



LARGE AND SMALL BEARS (*URSUS ARCTOS*): ARE THESE FEATURES OF THE PAST AND PRESENT?

Igor Zagorodniuk 

Key words

brown bear, microevolutionary processes, long-term dynamics, Ukraine.

doi

<http://doi.org/10.53452/TU3003>

Article info

submitted 06.10.2025
revised 06.12.2025
accepted 30.12.2025

Language

English, Ukrainian summary

Abstract

The hypothesis that the size of bears in Ukraine decreased over a century is considered, taking into account known facts, legends, statements, and assumptions about this phenomenon. The analysis was conducted considering studies of the variability of bear sizes (including geographical and sexual variation) from different neighbouring regions. The possible role of artificial selection through many years of hunting pressure with the removal of large individuals and ‘pseudo-selection’ through a decrease in the lifespan of animals due to environmental changes and population decline are analysed. Such hypotheses primarily concern the Carpathian region, unlike Polissia, where bears have always been smaller. An analysis of literature and factual data from different periods showed that sources from 100–150 years ago, which paid considerable attention to descriptions of notable trophies, feature specimens with large body sizes and weights (around 400–450 kg). Values of such magnitude have already disappeared in works from the middle and, even more so, the second half of the 20th century, despite the continuation of trophy hunting, which suggests a reduction in the size of these animals over time. As an alternative system for assessing the size structure of the population, it is proposed to use the analysis of paw print sizes (length of the hind foot and width of the front foot), which is successfully used in some regions of Europe and is a much more accessible type of data compared to body size or weight. Hypotheses for the shrinkage of body size are considered, including artificial selection (shooting of large individuals), the trophic hypothesis (deterioration of the food base), the climatic hypothesis (disappearance of the need to accumulate fat for wintering) and the statistical hypothesis. Obviously, all these processes are taking place, and the common denominator and additional general factor may be the disappearance of large-body-size (= not numerous) classes due to small population sizes. The decline in bear body size may reverse as a result of improvements (essentially a restoration) in the age structure of the population, the main factors being a triad of ‘population growth’ + ‘improvements in the food base’ + ‘reduction in disturbance factors’. The above is only possible with a reduction in anthropogenic pressures on natural complexes and an increase in the scope and network of protected areas.

Affiliations

National Museum of Natural History, NAS of Ukraine (Kyiv, Ukraine)

Correspondence

Igor Zagorodniuk; National Museum of Natural History, NAS of Ukraine; 15 Bohdan Khmelnytsky Street, Kyiv, 01054 Ukraine; Email: zoozag@ukr.net
orcid: 0000-0002-0523-133X

Cite as

Zagorodniuk, I. 2025. Large and small bears (*Ursus arctos*): are these features of the past and present? *Theriologia Ukrainica*, **30**: 3–17. [In English, with Ukrainian summary]

Ведмеді бурі (*Ursus arctos*) великі й малі: чи є це ознаками минулого і сучасності?

Ігор Загороднюк

Резюме. Розглянуто гіпотезу зменшення розмірів ведмедів з території України упродовж століття з огляду на відомі факти, перекази, твердження і припущення щодо такого феномену. Аналіз проведено з урахуванням досліджень мінливості розмірів ведмедів (у т.ч. географічної і статевої) з різних суміжних регіонів. Проаналізовано можливу роль штучного добору через багаторічний мисливський прес із вилученням крупних особин і «псевдодобір» через зменшення тривалості життя тварин внаслідок змін середовища і депресії чисельності. Такі гіпотези стосуються передусім карпатського регіону, на відміну від Полісся, де ведмеді і без того завжди були дрібнішими. Аналіз літератури і фактичних даних різного часу засвідчив, що у джерелах 100–150-річної давнини, в яких значну увагу приділяли описам визначних трофеїв, фігурують зразки з високими значеннями розмірів і маси тіла (порядку 400–450 кг). Величини такого порядку вже у працях середини і тим паче другої половини ХХ ст. зникли, попри продовження трофейних полювань, що дозволяє говорити про подібнення цих звірів у часі. Як альтернативну систему оцінки розмірної структури популяції пропонується використовувати аналіз розмірів відбитків лап (довжина задньої і ширина передньої ступні), що з успіхом використовують в частині регіонів Європи і що є значно доступнішим типом даних порівняно з розмірами чи масою тіла. Розглянуто гіпотези подібнення розмірів тіла, у т.ч. штучний добір (відстріл великих), трофічну гіпотезу (погіршення кормової бази), кліматичну гіпотезу (зникнення потреб накопичення жиру на зимівлю) і статистичну. Очевидно, мають місце всі ці процеси, а спільним для них знаменником і додатковим загальним фактором може бути зникнення великорозмірних (= нечисленних) класів через малі розміри популяцій. Зменшення розмірів тіла ведмедів може отримати зворотній тренд внаслідок покращення (по суті відновлення) вікової структури популяції, основним фактором чого має стати тріада «зростання чисельності» + «покращення кормової бази» + «зменшення факторів турбування». Все це можливе тільки при зменшенні антропогенних навантажень на природні комплекси і збільшенні площі мережі заповідних територій.

Ключові слова: ведмідь бурій, мікроеволюційні процеси, багаторічна динаміка, Україна.

Introduction

Bears (*Ursus*) demonstrate extremely wide variability in body size, which occurs both in space (geographical variability of species) and in time (evolutionary changes), and commonly in both components, especially in the appearance of isolated, often insular, forms. In the literature and media reports, it is often claimed that bears in ancient times were much larger than modern ones. The author has heard this thesis many times in various parts of the Ukrainian Carpathians, such as in Mizhhiria, Rakhiv, the Gorgany Mountains, and the Skolivski Beskydy Mountains. This phenomenon seems to have actually taken place, as all available ancient sources confirm the considerable size of bears among ancient hunting trophies (examples below).

The phenomenon of size decreasing over time (for various reasons) has been observed repeatedly in many mammal species. Examples include comparisons of descriptions of Danish mammals at different times [Schmidt & Jensen 2003], based on an analysis of metric characters of 25 species over the period from 1800 to 1972. Changes are ongoing, and changes in traits across generations, including size, are entirely expected, but have not been studied in representatives of the fauna of Ukraine. Changes in metric parameters can mean many things: they can indicate a place in the guild, could be an adaptive character or evidence of microevolutionary changes. Such changes are even recorded among synanthropic species, including European bats [Tomassini *et al.* 2014; Salinas-Ramos *et al.* 2021].

The aim of the study is to analyse hypotheses regarding the decreased size of bears in Ukraine over a long period of time (the last 150–200 years) and the factors causing this, and to assess the availability of various data for such research—from body weight to paw print size.

Some abbreviations used (in alphabetical order): DPM—State Natural History Museum NAS of Ukraine; ZMD— B. Dybovsky Zoological Museum of Ivan Franko National University of Lviv; ZMKU— Zoological Museum of Taras Shevchenko National University of Kyiv; IZAN—Institute of Zoology NAS of Ukraine; MNHU—Museum of Nature of Kharkiv University; NMNH—National Museum of Natural History NAS of Ukraine; CBL—skull length (condylobasal).

