. 6. Occurrence of well-nourished sables in North-western Yakutia in 2003–2010.

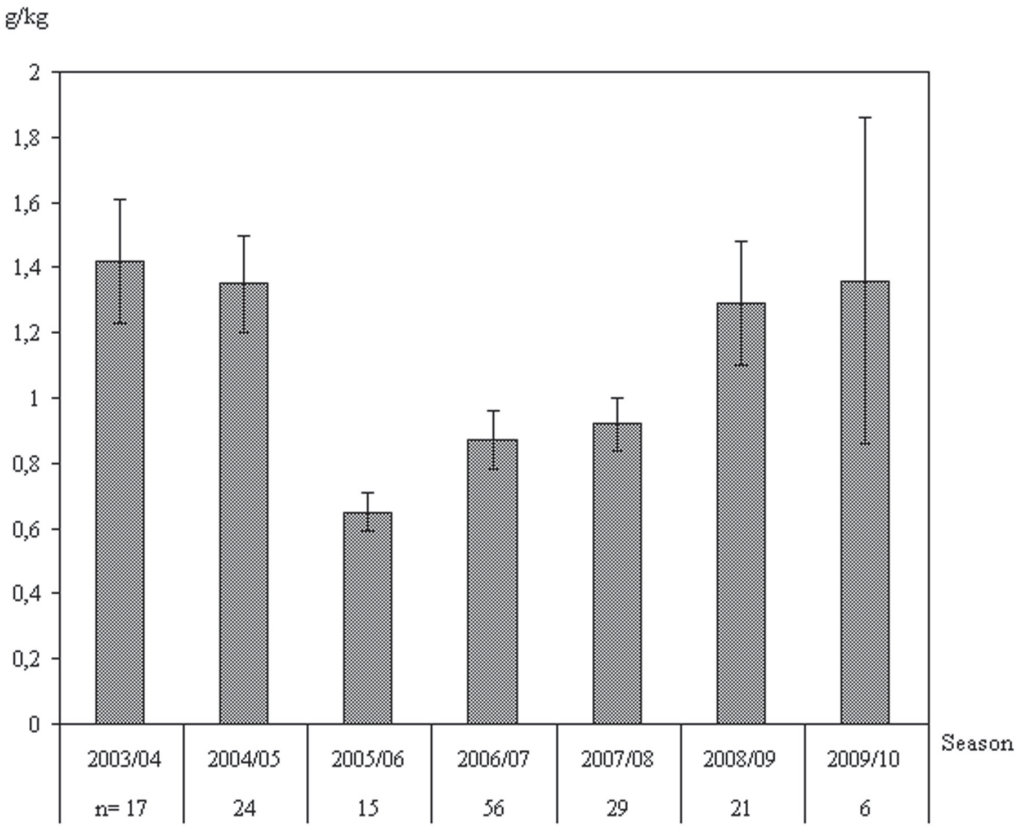

Fig. 7. Paranephric fat relative mass variations in sable of North-western Yakutia during 2003–2010.

