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Variability of the Brown Bear and the Problem of Decreased Individual Size

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Abstract—A review of published materials on the body weight of brown bears in the Northern Hemisphere is presented. The territories of Europe, Russia, Japan (Hokkaido island), Canada, and the United States are covered. The data reflecting the main forms of intraspecific variability of this trait are grouped: age, seasonal, geographic, and individual forms. The sex differences and differences in the weight of bears kept in captivity are taken into account. The life span of one generation of brown bears is on average close to 10 years. The share of bears aged 20 years or more in the population is small and decreases rapidly over the years, but signs of bear aging are progressing, and their contribution to the reproduction of the population is decreasing. Bears over 30 years old are very rare in natural populations; long-livers, whose age exceeded 40 years, were recorded singly in captivity. The reproductive contribution to the demography of the population for male and female brown bears that have reached the age limit is close to zero. The age trend in the dynamics of body weight corresponds to the rule of biological growth by L. von Bertalanffy and includes four age phases, which are distinguished by the predominant function (growth, maturation, reproduction, aging). There is also fifth phase: negative growth (degeneration). Negative growth is inherent in rare extremely old individuals and shatun bears. The age-related dynamics of body weight are complemented by an annual increase in weight (accumulation of fat reserves) and their consumption during hibernation. The controversial topic of body reduction in brown bear populations is considered, and different points of view are given. A more convincing explanation is that significant hunting pressure leads to a rejuvenation of the age composition of the population and, as an additional consequence of selective hunting, to a decrease of individual body-weight in the population. The dynamics of the weight characteristics of the population due to hunting selectivity by size and sex are reversible. The elimination of bears in the age phase of degeneration (extremely old bears and shatuns), whose contribution to the reproduction of the population is extremely small (or equal to zero), can hardly significantly worsen the gene pool of the population.

Keywords: brown bear, body weight, age phases, selective hunting, decrease in individual size
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INTRODUCTION

The hunting of large mammals raises questions, one of which is of practical significance: what are the consequences of hunting based on the trophy qualities of the hunting object? The immediate and distant consequences are revealed; they are assumed to be reversible and irreversible. For example, the owner and organizer of hunts must be sure that the trophy value of individuals in the local population of the brown bear *Ursus arctos* L. will not decrease over the years. Among domestic specialists (game managers and zoologists) is not agreement on the reality and reasons for probable changes in the properties, including trophy-significant properties, of hunted individuals. Accordingly, it is difficult to predict the long-term exploitation of the brown bear population. On the one hand, "There is no scientific evidence of a negative impact by trophy hunting on the morphometric parameters of Kamchatka bears ... " (Mel'nikov, V.K. and Mel'nikov, V.V., 2008, p. 162). On the other hand, it was noted (Stepanenko, 2020) that a body reduction is observed in bears in many populations of Russia, including Kamchatka; according to the latest author, a progressive body reduction in other populations is also expected in the future.

A well-grounded answer to the raised question requires generalizations of the facts that can be obtained as a result of long-term and fairly fully organized monitoring of the state and dynamics of variability in the brown bear. However, such monitoring has yet to be brought to a satisfactory state; only then can it be used as a basis to accumulate factual material. The intraspecific variability of mammals has many manifestations (Yablokov, 1966; Shmalgauzen, 1968; Mayr, 1968, 1971; Filipchenko, 1978; Hallgrimsson and Maiorana, 2000). The article discusses several types of variability: ontogenetic variability, age vari-

ability, and individual differences. The goal of this study is to review publications containing materials and generalizations on the variability of the brown bear that are useful for consideration of the influence of hunting on the size of individuals of this species and to discuss the results of the review. The main topics of discussion are as follows: duration of an individual life; age dynamics of body weight as an indicator of overall dimensions; seasonal dynamics of body weight; geographic variability in body weight; individual variability; and the causes of body reduction in brown bear populations.

The work is geographically limited to Europe, Russia, Japan (Hokkaido), Canada, and Alaska and other states inhabited by brown bears (United States), which basically corresponds to the boreal and temperate zones of the climatic map of the Northern Hemisphere. A certain and very common difficulty is presented by the following circumstance: when studying populations are the objects of hunting, a researcher is usually forced to use a sample obtained as a result of hunting, i.e., the composition of a hunting sample. A hunting sample distortedly represents the real composition of the population as regards sex, age, and other characteristics. There are at least two probable reasons for this distortion: the selectivity of hunting (or capture) and, as a consequence of the selectivity, the probable change in the composition of the surviving part of the population due to the removal of the other part. We also have to contend with the fact that the authors of the reviewed publications provide quantitative indicators with different completeness.

LENGTH OF AN INDIVIDUAL LIFE

In a discussion of the life span of the brown bear, it is necessary to take into account individual differences and the dynamism (variability over time) of any demographic indicator in populations. Dynamism is due to mortality, which, on the one hand, is peculiar in any age group and, on the other hand, can change significantly depending on a number of environmental factors. The article mainly uses data from authors who observed bears in captivity and tracked their age or those who determined the age of animals living in the wild based on teeth cuts (Klevezal, 2007). According to the authors of the reviews (Tumanov, 2017; Sato, 2009), the maximum age of brown bears in captivity reaches 28–30 years in males and 35–38 years in females. Another review publication (Schwartz et al., 2003) indicates that a long-lived male lived in captivity for 50 years and a female lived for 42 years (zoo in Memphis, United States). These values stand out from other data on the life span of brown bears, but they can be considered indicators of the population-species potential.

