

# Biomechanic Potentials of the Canine and Carnassial Teeth in the Strains of American Mink (*Neogale vison* Schreber 1777) Following Selection for Defensive Behavior Traits as Compared to a Natural Population and Related Species

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**Abstract**—Differences between the strains of aggressive and tame American minks that arose as a result of selection for traits of defensive behavior (16–17 generations) were revealed based on the biomechanical indices of the mandible characterizing the mechanical potentials of the canine and carnassial teeth. The results are consistent with D.K. Belyaev's theory of destabilizing selection: along with an increase in the variability of functions and the destabilization of the historically established system of their sexual differences (sexual dimorphism), new biomechanic features of the mandible were formed in the strain of tame minks. In contrast, the control strain of nonselected minks unaffected by selection retained significant sex differences in the biomechanical indices. Between the American minks from a Canadian natural population and the strains of aggressive and tame individuals, the differences in biomechanical indicators were less pronounced than between the strains themselves. Differences among the American mink, the European mink (*Mustela lutreola* L. 1758), and the Siberian weasel (*M. sibirica* Pallas 1773) in the biomechanical potentials of the canine and carnassial teeth of the mandible which reflect specializations in the genus *Neogale* and the specifics of the hunting behavior of the species were found. In the invasive American mink, the mechanical potential (MP) of the canine tooth prevails, compared to the MP of the carnassial tooth in both the European mink and the Siberian weasel, this trait being capable of ensuring the divergence of their trophic niches and contributing to the preservation of native species in areas of their sympatry with *N. vison*.

**Keywords:** mink, weasel, mandible, bite force, variation, domestication

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## INTRODUCTION

The phenomenon of domestication has long been of interest to researchers, especially after the publication of the work of C. Darwin (Darwin, 1868). The problem of the emergence of a rapid selective response to selection based on the traits of defensive behavior in animals is closely related to the problem of the formation of the morphogenetic effects of domestication (Belyaev, 1979a, 1979b; Trut, 1981; Trapezov, 1987; Belyaev and Trut, 1989; Kaiser et al., 2015; Singh et al., 2017). According to the data obtained (Trapezov, 2012; Singh et al., 2017; Trut et al., 2021), the rate of morphogenetic restructuring processes identified during domestication in dog breeds, silver foxes, American minks, brown rats, and other animals is usually high. The morphological differentiation revealed over historical time using the example of dog breeds

exceeded the levels of morphological diversity not only of their ancestral forms (wolf, coyote, and jackal), but was comparable to the diversity of the main representatives of the entire order of predatory mammals (Drake and Klingenberg, 2010). Morphometric differences between the strains of tame and aggressive American minks become apparent after just a few generations of selection for defensive behavior traits (Kharlamova et al., 2000). Such rapid transformations of domesticated species probably cannot be caused solely by the selection of random genome mutations that affect morphogenesis processes (Kukekova et al., 2018). First, different species often show similar morphogenetic changes during selection (Wilkins et al., 2014; Singh et al., 2017; Lord et al., 2020); second, the scope of targeted morphological

changes in such a short time (number of generations) turns out to be too large.

It can be assumed that an alternative probable factor accelerating the selective response may be morphogenetic processes initiated by stress-induced epigenetic changes (DNA methylation, transpositions of mobile elements of the genome, etc.), the leading role of which in microevolutionary processes has been increasingly discussed in the past decade (Jablonka and Raz, 2009; Burggren, 2016; Donelan et al., 2020). Such a mechanism of rapid genetic, epigenetic, morphogenetic, and ethological rearrangements of experimental animals is in good agreement with the idea of destabilizing selection proposed by Academician Belyaev (Belyaev, 1979a, 1979b; Belyaev and Trut, 1989). This mechanism allows the theory of destabilizing selection to be supplemented with new molecular genetic data (Kukekova et al., 2018; Trut et al., 2021) and epigenetic concepts (Jensen, 2013; Burggren, 2016; Bošković and Rando, 2018) about the nature of this phenomenon.

Earlier, at the experimental fur farm of the Institute of Cytology and Genetics, Siberian Branch, Russian Academy of Sciences, strains of aggressive and tame American minks were obtained as a result of selection for defensive behavior. During their further morphometric comparison (Kharlamova et al., 2000), the biomechanical characteristics of the mandible associated with the bite force and hunting behavior of the animals remained almost unstudied. It is of interest to compare these characteristics of caged American minks with those of natural representatives of the species, as well as other species of mustelids (Carnivora, Mustelidae).

When comparing the American mink strains, it remains unclear how the change in the shape of the mandible after experimental “domestication” of minks is associated with its biomechanical functioning. Another unstudied aspect is whether the mechanical potential proportional to the “bite force” of animals increases after selection in the aggressive mink strain and whether this potential decreases in tame individuals. It is also important to assess whether the opposite selection has affected the functional sex differences in the mandibles of representatives of different strains. Does the level of achieved functional mandibular differences between the strains of aggressive and tame minks reach the level of sex differences? Are there differences in the biomechanical potential of the mandibles in the invasive species—the American mink and the closely related European autochthonous competitor species? Therefore, it was of interest to conduct additional studies using new material on the American mink obtained after 16–17 generations of selection.