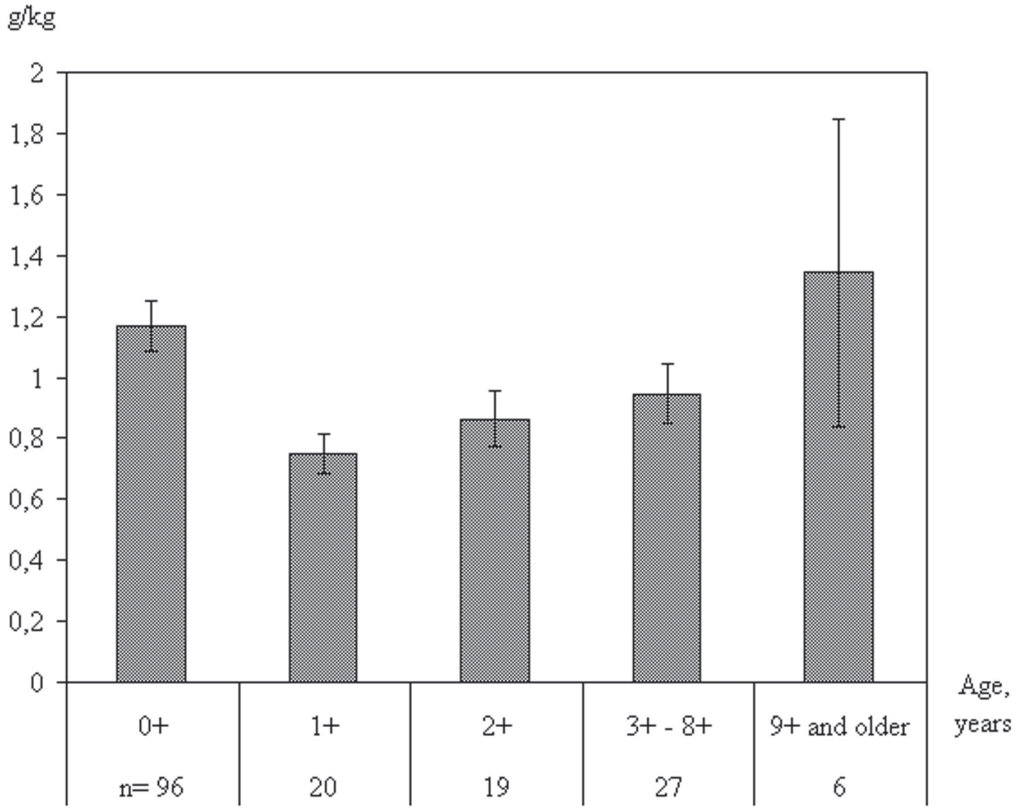

Fig. 8. Relative mass of paranephric fat in sables of various age in North-western Yakutia (2003–2010).

Vilyuy River basin, situating to the south, are inhabited by mongrel sables, probably appeared as a result of cross-breeding of Olenek-Zhigansk animals with introduced Olekma subspecies penetrating to the north from the Olekma River basin and the near-Lena region. According to the number of ecological parameters, Vilyuy sables take an intermediate position between the two original populations, while their morphological characteristics are more close to the aboriginal Zhigansk form (Zakharov & Safronov, 2012).

Chronological variations of fur colour of Zhigansk sables were characterized by gradual increase of the portion of light-coloured specimens which had lasted since the middle of the last century till nowadays (Table). Lightening of fur in the sables from Baikal region introduced to different regions of Siberia, with or without aboriginal populations of sables has been discussed in detail in the literature (Monakhov *et al.*, 1982). The facts of fur lightening in the sables of aboriginal populations are less known. Phenotype bias to prevalence of light colours could be explained by increased population number, migrations, gene pool mixing of different populations (Bakeyev, 1976; Safronov & Zakharov, 2014). According to K.D. Numerov (1973), colour change in sables in Central Siberia takes place simultaneously in large areas and includes the periods of lightening and darkening lasting 15 years or more. Thus, during the general process of fur colour lightening in Zhigansk population, darkening took place in 1960–1964 (Table).

After uncontrolled hunting in 17–18th centuries, in 19th century sable remained in the north-west Yakutia in remote isolated areas only (Doppelmair, 1927; Tavrovsky *et al.*, 1971) (Fig. 2). Increase of sable number in North-Western Yakutia with subsequent natural dispersion over the vast territory started since 1940s after hunting had been prohibited in 1930–1933, 1936–1941 and 1946–1950. In 1952–1953, the estimated number of sables was 3.4–4.0 thousand animals (Tavrovsky, 1958). By 1970–1980, post-hunting resources increased up to 18.0 thousand animals, but later declined to 8.0–11.7 thousand (Belyk *et al.*, 1990). Population number increased during 1990s. It reached 15.1 thousand in 1994, and 25.9 thousand animals in 2000 (Sedalischev & Popov, 2001). At the north, sable reached the near-tundra forests, beyond N 71°.