The following are the results of the study of the age of bears living in nature. The average age without sex subdivision in a sample of 89 adult brown bears caught in Slovakia (Hell and Sládek, 1979) was 10 years. In Slovenia, the local population is subject to significant pressure from legal hunting (Krofel et al., 2012): over the period 1998–2008, 20% of the population was removed. This is apparently the only example of such a high hunting percentage in the world. The highest age of individuals was recorded in a sample of 547 bears caught over the entire observation period: 15 years for a male and 18 years for a female. Thus, bears of this population do not live up to the maximum age for the species. A study of bear dens in Sweden using noninvasive methods (Elfström and Swenson, 2009) recorded 114 bears ranging in age from 2 to 30 years, with an average of 7.7 years. In a hunting sample from 1990–2015 taken in the same country, the average life span of bears was 5 years (Frank et al., 2017). The data from Sweden show how materials from the hunting sample can differ from the estimate of the age composition of the population obtained with the noninvasive method: the composition of the hunting sample is noticeably younger.

Brown bears in Russia reach sexual maturity at the age of 5–6 years (males) and 4–5 (females) (Zavatskii, 1987; Pazhetnov, 1990). According to visual observations on a spawning river at the Kronotsky Nature Reserve, 11.6% of bears of both sexes had signs of aging (Seryodkin and Pachkovskii, 2004). In the same reserve, two males were observed in the wild nature for 20 years in a row (Nikolaenko, 2003); males survived to the age of 28 and 29 years. The oldest bears from the Turukhansk district of the Krasnoyarsk Territory that were shot in nature were 39 and 29 years old (a male and female, respectively) (Zavatskii, 1981). Observations in captivity (Colmenares and Rivero, 1983) and in nature in landscapes with low forest cover (where bears are more accessible to visual observation) have shown that aging males with very impressive sizes often lose to younger, active, and aggressive males in the struggle for the right to mate with a receptive female bear (Nikolaenko, 2003; Gordienko, 2012; Puchkovskiy, 2017). As follows from a review (Geptner et al., 1967, p. 450), "one bear cub is more often born by young and old female bears."

At Glacier National Park (United States), four females aged 9 to 30 years were shot for the purpose of regulatory removal (Martinka, 1974). Materials on reproductive maturation (age of the first brood) and aging in female brown bears obtained from 18 populations of North America and two populations from Sweden (Schwartz et al., 2003) combined 4726 records of radiolabeled bears. Most bears mature at the age of 5 years, but the first brood is usually brought by bears in the wild nature a few years later. The greatest reproductive contribution is made by female bears aged 9–15 years; reproductive aging becomes noticeable from the age of 16 years, but it occurs especially rapidly after the age of 25 years. Not a single female bear over 29 years of age had cubs (van Daele et al., 2001; Stey-

Table 1. Age phases of the brown bear ontogeny as distinguished by the predominant function and the age trend of the body-weight dynamics

Indicators	Age phases				
	growth	maturation	reproduction	aging	degeneration
Age range, years	0–6	4–6	7–15	≥16	≥25
Growth dynamics	Rapid	Moderately rapid	Decelerating	Decreasing	Negative

aert et al., 2012), while the oldest female recorded in the wild nature was 34 years old.

Of 344 brown bears on the Alaska Peninsula, the oldest bears were a male 13 years old and a female 15 years old (Glenn, 1980). Long-term studies of the brown bear populations of the Great Yellowstone ecosystem and a number of other regions of North America and Sweden (van Manen et al., 2014; *Yellowstone Grizzly*..., 2017) showed that the decrease in the reproductive contribution to population demography in males may be caused not so much by a weakening reproductive function as by the diminishing ability to physically compete for females with younger males. Although males live up to 30 years of age in the wild nature, not a single male brown bear over 27 years old has been recorded as reproductively successful (Steyaert et al., 2012). In Japan (Hokkaido Island), 98% of problem brown bears (n = 823) that were shot during sport hunting and for the purpose of regulatory hunting were not more than 16 years old (Sato, 2009). The oldest of all were a 30-year-old male and a 34-year-old female.

The generation age of brown bears in the central part of European Russia is on average 8 years in the exploited population and 9–10 years in the protected population (Pazhetnov, 1993a). When the preservation of the reproductive potential and real life span of animals that make up the reproductive core of the population are taken into account, the available demographic data (Danilov, 1988; Pazhetnov, 1993b; Chernyavskii and Krechmar, 2001; Tumanov, 2017; Bunnell and Tait, 1985; Swenson et al., 2001; Schwartz et al., 2003) lead to estimation of the life span of one brown bear generation to be on average close to 10 years (Puchkovskiy, 2005; Pazhetnov, 2011). It should be clarified that an important role is played in this case by the average life span of not all born individuals but only those that make up the reproductive part of the population and ensure the birth of the next generation. The share of bears aged 20 years or more is small and decreases rapidly over the years, but the signs of bear aging are progressing, and their contribution to the reproduction of the population is also decreasing. Bears over 30 years old are very rare in natural populations; long-livers, whose age exceeded 40 years, were recorded singly in captivity. The reproductive contribution by male and female brown bears that have reached the age limit to the population demography is reduced.