1. Phenomenology and initial hypotheses

1.1. Dwarfism and size changes in mammals

The size of animals is one of the basic characteristics of each species, and sometimes of individual age or sex groups. In general, the phenomenon of size change over time, i.e. evolutionary changes, is not unrealistic, although it is believed that the rate of evolution is so slow that it is impossible to observe it during one creative life or even the existence of a particular scientific group (school). Nevertheless, we have many examples of this.

One of the most famous phenomena of size change is island dwarfism, when only small species can survive in small areas, while large forms are found on the neighbouring mainland [Lomolino 2005]¹. In the case of predators, the availability of prey is considered a key factor [Raia & Meiri 2006]. Among the well-known ‘bear’ stories is ‘The Little Bear as a Wonder from Oregon’ [Ingram 1917], known as the ‘lava bear,’ ‘dwarf grizzly,’ and ‘sun bear’ (URL). It, slightly larger than a badger, was considered a separate species from *Ursus americanus*, but is now included in the latter.

One of the most interesting recent works is devoted to comparing the sizes of mammals in works from different periods [Schmidt & Jensen 2003]: in the 25 species of mammals selected for analysis from the Danish mammal fauna, both fluctuations in size (body length) and clear changes towards smaller or larger sizes have been revealed over 175 years of observation.

For example, the hazel dormouse (*Muscardinus avellanarius*) gradually became smaller between 1880 and 1972 (17.0, 15.7, 15.0, 13.8, 14.1 mm), while the hedgehog (*Erinaceus europaeus*) grew larger (20.9, 24.9, 25.1, 29.0 mm), the squirrel (*Sciurus vulgaris*) clearly became smaller (49.7, 45.8, 44.5, 39.0, 37.5 mm), and the field mouse (*Apodemus agrarius*) increased in size (14.7, 15.0, 15.9, 18.7 mm). It is obvious that such processes could also affect other species and regions, including the noticeable changes in synanthropic bats mentioned in the introduction [Tomassini *et al.* 2014; Salinas-Ramos *et al.* 2021].

It is also important to remember the geographical variability in size and sexual differences in animals (not to mention age-related changes), including bears. Male bears are always larger than females, the Carpathian (and Balkan) bears are significantly larger than northern (and obviously Polissia) bears, there is significant differentiation in size between age groups, and bears can vary greatly in size before hibernation and in other seasons (up to 100 kg) in their fat reserves, which will affect size estimates based on weight indicators (previously, weight was one of the key indicators). All these factors may affect estimates of differences between samples from different times and regions, as well as samples that are heterogeneous in terms of sex. This is discussed in more detail in the section on ‘Ecogeographical rules’.

1.2. Carpathian legends and evidence of large bears

The author remembers a story told by an old bear hunter in the vicinity of the modern Zacharovany Krai National Nature Park (Transcarpathia) during field research in 2004, according to which bears have become smaller by almost half; that ‘in his youth, he and his father hunted bears weighing over 150–200 kg, and now that is the maximum weight.’

The author heard similar stories from hunters while working in the Kamianka River valley near Skole, where, among other things, there was a large collection of trophy skulls of various carnivores. In 1996–1998, foresters from the Chornohora branch of the Carpathian Reserve repeatedly told the author about bears that were clearly becoming smaller, and the author himself had an encounter with a bear the size of a human (80 kg) in the Bretskul forest.

¹ The topic is available in Ukrainian (>>>) and English Wikipedia (>>>).

There is quite a bit of direct evidence of ancient large bears that were hunted in the Carpathians. Examples of such specimens, which became famous hunting trophies, are shown in Fig. 1.

In O. Slobodian's monograph [2008], in the chapter 'References to bears in the history of the Carpathians', there are references to various large bears, which are summarised in Table 1. Although the maximum sizes of animals are not statistically significant values due to their randomness², hunting chronicles focus only on them, as this is their main value, and the high frequency of such data on large bears in ancient sources indicates that such data are not random.



Fig. 1. Trophy bears from the Carpathians: (a) 'Solotvyno Mizunsky,' 1932, a group of Lviv hunting enthusiasts (from an article in the media: O. Protsiv, 2012, <https://gk-press.if.ua/x5877>); (b) Great-grandfather hunter with Manlicher, Carpathians, village of Perkalaba, 1906. Source: Mox Perkalaba, 2013, pers. com. (family archive, photo of great-grandfather); (c) bear hunted on 15 December 1915 in the Ilemnia forest district of the Dolynsky district by Polish President I. Mościcki, one of the largest bears hunted in the Carpathians at that time, body length to the end of the tail 225 cm, fore foot width 18 cm (photo from the book by I. Chudiyovych [Chudiyovych 2017], edited by I. Skilsky); (d) a 15-year-old bear weighing 400 kg, hunted in 1905 in the Stanislav Voivodeship ('reproduction from V. Buzhynsky' in the book by O. Slobodian [Slobodian 2008]).

Рис. 1. Трофейні ведмеді з Карпат: (а) «Солотвин Мізунський», 1932, гурт львівських любителів ловів (зі статті в масмедіа: О. Проців, 2012, <https://gk-press.if.ua/x5877>); (б) мисливець прадід з Манліхером, Карпати, с. Перкалаба, 1906 р. Джерело: Мох Perkalaba, 2013, особ. повід. (сімейний архів, фото прадіда); (с) ведмідь здобутий 15.12.1915 у надлісництві Ілемня Долинського повіту президентом Польщі І. Мосьціцьким, один з найбільших ведмедів, здобутих на той час у Карпатах, довжина тіла до кінця хвоста 225 см, ширина передньої ступні 18 см (фото з книги І. Чудійовича [Chudiyovych 2017], редаговано І. Скільським); (д) 15-річний ведмідь, що важив 400 кг, здобутий 1905 р. у Станіславському воєводстві («репродукція з В. Бужинського» у книзі О. Слободяна [Slobodian 2008]).

² It is important to remember that maximums in statistics are random values, but in trophy hunting they are the only characteristics and are therefore mentioned in various sources. In other words, the repeatability of such data acquires statistical meaning as the frequency of its occurrence increases.