Based on hunting statistics provided by the Game Department of the Republic of Sakha (Yakutia), in Zhigansk population, 2–5-year cycles, as well as more prolonged 9–12-year cycles of sable numbers variation were revealed that had taken place during the last decades. The latter was more noticable in Zhigansk region (Fig. 3), where the peak number persisted from 1979 to 1991. Lesser cycles are related to 2–4-year periodicity

of numbers of forest dwelling voles, characteristic for those latitudes (Revin *et al.*, 1988).

Quantitative predomination of juveniles in samples proves high reproduction rates. Males prevailed over females, which is characteristic for the species as a whole, though the cases of female prevalence occur due to natural reasons (Monakhov, 1968; Bolshakov & Kubantsev, 1984). Numerical superiority of females among young animals in northern populations was noticed by G.A. Sokolov (1979). This tendency can be an adaptation of females to their increased mortality in elder age.

Fertilty and fecundity in females of Zhigansk population was rather higher as compared to Vilyuy and Olekma populations. The increasing in sable fecundity rates in the regions of long-term intensive hunting as a feedback to increased elimination was pointed out in the publications (Monakhov, 2007). However, in North-Western Yakutia, this process was observed under moderate hunting pressure which proves its possible dependence on more general factors including the current climate warming.

North-Western Yakutia, where Zhigansk sable lives, is characterized by the less favourable forage resources for sable due to rather limited plant food (Tavrovsky *et al.*, 1971). According to published data, in 1950–1970s, rather small population size allowed sables to occupy forest habitats most optimal for life. So its diet was based on forest dwelling rodents (Tavrovsky & Shitarev, 1957). Meanwhile our study showed that root vole composed the diet basis (42.2–61.4%) together with reduced consumption of northern red-backed vole (3.0–25.0%) during six winter periods (2003/04, 2004/05, 2005/06, 2007/08, and 2008–2010). Increased consumption of root and grey red-backed voles could be explained by sable distribution over all suitable habitats, from ripe larch forests to shrubby mires that are inhabited by polydominant population of small rodents. Thus, the expansion of biotopic distribution of sable following its population growth, has led to fuller use of small rodent resources.

It is known that during lean winters the number of Zhigansk sables with empty stomach reached 32.7% (Tavrovsky & Shitarev, 1957), while in our study they composed only 6.7%. This proves favourable food conditions during our study period.

Certain age-related variation in diet composition was observed. Growing up, juvenile sables have little choice for settling. Usually their habitats represent semi-open biotops non-preferable for this species, such as valley or swamped landscapes, while adult sables inhabit forests. Owing to this, forest dwelling voles were observed more often (48.3%) in the diet of adult animals living in habitats with better protective and forage conditions (forests), as compared to that of juveniles (29.5%). On the contrary, occurrence of root vole in the diet of juveniles was higher (37.5%) as compared to adult animals (25.0%). The same was observed in sables inhabiting the western part of the range (Zaleker & Poluzadov, 1955).

We discussed the geographical peculiarities of Yakutian sable diet in details earlier (Zakharov *et al.*, 2016). In South-Western Yakutia, the distribution range of Olekma population, purely animal food items were recorded in stomachs of 56.0% of sables, mixed animal-plant food in 41.2%, and only plant food in 2.8% (n=323). In the north-western regions, where Zhigansk sable lives, animal food consuming made up 84.2%, mixed food was eaten three times less (13.9%), while plant food was recorded at the same rate (2.9%). Insufficient provision with mixed food of Zhigansk sables increased its dependence on the number of voles. This was compensated by richer species composition of rodents recorded in sable stomachs, as compared to that in 1950s.

In separate years, pikas play an important role in sable's diet. One pika is equal to 3–6 northern red-backed and grey red-backed voles in body mass, thus notably reducing the energy cost of foraging (Safronov & Anikin, 2000).