AGE-RELATED BODY WEIGHT DYNAMICS AND AGE PHASES

Adult, male brown bears surpass females in weight by 30–50%; therefore, weight indicators are considered separately in the review materials when possible. It was established (Zavatskii, 1987) that local bears in the Turukhansk district of the Krasnoyarsk Territory grow and gain weight up to the age limit (25–30 years), but the growth is uneven. After reaching sexual maturity, the gain in weight and overall size slows as the bears age. Of the bears shot in the Turukhansk district, 25 adult males had an average age of 15.4 years and 13 females had an age of 10.2 years (Zavatskii, 1991). Weighing involved only bears shot in the summer months, when the fatness of the animals is minimal. The average weight of males was 189 kg, and their highest weight was 264 kg. The average weight of females was 111 kg, and their highest weight was 125 kg.

The materials already mentioned above show that the oldest bears make up an insignificant share of the population, one that eventually dies out. Therefore, the study of the weight dynamics in aging individuals is not provided with a sufficient number of facts that are suitable for processing with methods of mathematical statistics. In a den near the town of Belozersk (at that time, Novgorod province) a very large, "remarkably old and thin" male was shot (Melnitskii, 1915). It is assumed (Lazarev, 1979) that the weight of the oldest specimens in Kamchatka is decreasing. Visual observations also give some reason to assume that the weight of sick or aging individuals may decrease at the limit of life (Revenko, 1993). The last weeks of life of a large, emaciated, and, apparently, very old bear were traced in the winter of 2008 in Kamchatka (http://shpilenok.livejournal.com/2011/01/11/, accessed on February 13, 2021). There are few examples, but they give reason to believe that the weight of extremely old bears is changing downward. This vector of dynamics may correspond to the phase of age-related degeneration (Table 1).

Brown bears on the Alaska Peninsula reach 95% of the maximum weight at the age of 6.5 years for males and 4.5 years for females (Glenn, 1980). Bears that are older than this age continue to gain weight, but the rate of this process slows. The average weight was 389 kg in five males over 9 years old and 207 kg in 25 females over 9 years old. The maximum weight was 442 kg in a

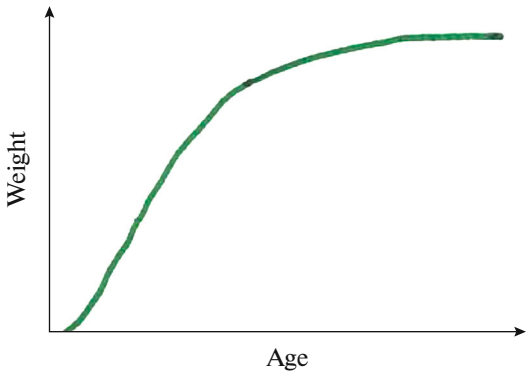

Fig. 1. Graphic expression (sigmoidal curve) of the biological growth rule of L. von Bertalanffy. Vertical axis, weight; horizontal axis, age.

male aged 10 years; the weight in the largest female (15 years old) was 277 kg. Estimates of the age dynamics of body weight in North American brown bears based on materials from later publications (Hilderbrand et al., 1999, 2019) generally confirm the conclusions of the author of the article cited above.

Foreign experts tend to discuss the calculated asymptotic body mass (Kingsley et al., 1988; Swenson et al., 2007), which is the result of age-related weight dynamics interpreted as an asymptotic process: a constant increase with a constant slowdown in the increase. In this regard, the authors refer to the general biological rule of the growth of living systems (in this case, those at the individual level) and the corresponding equation and curve on the graph, which were proposed by Bertalanffy (von Bertalanffy, 1969). As an illustration, Fig. 1 shows a unimodal curve that expresses the relationship between the age and body weight of an individual (https://animalbiosciences.uoguelph.ca/~swatland/HTML10234/LEC20/LEC20.html, accessed on March 5, 2021). Having data on the age of a particular bear and its body weight at the time of the study and using the equation of the growth rule, foreign colleagues obtain a curved line that must demonstrate the trend of the age dynamics of the individual's weight. Similar graphical materials have found a place in a number of publications (Kingsley et al., 1988; Hilderbrand et al., 1999, 2019; Swenson et al., 2007). Such graphs do not reflect the degenerative phase of body-weight dynamics (Table 1).

Based on the generalization of the aforementioned materials on the body weight of bears at different ages and taking into account the Bertalanffy growth rule, we distinguished the age phases of the growth dynamics (Table 1), which, in general, constitute the main trend of the dynamics. The phases are distinguished according to the most characteristic function. The growth phase is characterized by a rapid increase in body weight. During the maturation phase, bears reach sexual maturity and the growth rate slows. In the reproductive phase, the reproductive contribution to the population demography is the greatest, and the body weight continues to increase, but the rate of increase is noticeably reduced. In the aging phase, the reproductive contribution decreases, and the rate of body weight gain is minimal. In the degeneration phase, the reproductive contribution tends to zero, and the body weight may decrease.

The number of individuals in the population that represent these phases also decreases with age, which is especially noticeable for phases 4 and 5. Moreover, exploited populations may have no bears with obvious signs of aging at all (Glenn, 1980; Krofel et al., 2012). For this reason, the availability of materials that are suitable for research on the phases of aging and degeneration is minimal. Accordingly, it is still possible to characterize the representatives of these phases based on individual examples and assumptions until sufficient factual materials are accumulated. It can be more definitely assumed that the contribution of aging bears (phases 4 and 5) to the reproduction of the population and to its gene pool is minimal. These categories from the age composition of the brown bear populations are examples of redundancy in relation to the reproduction function of living systems at the population-specific level of organization (Puchkovskiy, 1999). Let me explain: with minimal hunting pressure in specially protected areas, long-lived bears can survive in the population but are already excluded from the reproductive process.