Table 1. Size characteristics of bears from the Carpathian region according to various sources (chronological order): body length and weight

Таблиця 1. Розмірні особливості ведмедів із Карпатського регіону за різними джерелами (хронологічний порядок): довжина і маса тіла

Location	Period	Length, cm	Weight, kg	Note	Ref.*
Orava, Slovakia	1878 (2.12)	206	356 ♂	80 kg of fat	1
Yasen, Kalush Raion, Ivano-Frankivsk Oblast	1905	240 ♂ 160–190	400 ♂	gold medal (Fig. 1, d); skull in Table 2;	2
Ilemnia, Dolyna Raion, Ivano-Frankivsk Oblast	1915 (15.12)	225 (♂?)	–	width of front foot 18 cm (Fig. 1, c)	3
Zakarpattia Oblast	late 1920s	–	298–350 (10)		5
Krummholz of the Ukrainian Carpathians	until 1949	198	250	no statistics, possibly n = 1	4
Monastyrts, Khust Raion, Zakarpattia Oblast	1955 (12)	–	340 ♂		5, 9
Polish Carpathians	until 1964	150–250	100–450 (average 150–250)	–	6
Romanian Carpathians	until 1967	120–200 ♀ (6) (average 168) 161–257 ♂ (21) (average 218)	93–303 ♀ (12) (average 214) 84–440 ♂ (33) (average 268)	–	7
Ukrainian Carpathians	until 1975	186–248	256–340	skull measurements in Table 2; hind foot 19.3–19.8 cm	5
Ukrainian Carpathians	until 1975 & 2008	144–180 ♀ 186–248 ♂	82–160 ♀ 186–340 ♂	♀ L = 144 & w = 82 collected with juv.	9 (+5)
[Polish Carpathians?]**	until 1984	120–200 ♀ (6) 161–257 ♂ (21)	93–303 ♀ (12) 84–440 ♂ (22)	skull measurements in Table 2	8

* References: 1—Duda 1935 after [Slobodian 2008]; 2—[Niezabitowski 1933]; 3—[Chudiyovych 2017]; 4—[Strautman & Tatarinov 1949]; 5—[Turianyn 1975]; 6—‘Kovalsky 1964’, according to [Slobodian 2008]; 7—[Almășan & Vasiliu 1967]; 8—[Rucek 1984: 270]; 9—[Slobodian 2008]. ** These data are repeated as original in reviews of the fauna of Belarus [Savitsky *et al.* 2005: 108–111] and Ukraine [Mezhzherin & Lashkova 2013: 258], which is an obvious confusion. In turn, these data strangely coincide with the data for Romania (see 4 lines above, ‘Romanian Carpathians’). It not only devalues the data, but also generates distrust of such sources, which are already extremely problematic and full of unverified data.

An important and noteworthy fact is that large bears were recorded during periods of high population numbers. This fact is further included in the ‘synthesis’ section. Thus, in an interview with game expert O. Protsiv in 2012³, the following information is mentioned:

‘... in 1900, 36 bears were hunted in the hunting grounds of Galicia. ... Data have been preserved on the shooting of 15 animals in a single hunt. ‘Beyond the Chornohora Mountains, the Gorgany are the wildest part of the Carpathians, where you can most often see the largest deer, bears (up to 2.5 m long, weighing up to 400 kg), and lynxes,’ wrote the Lviv magazine *Lovestvo* in 1905.’

Olexiy Slobodian’s conclusions are similar [Slobodian 2008: 31]:

‘The above information shows that large bears were found in the Carpathians at the beginning of the last century. Observations in recent years (1966–1989) show that large individuals are now very rare. This is due to the desire of hunters and poachers to hunt the largest animals.’

³ Kushnirenko, N. 2012. Vuytsio Misio. In: *Galician Correspondent*. 26 January 2012. URL

2. Facts and statistics

2.1. Standard metrics

In general, statistics on the Ukrainian Carpathians are scarce, and those on Polissia are even scarcer. The main summary on the Carpathians is the work of O. Slobodian [2008], but its loose references and lack of bibliography significantly diminish its significance. In this review, the data are summarised in tables in chronological order, separately for the Carpathians and Polissia. Metric data on body size (Table 1), skulls (Table 2), and paw prints (Table 3) are analysed separately.

An attempt at graphical analysis did not reveal a clear trend (therefore, only tabular data is provided here), but it is possible to conclude that the size of animals has decreased, although not as significantly as described in legends. The situation is complicated by incorrect rewriting of data by some researchers in others. A significant portion of the data presented in Table 1 has been republished without references in other sources, often in other countries, frequently with obvious errors, but most often with complete coincidences of minimums and maximums. This is an unfortunate situation, which was discovered only by chance due to the need to analyse such data. For example, in the 2013 guide to mammals of Ukraine, the measurements of bears (and other animals) were clearly copied from the 2005 Belarusian edition, which copied them from the 1984 Polish edition, which, in turn, copied them from a 1967 work on Romanian bears (see Table 1). Rejecting such plagiarised sources, we have a more modest range, which shows a decline in size due to a decrease in mean and minimum values.

Northern (Polissian) bears. In January 2003, in Sumy Oblast, a hunter caught an adult specimen weighing 120 kg (sex unknown) in a den (Merzlikin 2004, in: [Zagorodniuk & Merzlikin 2025]). One of the bears kept at the MNKU was, according to legend, caught as a cub in Bryansk Oblast in 1831 and grew to a large size in captivity (skin-mount in Fig. 2 c). Measurements taken at the author's request by colleagues from the MNKU are as follows: (1) body length—167 cm; hind foot 21–22 cm (A. Lunyachek, pers. comm.).



Fig. 2. Bear mounts: (a) at the IZAN Zoological Museum (Kyiv), V. Antonovych and V. Bondarenko creating the mount; photo from the newspaper 'Vechirnyi Kyiv', 11.01.1955; (b) a bear mount in the exhibition of the NMNH, estimated to be 180–185 cm tall based on the height of the people in the photo, clearly the same as in the previous photo; according to legend, 'it went to Kharkiv, as part of an exchange' (L. Shevchenko); photo from c. 1980 from the IZAN photo-archive; (c) a bear mount in the Museum of Nature at the Kharkiv University, from Bryansk Oblast, 1931, seven-year-old animal [Iliukhin 2019]; photo by O. Zoria, 17 January 2009.

Рис. 2. Опудала ведмедів: (а) у зоомузеї ІЗАН (Київ) В. Антонович і В. Бондаренко монтують опудало; фото з газети «Вечірній Київ», 11.01.1955; (б) опудало в експозиції ННПМ, розмір оцінено через зріст людей як 180–185 см, за рисами явно те саме, що на попередньому фото; за переказами, «поїхав десь до Харкова, по обміну» (Л. Шевченко); фото близько 1980 р. з фототеки ІЗАН; (с) опудало в Музеї природи ХНУ (Харків), з Брянщини, 1931 р., семирічний звір [Iliukhin 2019]; фото О. Зорі, 17.01.2009.

2.3. Registrations on camera traps as a source of data

Due to the legislative ban on hunting and the declining interest of scientists in dead bodies of animals, there are less and less ‘classical’ morphometric data available. Statistics from over 1700 measured samples, cited by some researchers [e.g. Swenson *et al.* 2007], are currently impossible for the Ukrainian realities. However, some new data can be seen from the results of camera trap registrations. To estimate sizes from photos, the experience described by S. Gashchak may be useful [Gashchak *et al.* 2022], which uses several calibration rods placed at different distances from camera traps to superimpose on images of zoological objects, allowing the sizes of animals to be estimated (Fig. 3). The method proposed by S. Gashchak is a breakthrough in studies using camera traps and, moreover, in a number of cases it can be applied retrospectively to re-evaluate images if researchers can restore the position of camera traps at the time of shooting.

2.4. Craniometry

The available data are incomplete and scattered, but they do exist and provide some important results (Table 2). As can be seen, the available data show an increase in skull length. For correct comparisons, the ratio of total (LC) and condylobasal (CBL) skull lengths was calculated for the Romanian sample, which is the largest, and all data were converted to a single dimension, CBL.