Richer winter diet (in the case of increased number of pikas) yielded the increased number of well-nourished sables at rather small amount of interior fat proving the known disability of the animals to fat accumulation (Ternovsky, 1977). The minimal absolute mass of paranephral fat at favourable forage conditions can be explained by rather wide age spectrum in fat sables including migrating juveniles. Under regular forage conditions, fat depot is usually recorded in full-grown animals keeping sedentary life and having good capacity for accumulation of reserve substances, as opposed to migrating juveniles (Safronov *et al.*, 1985).

The earlier metabolism studies (Safronov, 2002) allowed us to state that low heat production (4.9 kcal/h) and inactive metabolism in sables during rest (3.3% per 1° of ambient temperature) are insufficiently compensated by heat-insulating properties of fur. According to nature observations, sable easily withstands strong cold stress by high muscle activity (22.4 kcal/1000 m) but dies quickly of hypothermia at lack of motion despite long and dense fur. Increased respiratory exchange ratio (0.8–0.9) proves involvement of proteins into energy exchange. By opinion of M.I. Titova (1950), this is characteristic for sables with developed muscles and low fat deposit. This suggests that the recorded increase in body mass under favourable forage conditions provides muscle thermogenesis optimization and is of great significance for maintaining energy balance during the winter period.

Conclusions

Sable of native population in North-Western Yakutia that belongs to Yenisey (or Zhigansk) subspecies, is distinct by its larger body size and light fur colour as compared to the introduced populations of Olekma sable inhabiting more southern regions. Morphological characteristics of the Vilyuy River basin population are similar to Zhigansk sable. The process of sable fur colour lightening in the studied region continues.

Three latitudinal zones with various population density have been discerned the latter decreasing towards the northern border of the range. Population dynamics has maintained its natural cyclicity due to moderate hunting pressure. The demographic structure featured rejuvenated age composition and increased death rates in adult animals, especially in females of the most productive age. The reproductive core was composed of females aged 2–5 years with the prevalence of 2-year-old specimens. Participation of 1-year-old females in reproduction was weak. There was a tendency to increase female number among juveniles as a sign of population's reaction to their increased mortality at a mature age. Fertility and fecundity in Zhigansk sable were higher, while participation in reproduction was lower as compared to Olekma and Vilyuy populations.

The diet was composed mainly of animal food mostly represented by voles of *Myodes*, *Craseomys*, and *Alexandromys* genera. The significance of mixed animal-plant food did not reach the level of that in Olekma population in the south of Yakutia. Carnivorous diet amplifies the dependence of population on the abundance of small rodents. However, their simultaneous disappearance is unlikely due to asynchronous fluctuations in various species that are known for adjacent territories (Revin *et al.*, 1988).

Low winter fatness in most sables was normal for Zhigansk sables which were related to constant significant energy costs in search of small and scattered food items under extremely low air temperatures. The exclusion was the winters of 2005–2008, when the role of pikas increased in sable's diet. It represented a large food item which did not require long searching and critical energy costs. That yielded an increase in amount of well-nourished animals at relatively little individual fat depot. The average body mass was also increased.

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References

Bakeyev N.N. 1976. [Geographic variation of sable fur colour and its dynamics] // Trudy VNIIOZ. Vol.26. P.26–54 [in Russian].

Belyk V.I., Sedalischev V.T., Anikin R.K. *et al.* 1990. [The results of sable reacclimatization in Yakutia] // Intensifikatsiya vosproizvodstva resursov okhotnichyikh zhivotnykh. Kirov: VNIIOZ. P.194–206 [in Russian].

Bolshakov V.N. & Kubantsev B.S. 1984. [Sex structure of mammal populations and its dynamics]. Moscow: Nauka. 232 p. [in Russian]

Doppelmair G.G. 1927. [Fur hunting in Yakutia] // Yakutia. Leningrad: Izdatelstvo AN SSSR. P.412–468 [in Russian].

Eremeyeva K.M. 1952. [Geographic variation of sable colouration] // Trudy Moskovskogo pushno-mekhovogo instituta. Vol.3. P.81–89 [in Russian].