SEASONAL BODY-WEIGHT DYNAMICS

Seasonal body-weight dynamics in brown bear populations are usually well expressed. In autumn, animals feed intensively, gaining fat reserves that are necessary for consumption during hibernation and in the first weeks after leaving the den (*Medvedi*..., 1993; *Bears*..., 1994; *Yellowstone Grizzly*..., 2017). A noticeable accumulation of fat mass begins in the second half of August, with the transition to fairly high-calorie mass feed. During the fattening period (the period of hyperphagia in English-language publications), the body weight increases, reaching the maximum before laying to dens. In the taiga regions of Russia, the fat reserves in adult bears can reach 30% of the total body weight (Pazhetnov, 1990).

A review by European authors compared the body weights of brown bears in northern (Sweden and Norway) and southern Europe (Slovenia and Croatia) (Swenson et al., 2007). Northern bears used up the fat reserves and lost by spring 26% of the body-weight, determined in autumn (males), and 39% (females). Southern females lost 18% of the body-weight to spring; males had no noticeable differences. At the same time, the authors of the study noted that the hibernation of southern bears was half as long; moreover, some male bears of southern region do not den at all.

According to the data of Zavatskii (1987), the fat reserves of bears in the Turukhansk district of the Krasnoyarsk Territory amount to 17 to 25% of the live body weight by the time of denning. A male shot in northeastern Siberia (Chernyavskii and Krechmar, 2001) had 55 kg of fat at a body weight of 211 kg. A review of publications on the regions of Siberia (Smirnov, 2017) shows that the autumn–winter fatness of brown bears of both sexes is 20–25%.

Thus, the seasonal trend in the body weight dynamics of the brown bear reflects the accumulation of fat reserves, which reach their maximum values in late autumn, by the time of denning. By the spring, the total body weight decreases due to the expenditure of fat reserves. The intensity of these dynamics directly depends on the severity and duration of winter and, accordingly, on the duration of hibernation (Stroganov, 1962; Geptner et al., 1967; *Medvedi*..., 1993; Smirnov, 2017; Hilderbrand et al., 1999, 2019; Friebe et al., 2001). Modeling of the energy of winter sleep has shown that the fat reserve for a female bear's reproductive success cannot be less than 19% of its autumn body weight in the case of a hibernation period of more than 120 days (López-Alfaro et al., 2013).

According to studies in Russia, some of the bears' fat reserves are still preserved when they leave their dens (Pazhetnov, 1990; Ustinov, 1993; Chernyavskii and Krechmar, 2001; Tumanov, 2017), but they are completely consumed within a few weeks.

A special category is represented by shatun bears (Bromley, 1965; Geptner et al., 1967; Formozov, 1976; *Medvedi*..., 1993), which were recorded in some years in a number of regions of Russia (Puchkovskiy et al., 2019). Shatun bears are recorded in autumn and winter. The presence of shatun bears is characteristic of regions with severe, long, and snowy winters; they appear during the years of poor harvest of main fattening feed, suitable for hyperphagia (Gudritis, 1963; Pavlov and Zhdanov, 1972; *Medvedi* ..., 1993; Smirnov, 2017). The shatun bears that were examined by specialists were quantitatively dominated by adult males (Smirnov, 2017; Kozhechkin and Smirnov, 2017; Mordosov, 2005). Shatun bears are also characterized by a high or extreme degree of exhaustion and, accordingly, reduced body weight (Gudritis, 1963; Formozov, 1976; Smirnov, 2017; Puchkovskiy and Butkalyuk, 2020). The mortality rate among shatun bears is increased; this category of bears dies out during the first months of winter. There is reason to believe that the body-weight dynamics in shatun bears are similar to that of extremely old bears and correspond to the degenerative phase (Table 1).

GEOGRAPHICAL VARIABILITY OF BODY WEIGHT

The significant geographical variability of the brown bear of the Old World has been written about by many authors (Middendorf, 1851; Ognev, 1931; Stroganov, 1962; Geptner et al., 1967; Davitashvili, 1970; Chernyavskii and Krechmar, 2003; Couturier, 1954; Kurtén, 1973). Studies on the population genetics and phylogeography of the brown bear based on the use of paleozoological and molecular genetics methods paint a rather complex picture of the formation and status of modern subspecies and geographical populations (Baryshnikov, 2007; Kitchener et al., 2020) and are not considered in this article.

The fundamental report (Couturier, 1954) indicates the highest weight of brown bears from the Pyrenees: 350 kg for a male and 250 kg for a female. According to a modern publication (Swenson et al., 2007), male bears from southern Europe (Slovenia and Croatia) had an average body weight of 248 kg (n = 111) in spring and females had an average body weight of 115 kg (n = 67). Bears of northern Europe (territories of Sweden and Norway) weighed 201 kg (males, n = 412) and 96 kg (females, n = 446) in spring. The data on body weight in autumn for southern populations are as follows: 243 kg (males, n = 83) and 141 kg (females, n = 69); the weight values in autumn for northern populations are 273 kg (males, n = 301) and 158 kg (females, n = 281). That is, if the weight of animals that have accumulated fat reserves for hibernation is used for comparison, northern bears look somewhat heavier than southern ones. However, southern bears are found to be superior in weight according to the results of spring determinations.