The collection of brown bear skulls at the Zoological Museum of Lviv University (ZMD) is the largest in Ukraine. Moreover, all of these are probably ancient specimens associated with B. Dybovsky, the founder of this museum. None of these specimens have labels, so their connection to the Carpathians is provisional (I. Shydlovsky, pers. comm.).



Fig. 3. An example of determining the size of a bear in photographs by superimposing photo duplicates with calibration poles on images. Photo courtesy of S. Gashchak, author of this know-how. A more detailed description of the methodology is presented in [Gashchak 2025].

Рис. 3. Приклад визначення розмірів звіра на фотореєстраціях шляхом накладання на зображення фотодублів з калібрувальними жердинами. Фото люб'язно надано С. Гащак, автором цього ноу-хау. Докладніший опис методики представлено в [Gashchak 2025].

Table 2. Size characteristics of bears from Ukraine according to various sources (chronological order): skull length (cm) largest (LSL) or condylobasal (CBL), in mm

Таблиця 2. Розмірні особливості ведмедя з України за різними джерелами (хронологічний порядок): довжина черепа (см) найбільша (LLS) або конділобазальна (CBL), в мм

Location	Period	Skull length (LSL)	Skull length (CBL)	Source *
Ivano-Frankivsk Oblast	1905	260–350 ♂	240–323 ♂*	Niezabitowski 1933
[Ukrainian Carpa- ?hians]	until 1920	–	322–382 (16), mean 344	collection of ZMD**
[Ukrainian Carpa- ?hians]****	1952–1952, – 1957	–	312–370 (3), mean 317 [specimen with 370 ♂]	collection of ZMD and ZMKU**
Romanian Carpathians	until 1967	290–354 ♀ (12), mean 317 296–378 ♂ (40), mean 348	272–323 ♀ (11), mean 293 291–353 ♂ (32), mean 319	Almășan & Vasiliu 1967, = Rucek 1984***
Ukrainian Carpathians	until 1975	–	289–358, mean 333	Turianyn 1975
Ukrainian Carpathians	1980–1986	–	289–315 (3), mean 304	collection of NMNH**
Bukovyna	unknown	336–391 ♂ (4), mean 360	308–359 ♂ (4), mean 330*	Volokh & Tkachuk 2025

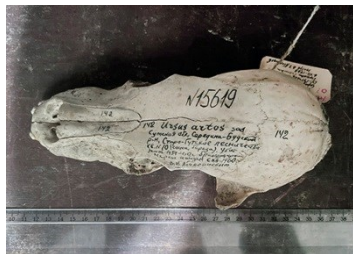
* CBL calculated using the ratio established based on the data in the row ‘Romanian Carpathians’ (LSL/CBL = 1.08 ♀ and 1.09 ♂); ** measurements of collection specimens were carried out by: ZMD—I. Vdovychenko (c/o I. Shydlovsky); NMNH—D. Lazarev and the author, ZMKU—Zh. Rozora; *** as in the case of Table 1, I believe that these data were copied (with errors) from descriptions of bears from Romania: the coincidences of minimums and maximums and sample sizes are obvious; **** the specimens from 1952–1953 originate from the Kyiv Zoo, and are believed to have been obtained from the Carpathians.

The zoological collection of NMNH contains four skulls from 1980–1986, all from Transcarpathia, including one from the vicinity of the village of Synevyr and three others from the hunting grounds ‘Soviet Carpathians’ (Yasynia district) [Shevchenko 2007]. Two of them have actually been found; their measurements are generally smaller than the mean values for all other samples (see Table 2). It is possible that these are females, which would explain their small size. However, another specimen (♂) found in the ZMKU, obtained 20 years earlier, in 1957, has a clearly longer skull length, CBL = 370 mm (Fig. 4, bottom row).

From the data presented in the table (arranged chronologically), it can be seen that, in general, the size of the skull has not undergone significant changes, although there are some. Since there are clear sexual differences, it is worth analysing the sexes separately. Here, the analysis focuses on males, as their skulls are more often the subject of attention as trophies. We have the following changes in skull length over time: 240...323 → 291...353 → 308...359 mm (Table 2).

Old specimens from the ZMD collection (three clearly young specimens and one very large, probably non-local specimen with CBL = 422 mm were excluded from the sample), whose sex is unknown, are characterised by their large size. On average, they are 10–30 mm larger than the values for post-war samples. The nature of these differences is unknown, and it cannot be ruled out that B. Dybovsky took them from other regions (e.g., Transbaikalia), where larger bears live.

The changes in size are ambiguous and, in general, there are irregular fluctuations, but in the case of males, there is actually an increase rather than a decrease in values, which contradicts the data on changes in body size. It can be assumed that the decrease in size was primarily due to a reduction in fat reserves in connection with a shorter hibernation period in a warming climate. However, the increase in skull size, if confirmed by new data, is paradoxical and can be explained by the increased load on the masticatory system due to an increase in herbivory and decrease in carnivory.



No. 15619 (223 mm)



No. 11006 (289 mm)



No. 11005 (315 mm)



Fig. 4. Bear skulls from Ukraine in the collections of Kyiv museums: top—a row of skulls demonstrating the differences in size between animals of different ages. Samples from the National Museum of Natural History (Kyiv); photos by D. Lazariev and the author.

Рис. 4. Черепи ведмедів з України в колекціях київських музеїв: вгорі — ряд черепів, що демонструє розмірні особливості тварин різного віку (матеріали ННПМ; фото Д. Лазарєва і автора); внизу — один із найбільших за розмірами колекційних зразків (♂ CBL = 370 мм), здобутий 14.10.1957 О. Кириченком в Закарпатті (напевно, в господарстві «Радянська Україна» біля Ясиня) (матеріали ЗМКУ, фото І. Костюка та Ж. Розори).

An example of an age series according to the degree of ‘maturity’ of the skull (increase in size and sculpturality, formation of ridges, overgrowth of sutures) is shown in Fig. 4. It is obvious that thanks to prolonged growth and under appropriate conditions, and above all, minimal age mortality, bears can reach large sizes. The difference between the sizes of the average and larger skulls shown in Fig. 4 (if we take the average as 100%) is almost 10% of the length.

2.5. About ‘plantometry’

Since bears can no longer be hunted, poaching data are unavailable, and, moreover, no one would now weigh or measure the animals; thus, such data are no longer relevant. Cranial data are also difficult to obtain. However, researchers with experience in non-game fauna have at their disposal important estimates of body size and, in some cases, characteristics of sex, age, and geographical lineage based on paw measurements. Like most Arctoidea, especially the larger species, bears are plantigrade, and paw length correlates with body size in all carnivores, including bears [Viranta 1994; Harris & Steudel 1997; Brooks *et al.* 1998]. Moreover, due to their large size, bears make clearly visible paw prints, and a substantial amount of data can be collected by analysing tracks on shores of water bodies, sand hills, mud roads, or snow.