Formozov A.N. 1932. [Formula of quantitative assessment of mammals by footprints] // Zoologicheskii zhurnal. Vol.11. P.66–69 [in Russian].

Gusev O.K. 1966. [Sable ecology and censuring]. Moscow: Lesnaya promyshlennost. 124 p. [in Russian]

Klevezal G.A. 2007. [Principles and methods of age estimation in mammals]. Moscow: KMK Sci Press. 283 p. [in Russian]

Monakhov G.I. 1968. [Population structure, reproduction dynamics and questions of rational use of sable resources in Prebaikalia and Transbaikalia] // Zoologicheskii zhurnal. Vol.47. No.4. P.602–609 [in Russian].

Monakhov G.I., Kryuchkov V.S., Monakhov V.G. & Shurygin V.V. 1982. [Results of introduction of East-Siberian sables in the Yenisey Siberia and the Vysyugan River basin] // Promyslovaya teriologia. Moscow: Nauka. P.136–148 [in Russian].

Monakhov V.G. 2007. [On changes in reproduction cycles in sable of Trans-Urals in late 20th century] // Sibirskii ekologicheskii zhurnal. No.4. P.635–637 [in Russian with English summary].

Numerov K.D. 1973. [Sable. Middle Siberia] // Sobol, kunitsy, kharza. Moscow: Nauka. P.70–78 [in Russian].

Revin Yu.V., Safronov V.M., Volpert Ya.L. & Popov A.L. 1988. [Ecology and population number dynamics of mammals in Pre-Verkhoyanie] // Novosibirsk: Nauka. 200 p. [in Russian]

Rokitsky P.F. 1973. [Biological statistics]. Minsk. 319 p. [in Russian]

Romanov A.A. 1938. [On Zhigansk sable] // Priroda. No.4. P.112–113 [in Russian].

Romanov A.A. 1941. [Fur animals of Lensk-Khatanga Krai and ther hunting] // Trudy Instituta polyarnogo zemledeliya, zhivotnovodstva i promyslovogo khozyaistva. Vol.17. 139 p. [in Russian]

Safronov V.M. 2002. [Ecological and physiological peculiarities in Mustelids under winter conditions of Yakutia] // Nazemnye pozvonochnye Yakutii: ekologiya, rasprostranenie, chislennost. Yakutsk: YaF "Izdatelstvo SO RAN". P.50–67 [in Russian].

Safronov V.M., Nikolaev A.N. & Odnokurtsev V.A. 1985. [Essay on sable (*Martes zibellina* L.) winter ecology in West Pre-Verkhoyanie] // Fauna i ekologia mlekopitayuschikh Yakutii. Yakutsk: YaF SO AN SSSR. P.24–55 [in Russian].

Safronov V.M. & Anikin R.K. 2000. [Ecology of the sable, *Martes zibellina*, in northeastern Yakutia] // Zoologi-

cheskii zhurnal. Vol.79. No.4. P.471–479 [in Russian with English summary].

Safronov V.M. & Zakharov E.S. 2014. [Fur colour change in sable (*Martes zibellina,* Carnivora, Mustelidae) of various age groups in the Middle Aldan River basin] // Zoologicheskii zhurnal. Vol.93. No.4. P.595–599 [in Russian with English summary].

Safronov V.M., Zakharov E.S. & Sedalischev V.T. 2006. [Sable numbers in Yakutia] // Problemy sobolinogo khozyaistva Rossii. Proceedings of the 5th All-Russian research-and-practice Internet-conference on sable. Kirov. P.198–205 [in Russian].

Schwarz S.S., Smirnov V.S. & Dobrinsky L.N. 1968. [Method of morphophysiological indicators in ecology of terrestrial vertebrates] // Trudy Instituta ekologii rasteniy i zhivotnykh. Sverdlovsk. Vol.58. P.346–348 [in Russian].