Our compatriots write that "there is no reliable information about the killed bears weighing 300 kg in the Komi Republic" (Polezhaev and Neifeld, 1998: p. 67). In the Lapland Nature Reserve, the maximum weight of adult males was 315 kg; the average weight for 13 individuals was 185 kg. For females (n = 10), these indicators were 175 and 135 kg (Gilyazov, 2011). In Karelia, of 75 weighed males, only three adult males weighed more than 300 kg (320, 340 and 370) (Danilov and Tirronen, 2017). The weight of shot bears from Arkhangelsk oblast was in the range of 100–300 kg (Weisfeld, 1993). The weight of adult bears shot in Tver oblast was 175 kg for one female and from 230 to 315 kg for six males (Pazhetnov, 2006). Of the 223 bears shot in Udmurtia in 1986–1989, 162 bears weighed within 100 kg and only four bears exceeded 200 kg in weight (Loskutov et al., 1993). The maximum weight of bears from Bashkiria was 300–320 kg (Loskutov et al., 1993).

Of the more than 120 bears shot in the Tomsk oblast, only two were heavier than 300 kg. They weighed from 100 to 150 kg for the most part (Lyalin, 1983). The weight and size of the brown bear inhabiting the western Sayan do not differ from the popula-

tions of central Siberia (Turukhansk district of the Krasnoyarsk Territory) (Zavatskii, 2004). In terms of body size, bears from Yakutia are smaller than those in other regions of Siberia and the Far East (Tavrovskii et al., 1971; Akhremenko and Sedalishchev, 2008); in particular, the weight of adult males in Yakutia did not exceed 140–150 kg (Tavrovskii et al., 1971). For Kamchatka bears, it was established (Lazarev, 1979) that females reached their maximum weight at 9–10 years old and males reached it at 18–20 years old. The weight data for Ussuri brown bears collected in the 1970s on the Amur–Ussuri Territory (Kucherenko and Batalov, 1979) are especially impressive. The carcasses were weighed (without skin, entrails, head, or paws): 437, 470 and 505 kg; sex was indicated only for the last carcass (male). The authors suggested that the live weight of the last bear was close to 750 kg. There is data on brown bears from Hokkaido Island (Sato, 2009). The average weight of live bears in the wild was 192.4 for males ($n = 7$) and 102.9 kg for females ($n = 31$). The maximum weight recorded in November and October was 400 kg for a male and 152 kg for a female, respectively.

The trophy characteristics of brown bears from foreign Europe and Russia (measurements of the skulls and skins) slightly increase with advancement from west to east; they are most significant for the bears of Kamchatka (Kozlovskii and Kolesnikov, 2007). The weights of bears in Kamchatka and the southern part of the Far East (Amur region) are also the highest (Geptner et al., 1967); they are approached in size by bears from Sakhalin and the Kuril Islands (Yudin, 1993; Chernyavskii and Krechmar, 2001, 2003), Hokkaido Island (Sato, 2009). The large size of the brown bear populations inhabiting the coastal regions of northeastern Asia may be due to the availability, variety, and high value of the food, which is primarily represented by spawning salmon fish (Voronov, 1974). The large size of the Kamchatka and Ussuri brown bear subspecies is also attributed (Formozov, 1976) to the diversity and abundance of food, and the smaller size of individuals from other geographical races is attributed to the conditions of a relatively poor diet.

The brown bear populations (including those commonly referred to as grizzlies) in North America also exhibit significant geographic variability in body length and skull size (Rausch, 1963; Kurtén, 1973; Kitchener et al., 2020). Bears of the Alaskan Peninsula and the Afognak and Kodiak Islands are the largest; bears of the interior territories of Alaska state and continental populations are noticeably smaller (Glenn, 1980; McDonough and Christ, 2012). The large sizes of individuals from the marginal populations are genetically determined and correspond to a rather harsh climate and good feeding conditions. According to many researchers, the weight indicators of bears, like linear indicators, are determined by factors of nutrition and population density and, depending on their favorableness, they vary among populations inhabiting different territories (Kingsley et al., 1988; Hilderbrandt et al., 1999, 2018, 2019; Schwartz et al., 2003; Zedrosser et al., 2006, 2007; van Daele et al., 2012). The body weight of adult brown bears ranges from 80 to over 600 kg; the most significant indicators of body weight (as well as the linear dimensions) are characteristic of coastal populations of Alaska state, where these predators have access to reservoirs with migratory salmon, to food objects on the ocean coast, to berry fields, and to areas in which the food conditions are generally the most favorable. Similarly favorable conditions for the brown bear population are characteristic of Kamchatka (Revenko, 1993; Chestin et al., 2006; Gordienko, 2012). The outstanding weight indicators of bears in the Amur–Ussuri Territory (Kucherenko and Batalov, 1979) have not yet been explained.

The aforementioned materials on the geographic variability in body weight of the brown bear show satisfactory agreement with the outline of the geographic patterns of variability in the size of the brown bear (Geptner et al., 1967). The weight characteristics of the populations inhabiting Europe (abroad and within Russia) and western Siberia (European-Siberian bears) (Geptner et al., 1967) are close. The bears of the Altai–Sayan mountain system and eastern Siberia, part of the territories of the Far East (eastern Siberian brown bears) are somewhat larger (Geptner et al., 1967). A special place is occupied by the populations of Yakutia, which are characterized by relatively small sizes of individuals. Geographic variability is also manifested within this vast region, but it is still insufficiently studied. The available materials suggest that the northern populations are smaller than those that inhabit the southern and eastern parts of Yakutia (Boeskorov et al., 2011). The bear populations inhabiting the Pacific coast of Russia, the northern Pacific islands (Sakhalin, Shantarskie, and Kurilskie islands, Hokkaido) and Kamchatka are notable for their larger linear dimensions and body weight. The largest bears for Eurasia are typical of Kamchatka and the Amur–Ussuri Territory. The latter case refers to the Ussuri bear (Geptner et al., 1967; Chernyavskii and Krechmar, 2003), the weight characteristics and distribution of which need to be clarified.