Examples of bear paw prints on different substrates are shown in Fig. 5. The top row shows Carpathian samples, while the bottom row shows Polissia samples (the latter often on sand). Unfortunately, despite well-known recommendations [Miropolsky 2017], researchers often photograph tracks without measuring them; in some cases, the frames contain improvised measuring devices—a camera lens cap, a matchbox, a hat, a radio, a telephone, or a tape measure (see Fig. 5).

The examples of bear paw measurements are as follows:



Fig. 5. Examples of bear paw prints on different substrates (based on materials provided by colleagues): (a) Carpathian Biosphere Reserve, Y. Dovhanych, scale 8.0 cm, hind paw length = 30.0 cm; (b) Uzhansky National Nature Park, N. Koval, scale 5.0 cm, hind paw length = 26.0 cm; (c) Uzhansky National Nature Park, N. Koval, scale 28 cm, hind paw length = 26.6 cm; (d) Polissia, S. Zhyla, no scale, front paw width = 18 cm; (e) Polissia, S. Gashchak, scale 58 mm, hind paw length = 22.6 cm; (f) Chornobyl zone, A. Simon, ruler, hind paw length = 26.3 cm.

Рис. 5. Приклади відбитків задніх лап (слідів) ведмедя на різних субстратах (за матеріалами, що передані колегами): (a) Карпатський БЗ, Я. Довганич, мірка 8,0 см, = 30,0 см; (b) Ужанський НПП, Н. Коваль, мірка 5,0 см, = 26,0 см; (c) Ужанський НПП, Н. Коваль; мірка 28 см, = 26,6 см; (d) Полісся, С. Жила, без мірки («дорослий — це 18 см ширини сліду передньої лапи»); (e) Полісся, С. Гащак, мірка 58 мм, слід = 22,6 см; (f) Чорнобильська зона, А. Сімон, лінійка, слід = 26,3 см.

Table 3. Hind paw length and front paw width for main age groups (excluding young bears), based on data from the Bulgarian population [after: Spassov *et al.* 2016]

Таблиця 3. Розміри відбитків лап ведмедя для основних його вікових груп (без молодих), за даними для болгарської популяції [за: Spassov *et al.* 2016]

Age group	Hind paw length (cm)	Front paw width (cm)
Adults ♀♀ and immature ♂♂ (100–200 kg)	19–20 to 23–24	12–13 to 13.5–14
Mature ♂♂ aged > 5 years (200–250 kg)	24 to 26–27	14.5 to 17
Old ♂♂ aged >10 years (>250 kg)	27 to 30–31	17 and more

1) Ukrainian Carpathians, Uzhansky National Park, two photos with hind paw length measurements—16.9 and 26.6 cm (received from N. Koval); 2) Polissia Biosphere Reserve, five photos, one with hind paw length—22.6 cm (received from S. Gashchak); 3) Sumy Oblast, Desniansko-Starogutsky National Park, footprint description 18×29 cm (data from Y. Kuzmenko [Zagorodniuk & Merzlikin 2025]); 4) Polissia Nature Reserve, four photos, front paw width in adults over 15 cm, often 18 cm (S. Zhyla, pers. comm.); 5) Chornobyl zone, 14 photos with clear prints—hind paw length: 26.0, 26.3, 26.6, 27.0, 27.0 cm (received from A. Simon with the assistance of S. Gashchak).

For Polissia bears, footprints are the primary source of morphometric data, emphasising their importance. Although Carpathian bears are expected to be larger than Polissia bears based on paw size, the largest measured prints from the Carpathians (24.0, 26.0, 26.6 cm) are comparable to Polissia prints (24.0, 27.0, 29.0 cm). Paw prints from Bulgaria, representing more stable populations with all size classes, are naturally larger (Table 3).

Based on these parameters, the largest size class (27–31 cm) is essentially absent in our populations. Assuming Carpathian bears should be roughly comparable to Bulgarian bears, this suggests either a reduction in size or a lack of individuals surviving past 10 years, likely due to hunting pressure. Historical and current poaching data support this conclusion.

Finally, a historical anecdote illustrates the situation. A colleague, now deceased, was once tasked by a Carpathian nature reserve management to acquire several bear skins from mountain villages for an exhibition. Despite the difficulty, he collected several dozen skins, including some very large ones. During travels through the Carpathians in the 1980s and 2000s, the author also collected accounts of bear shootings. For instance, on the Borzhava ridge (summer 1995), shepherds recounted past shootings and new incidents, and in 1997–1998, cartridges were found in the Chornogora massif of the Carpathian Reserve. All of this demonstrates significant hunting pressure, corroborated by other sources.

3. Hypotheses

3.1. Ecogeographical rules (Bergman and ‘anti-Bergman’)

Studies have shown that bears exhibit geographical variability, which is often interpreted in terms of ecogeographical rules. In particular, it was reported that northern bears are smaller than southern bears [Swenson *et al.* 2007]. This pattern is commonly discussed alongside sex-related size dimorphism (females being smaller than males) and the need for bears to accumulate large fat reserves for winter dormancy. Overall, this interpretation appears problematic, because the application of ecogeographical rules related to thermoregulation to hibernating animals is no more justified than for migratory (e.g., bats) or subterranean mammals (e.g., moles)⁴. Could this explain why bears increase in size not toward the north but toward the east, with particularly large individuals in Kamchatka, where berry resources are abundant and bears feed extensively on large anadromous salmonids, their key food resource during spawning [Deacy *et al.* 2018]?

To be fair, it should be noted that the authors of the cited study analysed several hypotheses in addition to Bergmann’s rule, including the hypothesis of greater carnivorousity in northern bears, which would also explain their larger size, as well as hypotheses of greater ecosystem productivity and longer growing sea-

⁴ In the 1980s and 2000s, such ‘paradoxes’ were repeatedly mentioned in connection with another well-known phenomenon that ran counter to ecogeography—the ‘Dehnel effect’ [Dehnel 1949; Mezhzherin 1964].

sons and lower winter hibernation costs with higher population densities in the south, which would explain the larger size in the south. The value of the study lies in the use of models with body mass standardisation by age, adjusted for sex and season, which allowed the data series to be aligned. Finally, it was showed that northern bears gained more weight before hibernation and had the same large weight loss during winter sleep, which lasted twice as long for them.

In fact, this is why trophic hypotheses deserve special attention.

3.2. Trophic hypotheses

The author suggests (and there are relevant facts above) that bears, at least those in the Carpathians, have become smaller over the last 100–150 years. Shrinking of body size, like increasing in size, is a rare phenomenon in mammals. Size is usually a characteristic of a species and does not change depending on the status of populations, since in mammals, growth, its rate and periods are determined by, among others, sexual maturation, bioenergetics, biomechanics, and seasonal cycles. Bears are no exception.

At the same time, it is known that the size of individuals in a population can fluctuate when living conditions change. Thus, Myakushko [2021] writes that when living conditions deteriorate, there is a significant decrease in body weight in all size and age groups of the studied species [rodents]. Such deterioration may be caused, in particular, by an increase in anthropogenic pressure. Long-term data series show that the body condition scores [according to: Myakushko 2004]⁵ in model species decreased by 17–23% over 35 years, with an even more significant decrease of 32% in reproductive females.