Sedalischev V.T. & Popov A.L. 2001. [Sable resources in Yakutia and its conservation problems] // Ratsionalnoe ispolzovanie resursov sobolya v Rossii. Proceedings of the 4th All-Russian research-to-practice conference. Krasnoyarsk. P.46–53 [in Russian].

Shadrina E.G. 1988. [Comparative characteristics of age estimation methods for sable (*Martes zibellina*) and ermine *(Mustela erminea)*] // Zoogeograficheskiye i ekologicheskiye issledovaniya teriofauny Yakutii. Yakutsk. P.76–83 [in Russian].

Smirnov V.S. 1960. [Age estimation and age interrelationships in mammals. Case study of squirrel, musk-rat and five predator species] // Problemy flory i fauny Urala. Sverdlovsk. P.97–112 [in Russian].

Sokolov G.A. 1979. [The mammals of Siberian cedar forests in Siberia]. Novosibirsk: Nauka. 256 p. [in Russian]

Tavrovsky V.A. 1958. [Sable of North-west Yakutia and the ways of hunting recovery] // Vosstanovlenie promyslovykh zapasov sobolya v Yakutii. Trudy Instituta biologii Yakutskogo filiala SO AN SSSR. Moscow: Izdatelstvo AN SSSR. Vol.4. P.50–142 [in Russian].

Tavrovsky V.A. & Shitarev I.S. 1957. [Materials on sable nutrition in North-west Yakutia] // Zoologicheskii zhurnal. Vol.21. No.4. P.608–616 [in Russian].

Tavrovsky V.A., Egorov O.V., Krivosheyev V.G. *et al.* 1971. [Mammals of Yakutia]. Moscow: Nauka. 660 p. [in Russian]

Ternovsky D.V. 1977. [Biology of Mustelidae]. Novosibirsk: Nauka. 280 p. [in Russian]

Timofeyev V.V. & Nadeyev V.N. 1955. [Sable]. Moscow: Zagotizdat. 403 p. [in Russian]

Titova M.I. 1950. [Standards of maintenance feeding of adult sables] // Trudy NII pushnogo zverovodstva i krolikovodstva. Vol.5. P.5–49 [in Russian].

Tumanov I.L. 1988. [Fecundity estimation in marten and sable: express-method] // Okhota i okhotnichye khozyaistvo. No.10. P.15 [in Russian].

Vershinin A.A. 1976. [Methodology guidelines on sable census] // Moscow: NTI TsNIL Glavokhoty RSFSR. 35 p. [in Russian]

Zakharov E.S. 2005. [On ecology and numbers of sable in North-western Yakutia] // Estestvoznaniye i gumanizm: sbornik nauchnykh rabot. Vol.2. No.4. Tomsk. P.35–36 [in Russian].

Zakharov E.S. 2008. [Ecology and numbers of sable in North-western Yakutia] // "EREL-2007": materialy konferentsii nauchnoy molodezhi. Yakutsk. P.185–189 [in Russian].

Zakharov E.S. 2012. [Sable of South and West Yakutia (morphology, ecology, population structure)] // Autoreferat of Candidate Thesis. Yakutsk. 20 p. [in Russian]

Zakharov E.S. & Safronov V.M. 2012. [Ecology of sable (*Martes zibellina* L.) in West Yakutia] // Vestnik Tomskogo Gosudarstvennogo Universiteta. Biologia. Vol.17. No.1. P.73–84 [in Russian with English summary].

Zakharov E.S., Safronov V.M. & Pavlova A.I. 2016. [Winter diet of sable (*Martes zibellina L.*) in Yakutia] // Dostizheniya nauki i tekhniki APK. Vol.30. No.11. P.82–87. [in Russian with English summary].

Zaleker B.L. 1950. [Materials on sable (Martes zibellina L.) sex cycle] // Trudy VNIIOP. Vol.9. P.135–151 [in Russian].

Zaleker B.L. & Poluzadov N.B. 1955. [Fecundity and winter diet of sable in Ivdelsky region of Sverdlovskaya Oblast] // Trudy VNIO. Vol.14. P.145–152 [in Russian].