INDIVIDUAL BODY-WEIGHT VARIABILITY

Many authors have written of the significant individual variability of the brown bear in many features and the diversity of the supposed causes of variability (Middendorf, 1851; Shirinskii-Shikhmatov, 1900; Ognev, 1931; Stroganov, 1962; Geptner et al., 1967; Davitashvili, 1970; Couturier, 1954; Kurtén, 1973).

According to observations on the Alaskan Peninsula (Glenn, 1980), bears of the same age differ greatly in weight and size, including those within the same brood. There are a number of supposed reasons for this: competition for milk between cubs in a brood; the

care of the mother, which may not be enough for all the cubs; sometimes unequal nutritional conditions in the family and during the transition to an independent life, etc. The work on cubs kept in captivity in preparation for their release into natural conditions gave good opportunities to determine the variability of the cubs of a given year in terms of their fearfulness, activity, and other behavior traits, the weight and growth rate, the size indicators, and other morphological and physiological traits (Pazhetnov et al., 1999).

A bear killed in the Yekaterinburg district (Sabaneev, 1878), which probably weighed "no less than thirty poods" (480 kg), was described. The weight of nine adult bears in northeastern Siberia (Chernyavskii and Krechmar, 2001) varied from 145 to 270 kg. However, one male caught in October 1984 in the Anadyr River basin stood out for its enormous weight (approximately 600 kg).

There are data from the opposite extreme. Among cubs from the same brood, there is a cub that lags behind in growth, the "runt." Runts are described according to observations in wild conditions (Zavatskii, 2004). Such data based on observations in semifree conditions are available to specialists during the preparation of cubs for release into nature (Pazhetnov et al., 1999). A female bear is capable of giving birth to one to four (very rarely more) cubs (Stroganov, 1962; Danilov, 2017; Smirnov, 2017). Cubs from large broods are forced to compete for food, care, and protection from the female bear; in such broods, there is a greater likelihood of the appearance of runts, which will not have enough milk. The probability of the death of such cubs is increased. For example, it is well known that Kamchatka bears are notable for their large size. However, relatively small (for their age) individuals can be found even there. For example, a female bear with two young bear cubs on the territory of the South Kamchatka Game Reserve weighed 120 kg at the age of 18 years (Gordienko, 2012).

BODY WEIGHT IN CAPTIVITY

In wild nature, before denning, the bear cubs of a given year weigh 30–40 kg, while they grow up to 80 kg by December in zoos (Vereshchagin, 1978). The bear cubs of a given year raised in semifree conditions have time to gain about 1.5 times more weight than wild bear cubs by the time of denning (Ternovskii and Ternovskaya, 1972). "Under natural conditions, by the end of the fattening period (November), the bear cubs of a given year weigh 35–45 kg..., while they weigh 60–70 kg in case of artificial feeding" (Pazhetnov, 1990, p. 114). The cited author explains this difference "not only by the abundance and availability of food, but also by the different degree of physical activity."

In zoos, bears can reach enormous weights (Gilmutdinov and Malev, 2011): in the zoo in the city of Mena (Chernigov oblast), a brown bear weighed 600 kg; two brown bears in the zoo of the city of Buzuluk (Orenburg oblast') each weighed about 400 kg at the age of about 4 years.

THE FACTORS OF THE INDIVIDUAL SIZE SHRINKAGE IN THE BEAR POPULATIONS

The theoretical foundations of the dynamics of traits in living systems at the individual and population-species levels have been summarized in works on evolutionary biology (Shmalhausen, 1968, 1982; Grant, 1991; Puchkovskiy, 2013; Blanckenhorn, 2000) and on the management of populations of game animals (Watt, 1971; Schwartz, 1981; Pavlov, 1989). A comprehensive review of publications on the phylogenetics, taxonomy, and variability in species of the bear family Ursidae was presented in a monograph (Baryshnikov, 2007). The interpretation of the presented materials on body-weight variability in the brown bear is based on these theoretical principles.

The weight and overall size of the brown bear can theoretically change over time and vary in different populations in accordance with three different modes of adaptation: ontogenetic mode (1), demographic mode (2), and evolutionary mode (3).

(1) In the process of ontogenesis, the individual experiences the influence of environmental conditions that differ in the degree of favorableness, which is manifested by the age and geographical and seasonal body-weight variability, even for bears living in captivity. Ontogenetic, adaptive changes are not hereditary; that is, they are not reflected in genetic structures.

(2) Under the influence of a complex of factors, the demographic characteristics of a population, the age and sex composition, can change. In this case, the weight indicators of the population (average values, limits) may change. The ratios of the sexes and the age groups and the accompanying weight indicators can change in a single generation, which in itself will not be reflected in the gene pool and may be reversible.

(3) The combined action of evolutionary factors with the participation of selective hunting can change the weight and overall size of individuals in the population over time. This will be reflected in the genotype of individuals and the gene pool of the population.