As S. Myakushko notes, ‘shrinkage of body size can be achieved through various mechanisms. First, mortality results in the loss of the largest individuals and reproductive females with the highest energy requirements from the population. Second, young animals grow and gain weight more slowly. ... The reduction in the exterior parameters of individuals reduces their specific energy requirements and enables them to better survive unfavourable conditions. From this perspective, the reduction in size of its elements can be considered a specific population strategy for maintaining ecological balance’ [Myakushko 2021].

A consultation with a colleague who worked with carnivores at the zoo revealed similar results (conversation with E. Ulyura). In particular, the author found that dystrophy in bears is a common phenomenon, and not only in captivity. Moreover, the current state of the land, including the almost complete extermination of medium and large fish, significant pressure from hunters and poachers on game, deforestation, degradation of pastures, excessive harvesting of mushrooms and berries, excessive disturbance by thousands of holidaymakers, fragmentation of space by roads and resort areas all lead to the entirely predictable consequences of malnutrition. It is worth mentioning that historically bears in Ukraine (including in the Carpathians) certainly consumed fish, including trout and salmonids in general during spawning migrations, but modern anthropogenic conditions have essentially destroyed riparian habitats and this food component, which is now virtually absent [Kilfoil *et al.* 2023].

The author also found that zoo practices show that bears are very mobile in accumulating and expending fat reserves, which is why their body weight can vary significantly both seasonally and individually, not to mention different conditions of keeping, feeding, physical activity, and duration of sleep (E. Ulyura, pers. comm.). Hence, it is entirely expected that bears in the wild will become smaller, regardless of hunting pressure, although it is clear that the latter also plays a role and can have a significant impact (more on this below).

3.3. Bear size as a factor affecting hunting

The author raised the idea of shrinkage of body size as a result of prolonged (in essence, centuries-long) hunting as a form of artificial selection when analysing the small size of the European form of roe deer compared to the Siberian form [Zagorodniuk 2002]. Large-scale and prolonged

⁵ The body condition score is the ratio of body weight (W) to body length (L)—W/L, which is an index sensitive to reflecting any influence [Myakushko 2004, 2021].

hunting could and probably did contribute to its shrinking. If we assume a model in which 20% of the population is removed each year, which is equivalent to the population growth in the first approximation, then the loss of older age groups as extreme classes is highly likely. In addition, large animals are physically larger targets and more desirable prey in all types of hunting, especially trophy hunting. As mentioned above in an interview with O. Protsiv, this is the case, and it is ‘related to the desire of hunters and poachers to obtain the largest animals’ (loc. cit.).

That is, even with equal frequency of occurrence of animals of different sizes, large animals will be removed at a higher rate, and under excessive hunting pressure animals will become smaller due to greater removal of older size classes. It is important to note that larger size classes are also older age groups. Since age-related mortality exists in any species, the proportion of older individuals is already small and inversely proportional to age. Even for long-lived animals such as bears, 100–150 years of excessive hunting pressure is sufficient for a shift toward early maturation and reproduction, particularly in small populations.

As is well known, small classes in terms of frequency (including size) can disappear purely for statistical reasons when overharvested [Egorov 1975], especially when there is a significant reduction in the total population size. This is certainly what happened. The current increase in the total bear population may become a factor in the restoration of age structures typical for this species. Of course, this will be influenced by a number of factors, including wintering conditions, food availability, and the overall health of the population (which is currently the least discussed), which may support or offset such trends.

A review of the literature shows that under ‘standard’ conditions, with regular anthropogenic pressure, the proportion of each subsequent age group does indeed decline rapidly (data for Slovenia and Croatia) [Jerina *et al.* 2018], whereas in protected conditions with proper population monitoring (Pyrenees), the age group distribution often favours adults due to high survival rates and minimal age mortality [Sanz-Pérez *et al.* 2025]. In ‘critical’ populations with low abundance, significant disturbance, and excessive hunting pressure (poaching), older age (size) classes are extremely rare (Table 4). Numerous sources confirm the assumption that hunting can change the age structure of the bear population by ‘eliminating’ older age classes. This is, in particular, evidenced by both direct data on the distribution of age groups and modelling [Bischof *et al.* 2018].

Data from Slovakia show that in areas with high levels of poaching or hunting, older males often dominate among the individuals removed [Rigg & Adamec 2007]. An analysis of the frequencies of bears removed in Slovenia ($n = 927$) shows differences in age and sex among the removed animals, highlighting the selective impact of hunting on the population structure. In particular, 78% of those removed⁶ were under 4 years of age, but the proportion of individuals obtained by hunters in each age group was approximately the same, around 55–65% [Krofel *et al.* 2012].

Table 4. Proportions of different age groups in bear populations

Таблиця 4. Частки різних вікових груп у популяціях ведмедя

Population type	0–1 years	2–3 years	4–5 years	6–9 years	≥10 years
Protected populations (Pyrenees) [Sanz-Pérez <i>et al.</i> 2025]*	~32 %		~22 %	~46 %	
Free populations from the Carpathians (generalised estimate from various studies)	8–15 %	18–30 %	20–30 %	15–25 %	3–10 %
Estimate for lognormal distribution (step ‘1/3’ from the previous value)	38.4 %	25.6 %	17.1 %	11.4 %	7.6 %

* There is no detailed breakdown by year, but we are talking about juveniles, subadultus, adultus.

⁶ Apart from hunting (59 %), removals included problematic individuals (18 %) and roadkill (16 %). Up to 20 % of the population is removed annually—the highest rate in Europe. At high population densities, removal of a substantial non-trophy proportion does not adversely affect age structure and may even help balance it by regularly removing problematic juveniles.

The experience of Scandinavia (Sweden and Norway) is noteworthy, where during the 20th century the local brown bear (*Ursus arctos*) population almost disappeared due to excessive hunting, but legal protection measures and monitoring programmes contributed to the restoration of its abundance and range. This was accompanied by an increase in the proportion of adult individuals in the population, although hunting remains an important factor in mortality and affects the age structure of the population [Swenson 1995; Frank 2017; Christiernsson 2018].

4. Synthesis

Analysis of long-term data series on body size (body length and body mass) of brown bears from Ukraine and adjacent regions reveals weak but consistent changes toward a reduction in body size. However, these processes are not unambiguous: analyses of cranial dimensions (although based on smaller sample sizes) do not show a similar trend. Moreover, larger body size in older museum specimens may reflect both a larger overall sampling base (essentially, a larger population), in which all size classes—including very large males older than 10 (and even 15–20) years—were more fully represented, and a historical bias toward collecting and documenting hunting trophies, particularly in earlier collections.

Both direct and indirect evidence suggest that bears inhabiting Ukraine have indeed become smaller over time, especially in the Carpathians, where data availability is higher than in Polissia. The analysis also highlights the limited amount of reliable metric data and the frequent reuse of measurements across publications, sometimes borrowed from studies conducted in other regions. Factors contributing to size reduction include a combination of natural and anthropogenic influences, such as a deep demographic depression, size-selective hunting, reduced lifespan, deterioration of food resources, and a decreased need for large fat reserves associated with shorter winter dormancy.