It has been suggested that hunting selectivity "very quickly" and "everywhere" (Stepanenko, 2020, p. 31) leads to a size reduction in brown bear populations. What are the facts suitable for this topic, and what is known about the shrinkage of individual size in brown bear populations, to scientists, who were engaged in the collection, study of these facts and their understanding? It is known that the life span of bears is reduced in various foreign countries and in some regions of Russia due to the intensive hunting of them, and the bears do not reach their maximum size. That is, the most understandable explanation for a certain size reduction in shot bears within the exploited pop-

ulations is the rejuvenation of such populations. This explanation, which has not yet lost its significance, was proposed as early as the 19th century (Middendorf, 1851). Today, there are many examples of a certain reduction in the occurrence of the largest (in weight and size) individuals in exploited brown bear populations (Voronov, 1974; *Medvedi*..., 1993; Valentsev et al., 2006; Laisheva, 2006; Fil, 2006; Danilov and Tirronen, 2017; Smirnov, 2017; Krofel et al., 2012).

According to the data, the number of brown bears in many provinces of European Russia at the beginning of the 20th century was low due to intensive hunting; animals weighing over 200 kg were rarely hunted in dens (Melnitskii, 1915). The author presented an overview of data (his own data and those of his contemporaries) on the weight of killed bears: 82 adult bears in the Novgorod province weighed on average 8 poods (128 kg), and the heaviest of them weighed 13 poods (208 kg); in the Olonets and Novgorod provinces, of at least 600 bears, the average weight of which (including the weight of cubs) was 4.5 poods (72 kg), the largest bear weighed 16 poods 12 pounds (261.5 kg), while a bear weighed 18 poods 7 pounds (291 kg) in one recorded case. N.A. Melnitskii himself did not see bears weighing over 14 poods (224 kg). It is believed (Pazhetnov, 1990, p. 190) that the life of bears was short at that time (late 19th to the early 20th centuries) and they did not have time to reach the largest size. "In our time, there is no need to talk about size reduction in the brown bear in central Russia: an animal weighing 250–270 kg is not such a rarity" (Pazhetnov, 1990, p. 190).

In Sweden, the brown bear was exterminated in the past as a harmful, dangerous animal, and it became rare in the 1930s. The attitude towards this species changed, its number began to grow, and hunting for brown bears has been practiced in recent decades. Bears in the countries of northern Europe have not only restored their numbers; they are close in size to those that live in European Russia in our time. Their weight exceeds 300 kg in single cases (Swenson et al., 2007). It follows from these examples and from publications on European Russia (Pazhetnov, 1990; Pazhetnov et al., 2002; Danilov, 2017) that the body size reduction of bears due to intensive hunting is reversible within decades (possibly in the first centuries). That is, a slight decrease in hunting pressure, under which the average life span of bears increases, allows bears of modern generations to gain a fairly large body weight.

Foreign colleagues (Krofel et al., 2012) provided data on the shooting and other forms of the removal of bears from the population in Slovenia in 1998–2008 after analyzing the age (the age was determined by teeth cuts) and sex composition of the hunting sample. These materials have been partially cited above. Among adult bears, females accounted for 36.2%. Bears weighing over 150 kg (males reach this weight at the age of 6 years) made up no more than 10% of the sample. Males in such a population do not reach the maximum weight (330 kg for Slovenia); their trophy value is low. Obviously, the regime of bear hunting in this case is intended to maintain the population reproduction at a high level and to preserve its rejuvenated composition (Puchkovskiy, 2017).

A special case is the example of the bears of the Caucasus. An amazing but real phenomenon in the Caucasus is known and has been studied for many years (Kudaktin and Chestin, 1993): the coexistence (up to the formation of compound groups during the rut period) of three brown bear forms. The phenomenon is so unusual that scientists were forced to use the term "ecomorph" to refer to these forms. Such ecomorphs, which differ in individual size and a number of other biological characteristics, do not correspond to the formal criteria of the subspecies (it is believed that subspecies are always allopatric, that is, they do not live together (Mayr, 1968, 1971) but behave like different species that are capable of assortative (selective) crossing. The ecomorph *caucasicus* is notable for its largest size; therefore it is the most attractive for hunters and is more often subjected to hunting for this reason. In this case, the selective removal of a larger ecomorph is quite real (Kudaktin and Chestin, 1993; Laisheva, 2006). However, this case is unique; there are no other places with sympatric brown bear ecomorphs in Russia (perhaps nowhere else in the world). This unusual population of the Caucasus must be subject to special protection, organized evolutionary monitoring, and research with genetic methods.

A trophy bear hunt with a pronounced selectivity in the size of individuals has been practiced in Kamchatka since the 1990s. The hunting sample is dominated by adult males (often with signs of aging) (Valentsev et al., 2006). Accordingly, over many years of such removal, the authors have noted some rejuvenation of the population and a decrease in the likelihood of meeting extremely large males. Surveys over a number of years, including aerial surveys (Gordienko et al., 2006), showed that females predominated among adult Kamchatka bears in the wild (among live bears!) (Gordienko, 2012). The researcher also attributes these changes to trophy hunting on the peninsula and selective hunting (p. 58). The materials obtained as a result of the study of the Kamchatka brown bear populations show that the proportion of adult females that are less attractive to the hunter is increasing among survivors as a result of hunting (the main goal of which is the obtainment of a valuable trophy). At the same time, the proportion of adult males is decreasing, and the largest individuals (usually the oldest) among them are becoming increasingly rare. Ultimately, the noted changes in the sex and age composition are assessed as a shrinking of individual size in the bear population.

A review publication (Smirnov, 2017, p. 209) expresses the fear that the hunting of the largest dominant males "leads to a deterioration in the hereditary qualities of the offspring." On page 288, it was suggested that "the size reduction of new generations of animals indicates that the gene pool of the bear population is changing for the worse."

Here is another group of opinions on the facts of the size reduction in brown bear populations and the relation of these facts to the gene pool. "The hunting of large males, especially individuals with signs of aging, cannot be considered an impact that threatens the gene pool of the bear population" (Fil, 2006, p. 145). "Hunting only for very large animals is selective and, if this practice is maintained for a long time, it theoretically can lead to genetic selection towards a size reduction of individuals in the population" (Danilov and Tirronen, 2017, p. 13). Scientists who thoroughly study the brown bear of Kamchatka and admit the selective role of trophy hunting consider it premature to draw definite conclusions about the deterioration of the population gene pool, "at least until the results of genetic studies on this issue are obtained" (Valentsev et al., 2006, p. 49).

In general, the selective hunting of bears with a high trophy value leads to some rejuvenation of local exploited populations, and assumptions about a possible (over many years of trophy hunting!) decrease in the average size of local adult bears are not without grounds. However, trophy hunting in Kamchatka is not conducted throughout the entire habitat of brown bears, and there are other regions of Russia which contain specially protected areas, inhabited by bears, and where trophy bear hunting is not carried out in all areas that are open for hunting.

Let us turn to selection and its genetic basis. As far as it is known, no one has been specially engaged in the selection of brown bears, so we will use analogies from selection theory and examples from animal breeding. The genotype of an individual is relatively stable during an individual life (Dubinin and Glembotskii, 1967; Trapezov, 2009; Inge-Vechtomov, 2010). However, the properties of bulls as sires in the practice of cattle breeding have their own age optimum of 4–10 years (Markushin, 1983). After this, a period of gradual extinction of sexual functions begins, but the genotype of the sire remains the same. Strictly speaking, due to the appearance of genomic mutations, the genes of sex cells can change with age, which means that such genetic changes are more likely in aging individuals than in young sires (Inge-Vechtomov, 2010). In human genetics, a direct dependence of the frequency of newly emerging mutations on the age of parents is known (Fogel and Motulski, 1990; https://elementy.ru/novosti_nauki/433114/Chislo_mutatsiy_ u_detey_zavisit_ot_vozrasta_oboikh_roditeley, accessed on March 7, 2021). However, genetic studies of this level in populations of brown bears have not yet been carried out; science does not have precise knowledge in this area. It can only be assumed by analogy with the selection of domestic mammals and human genetics that the value of aging brown bears as carriers of a part of the population's gene pool cannot differ for the better. As noted above, the reproductive contribution of aging bears of both sexes is markedly reduced. Accordingly, the removal of the oldest males and shatun bears from the population is unlikely to worsen the gene pool of the population.

In principle, the selection of bears can be used to change the overall size and corresponding evolutionary shifts in the genotypes of individuals and gene pools of populations (Belyaev, 1981; Schwartz, 1981; Trapezov, 2009), but for their identification requires well-established, evolutionary monitoring. The issue of the evolutionary dynamics of brown bear populations belongs to a special topic of evolutionary biology, on which there are many publications. This issue requires separate consideration.

CONCLUSIONS

The life of brown bears is divided by us into five age phases (Table 1) that differ in their dominant functions: growth, maturation, reproduction, aging, and degeneration. The age phases are also characterized by differences in the body-weight dynamics. Foreign publications reflect the traditional view (Kingsley et al., 1988; Swenson et al., 2007; Hilderbrand et al., 2019) that the trend of age-related body-weight dynamics is satisfactorily described by the biological growth equation (von Bertalanffy, 1969) but is limited to four of the age phases given above. However, the real body-weight dynamics in the brown bear are somewhat more complicated. In some populations, bears live up to the degeneration phase, which is notable for a decrease in body weight (exhaustion) and complete elimination from reproduction. The age-related weight dynamics are also complicated by the annual accumulation of fat reserves during the period of hyperphagia and their gradual consumption during the period of hibernation and in the first weeks after leaving the den. In addition, shatun bears, which have not managed to gain the fat reserves necessary for a full winter sleep, appear in some regions of Russia in the years of a catastrophically low yield of fattening feed. Such bears are doomed to death, and their weight dynamics correspond to the phase of degeneration. However, the age of shatun bears can vary.

As follows from the reviewed materials on body-weight variability that are discussed against the background of age dynamics, hunting pressure can result in a rejuvenation of the age composition of the exploited population and, in this regard, a reduction in its weight indicators. Such changes are reversible; the age and weight indicators of individuals in the population are restored with a decrease in hunting pressure (Pazhetnov, 1990; Danilov, 2017). The hunting or trapping

regime can be an effective tool in the management of brown bear populations (Puchkovskiy, 2017), including body-weight, age, and sex composition. The practice of trophy hunting (Valentsev et al., 2006; Fil, 2006) and knowledge of the basics of animal selection (Belyaev, 1981; Schwartz, 1981; Trapezov, 2009; Inge-Vechtomov, 2010) do not yet provide sufficient grounds for certain conclusions about the real value of selective hunting (by body-size, age and sex) as a factor in the deterioration of the gene pool of brown bear populations.

COMPLIANCE WITH ETHICAL STANDARDS

Conflict of interests. The author declares that he has no conflicts of interest.

Statement on the welfare of humans or animals. This article does not contain any studies involving animals.

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