An additional factor affecting size estimates is the development of partial synanthropy, typical of younger bears, which is often accompanied by human–bear conflicts and ultimately by the removal of such individuals. As a result, metric datasets are increasingly dominated by records of smaller-bodied bears. Consequently, assessments of changes in population structure based on invasive methods are biased toward younger (and generally conflict-prone) individuals.

For the current and future periods of bear studies, especially within protected areas, size proxies such as paw print measurements (hind foot length and fore foot width) should be more widely applied, as they are informative and can be collected in large numbers. Particular attention should also be paid to the estimation of body size from camera-trap photographs.

The low population size during the mid and late 20th century and only a slight increase in recent decades do not allow expectations of a population age structure approaching its original state, due to persistent anthropogenic constraints and widespread poaching. In the early 1970s, the Ukrainian bear population (essentially restricted to the Carpathians) was estimated at more than 1100 individuals [Khoyetskyy 2017]. Hunting restrictions and the protected status of the species undoubtedly promote population growth, as clearly demonstrated in Poland since the 1980s [Jakubiec 2001]. In contrast, in Ukraine bear numbers continued to decline during the same period [Kryzhanivsky 1999], and only recently has a slight stabilisation been observed, with an estimated population of about 300 individuals in 2009 [Shevchenko & Shkvyria 2009] and 285 individuals in 2022 (according to official state statistical reports, ‘*Form 2tp-hunting*’).

Under these conditions, population growth and the establishment of a stable older age class appear unlikely. The ongoing redistribution of the human population toward the Carpathian foothills and the intensive development of recreation in the Carpathian region—resulting in excessive disturbance and profound habitat transformation—are not conducive to bear population recovery. Apparent positive trends are largely driven by media visibility and numerous ‘conservation’ projects that, in practice, provide little real support for population growth and long-term development.

Overall, a temporal reduction in body size is evident and is most likely driven by the simultaneous action of several factors: the loss of large individuals from the population (selective hunting, mortality of older age classes, higher mortality of adult males), climate change (shorter winter dor-

mancy and reduced need for fat accumulation), and trophic factors (deterioration of food resources, although consumer pressure may also be lower than in the past). Most likely, all these factors act concurrently. Whether compensatory mechanisms at the population level exist (e.g., earlier sexual maturity or increased fecundity) remains unknown; however, in the author's view, such mechanisms have not developed, and population decline therefore remains largely uncompensated. In any case, these are predominantly anthropogenic processes, and bears are effectively no better off than species experiencing more direct human impacts.

Acknowledgements

Sincere thanks to colleagues who contributed to the accumulation of information about the dimensional characteristics of bears, in particular D. Lazariev, A. Luniachek, I. Merzlikin, I. Shydlovskyy, as well as colleagues who participated in the development of discussions on the hypotheses expressed or involved in the discussion, in particular M. Kolesnikov, S. Myakushko, E. Ulyura, and L. Shevchenko. Thanks to S. Gashchak, Y. Dovhanych, N. Koval, and A. Simon for sending photos of footprints. Special thanks to one of the leading experts on changes in animal size in the process of historical population development, S. Myakushko, for his detailed analysis of the article and important comments on facts and hypotheses.

Declarations

Funding. The study was carried out as part of the planned research topic of NMNH (State Registration No. 0124U000572) under the section 'Dynamics of biota in conditions of climate change and warfare.'

Conflict of interest. The author has no conflicts of interest relevant to the content of the article.

Handling of material. The study was conducted in compliance with the requirements of the current legislation of Ukraine regarding work with live and collection material.

References

- Almāsan, N. A., G. D. Vasiliu. 1967. Zur Kenntnis des Rumänischen Karpatenbär. *Acta Theriologica*, **12**: 47–66. [CrossRef](#)
- Bischof, R., C. Bonenfant, I. M. Rivrud, A. Zedrosser, A. Friebe, [et al.]. 2018. Regulated hunting re-shapes the life history of brown bears. *Nature Ecology & Evolution*, **2** (1): 116–123. [CrossRef](#)
- Brooks, R. T., R. McRoberts, L. L. Rogers. 1998. Predictive relationships between age and size and front-foot pad width of northeastern Minnesota Black Bears, *Ursus americanus*. *Canadian Field-Naturalist*, **112** (1): 82–85. [CrossRef](#)
- Chudiyovych, I. 2017. *Hunting 'Atlantis' of the Lviv Carpathians (History and Mythology, Articles and Photos)*. Pyramid, Lviv, 1–268. [Ukrainian]
- Christiernsson, A. 2018. *Managing Strictly Protected Species with Favourable Conservation Status. The Case of the Swedish Brown Bear (Ursus arctos)*. Stockholm University, 1–24. [URL](#)
- Deacy, W. W., J. A. Erlenbach, W. B. Leacock, J. A. Stanford, C. T. Robbins, J. B. Armstrong. 2018. Phenological tracking associated with increased salmon consumption by brown bears. *Scientific Reports*, **8**: 11008. [CrossRef](#)
- Dehnel, A. 1949. Badania nad rodzajem *Sorex L. Annales Universitatis Mariae Curie-Skłodowska. Sectio C: Biologia*, **4**: 17–102. [URL](#)
- Gashchak, S., C. L. Barnett, N. A. Beresford, [et al.]. 2022. Estimating the population density of Eurasian lynx in the Ukrainian part of the Chernobyl exclusion zone using camera trap footage. *Theriologia Ukrainica*, **23**: 47–65. [CrossRef](#)
- Gashchak, S. 2025. Method for estimating animal size from camera trap images using reference objects. *Theriologia Ukrainica*, **30**: 97–108. [CrossRef](#)
- Egorov, Y. E. 1975. The stabilising effect of random elimination. *Journal of General Biology*, **36** (2): 220–226. [Russian]
- Frank, S. C. 2017. Indirect effects of bear hunting: a review from Scandinavia. *Ursus*, **28** (2): 150–164. [CrossRef](#)
- Harris, M. A., K. Steudel. 1997. Ecological correlates of hind-limb length in the Carnivora. *Journal of zoology*, **241** (2): 381–408. [CrossRef](#)
- Iliukhin, Y. 2019. Representatives of the family Ursidae in the collection of the Museum of Nature of V. N. Karazin Kharkiv National University. In: Zagorodniuk, I. (ed.). *Natural History Museology, Volume 5*. NMNH NAS of Ukraine, Kyiv, 170–173. [Ukrainian] [URL](#)
- Ingram, G. M. 1917. The Little Bear Wonder of Oregon. *The Oregon Sportsman*, **5** (4): 275–276. [URL](#)
- Jakubiec, Z. 2001. *Niedźwiedź brunatny Ursus arctos L. w polskiej części Karpat*. Instytut Ochrony Przyrody PAN, Kraków, 1–108. (Seria: Studia Naturae; vol. 47). ISSN 0081-6760 [URL](#)
- Jerina, K., E. Polaina, D. Huber, S. Reljić, M. Bartol, [et al.]. 2018. *Reconstruction of Brown Bear Population Dynamics in Slovenia and Croatia for the Period 1998–2018*. Prepared within C5 action of Life DinAlp Bear Project, 1–46. [URL](#)
- Khoyetskyy, P. 2017. Game fauna count in the '2-tp – hunting' statistical reporting format: features, advantages, disadvantages. *Novitates Theriologicae*, **10**: 206–216. [Ukrainian]. [CrossRef](#)
- Kilfoil, J. P., T. P. Quinn, A. J. Wirsing. 2023. Human effects on brown bear diel activity may facilitate subadults foraging on Pacific salmon. *Global Ecology and Conservation*, **42**: e02407. [CrossRef](#)
- Krofel, M., M. Jonozović, K. Jerina. 2012. Demography and mortality patterns of removed brown bears in a heavily exploited population. *Ursus*, **23** (1): 91–103. [CrossRef](#)
- Kryzhanivsky, V. 1999. Brown bear — *Ursus arctos*. In: Zagorodniuk, I. V. (ed.). *Mammals of Ukraine, Protected by the Bern Convention*. Kyiv, 118–120. (Series: Proceedings of the Theriological School; Vol. 2). ISBN 966-02-1280-1. [URL](#)
- Lomolino, M. 2005. Body size evolution in insular vertebrates: Generality of the island rule. *Journal of Biogeography*, **32** (10): 1683–1699. [CrossRef](#)
- Mezhzherin, V. A. 1964. Denel's phenomenon and its possible

- explanation. *Acta Theriologica*, **8** (6): 95–114. [Russian] [CrossRef](#)
- Mezhzherin, S. V., O. I. Lashkova. 2013. *The Mammals of Ukraine. Reference Book*. Naukova Dumka, Kyiv, 1–358. [Ukrainian]
- Miropolsky, V. 2017. Photographing of wild animals and traces of their life in the field. *Novitates Theriologicae*, **10**: 60–69. [Ukrainian] [CrossRef](#)
- Myakushko, S. A. 2004. Changes in body weight and body size of rodents under various forms of anthropogenic load. *Nature Reserves in Ukraine*, **10** (1–2): 92–95. [Ukrainian] [URL](#)
- Myakushko, S. 2021. Shrinkage of body size in rodents as a strategy of populations under anthropogenic conditions (results of 50 years of study of rodent populations). *Theriologia Ukrainica*, **22**: 133–143. [CrossRef](#)
- Niezabitowski, E. 1933. *Klucz do oznaczania zwierząt ssących Polski*. Nakładem Koła Przyrodników Uczniów Uniwersytetu Jagiellońskiego, Kraków, 1–124. [URL](#)
- Raia, P., S. Meiri. 2006. The island rule in large mammals: paleontology meets ecology. *Evolution*, **60** (8): 1731–1742. [CrossRef](#)
- Rigg, R., M. Adamec. 2007. *Status, Ecology and Management of the Brown Bear (Ursus arctos) in Slovakia*. Slovak Wildlife Society, Liptovský Hrádok, 1–128. [URL](#)
- Sanz-Pérez, A., V. Sazatornil, S. Palazón, C. Vanpé, P.-Y. Quenette, [et al.]. 2025. Mapping sex- and age-structure reveals lonely males at the front in an expanding brown bear population. *Biological Conservation*, **306**: 111122. [CrossRef](#)
- Salinas-Ramos, V. B., P. Agnelli, L. Bosso, L. Ancillotto, D. Russo. 2021. Body size of Italian greater horseshoe bats (*Rhinolophus ferrumequinum*) increased over one century and a half: a response to climate change? *Mammalian Biology*, **101**: 1127–1131. [CrossRef](#)
- Savitsky, B. P., S. V. Kuchmel, L. D. Burko. 2005. *Mammals of Belarus*. Published by the Belarusian State University Publishing Centre, Minsk, 1–320. [Russian]
- Schmidt, N. M., P. M. Jensen. 2003. Changes in mammalian body length over 175 years. Adaptations to a fragmented landscape? *Conservation Ecology*, **7** (2): 6. [CrossRef](#)
- Shevchenko, L. S. 2007. *Mammals. Issue 3. Carnivora. Lagomorpha (Supplement)*. National Museum of Natural History, NAS of Ukraine, Kyiv, 1–80. (Series: Catalogue of the Collections of the Zoological Museum). ISBN 978-966-02-4462-7 [URL](#)
- Shevchenko, L. S., M. G. Shkvyria. 2009. Brown Bear *Ursus arctos* (Linnaeus, 1758). In: Akimov, I. A. (ed.). *Red Data Book of Ukraine. Animal world*. Globalconsulting, Kyiv, 537. [Ukrainian]
- Slobodian, O. O. 2008. *A Brief History of Brown Bear Research in the Ukrainian Carpathians*. DKD, Ivano-Frankivsk, 1–160. [Ukrainian]
- Spassov, N., G. Spiridonov, V. Ivanov, L. Assenov. 2016. Bear footprints and their use for monitoring and estimating numbers of brown bears (*Ursus arctos* L.) in Bulgaria. *Historia Naturalis Bulgarica*, **23**: 119–126. [URL](#)
- Strautman, F. I., K. A. Tatarinov. 1949. Materials on the fauna of vertebrate animals of the Eastern Carpathian forests. *Scientific Notes (Biological Series)*. Ivan Franko State University of Lviv, **16** (5): 121–152. [Ukrainian]
- Swenson, J. E. 1995. The near-extinction and recovery of brown bears in Scandinavia. *Wildlife Biology*, **1** (1): 5–13. [CrossRef](#)
- Swenson, J. E., M. Adamič, D. Huber, S. Stokke. 2007. Brown bear body mass and growth in northern and southern Europe. *Oecologia*, **153** (1): 37–47. [CrossRef](#)
- Tomassini, A., P. Colangelo, P. Agnelli, G. Jones, D. Russo. 2014. Cranial size has increased over 133 years in a common bat, *Pipistrellus kuhlii*: a response to changing climate or urbanization? *Journal of Biogeography*, **41** (5): 944–953. [CrossRef](#)
- Turianyn, I. I. 1975. *Fur- and Game Mammals and Game Birds of the Carpathians*. Uzhhorod, 1–176. [Ukrainian] [URL](#)
- Viranta, S. 1994. Limb bone proportions and body mass of the cave bear (*Ursus spelaeus*). *Historical Biology*, **7** (3): 239–250. [CrossRef](#)
- Volokh, A., Y. Tkachuk. 2025. The brown bear (*Ursus arctos*) in Bukovyna (Ukraine): distribution, habitats, diet, morphological features. *Theriologia Ukrainica*, **30**: 88–96. [Ukrainian] [CrossRef](#)
- Zagorodniuk, I. 2002. Allopecies of the roe deer (*Capreolus*): nature of differences between them and status of populations from Ukraine. *Visnyk of the Luhansk Pedagogical University. Biological Sciences*, No. 1 (45): 206–222. [Ukrainian] <https://bit.ly/3oemHW9>
- Zagorodniuk, I., I. Merzlikin. 2025. The brown bear (*Ursus arctos*) in the Eastern Polissia in Ukraine: evidence of the species' recovery in the region. *Novitates Theriologicae*, **17**: 63–66. [Ukrainian] [CrossRef](#)