In this regard, it should be noted that a number of publications present approaches to direct and indirect assessment of the bite force and forces exerted on the teeth (incisors, canines, molars) of different mammal species. These approaches involve the use of different

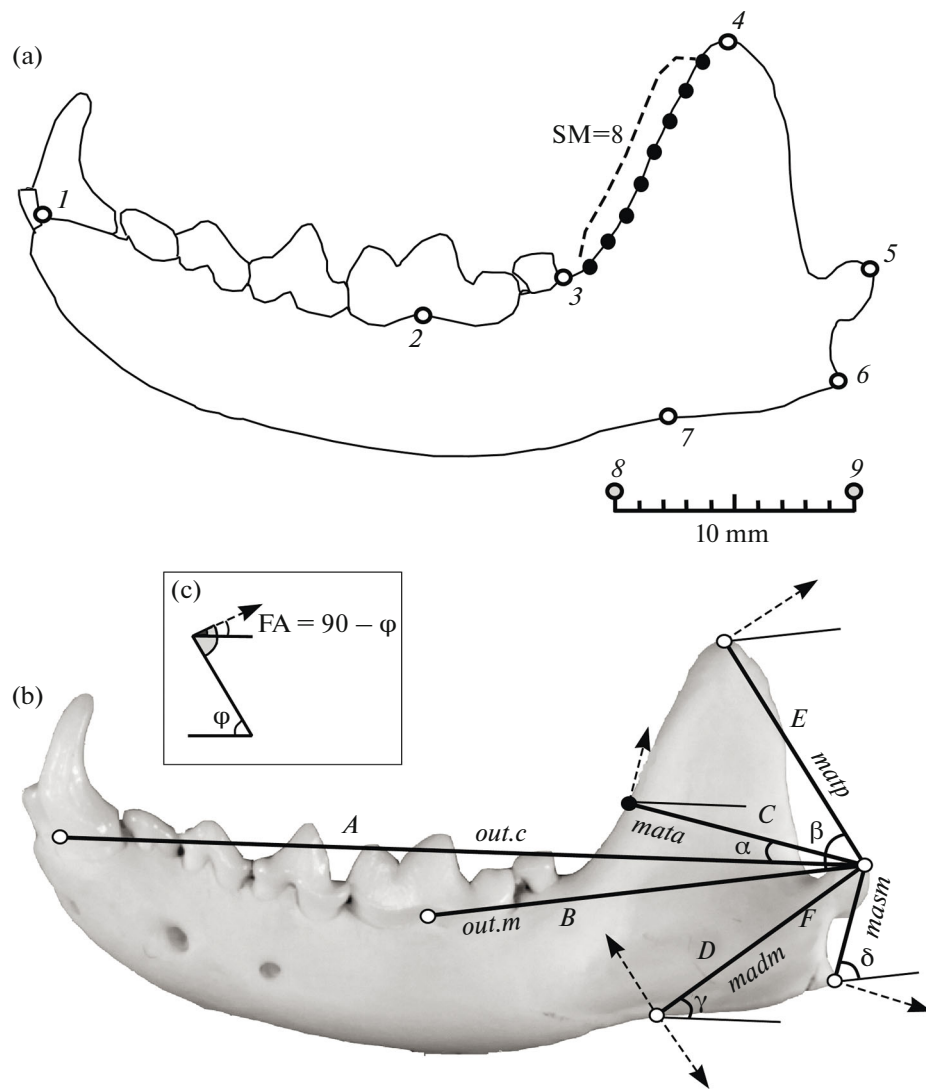
mandibular functional indices (Christiansen, 2008; Blanco et al., 2011; Anderson et al., 2014; Cornett et al., 2015; Vasil'ev et al., 2016; Gálvez-López and Cox, 2022). Therefore, it is of interest also to evaluate the biomechanical features of the mandible in experimental strains of American mink associated with the selective process based on defensive behavior traits.

The goal of this study is a comparative assessment of the biomechanics of nutrition and the mechanical potential in the area of the canine (c) and carnassial tooth (m1) in American minks based on the morpho-functional mandibular indices in males and females of strains of aggressive and tame animals obtained as a result of selection based on defensive behavior traits. Of particular interest was a comparison of their indices with the characteristics of nonselected minks and individuals of natural populations of the species from Canada, as well as closely related mustelid species—the European mink (*Mustela lutreola* L. 1758) and the Siberian weasel (*M. sibirica* Pallas 1773).

## MATERIALS AND METHODS

We used the collection of craniological material from two strains of aggressive (69 males, 51 females) and tame (30 males, 31 females) American minks obtained as a result of 16–17 generations of selection based on defensive behavior traits at an experimental fur farm at the Institute of Cytology and Genetics, Siberian Branch, Russian Academy of Sciences, under the supervision of O.V. Trapezov (1987, 2012). Nonselected minks (142 males, 113 females), which were kept on the fur farm in parallel with the experimental strains, were used as a conditional control for comparison with the experimental strains. All animals were represented by yearlings of similar age (seven months) and were obtained during the same season (in November). In addition, to make a comparison, we studied museum samples of mandibles of males of the natural American mink population from the province of Alberta in Canada (1933) (16 specimens) (age from 1+ to 3+) and two samples of relatively closely related mustelid species (Carnivora, Mustelidae) from the Museum of the Institute of Plant and Animal Ecology, Ural Branch, Russian Academy of Sciences, Yekaterinburg: seven European minks and ten Siberian weasels.

The objects of study were the branches of the mandible (digital photos) of American minks (and related species) from the buccal side (Fig. 1), which is part of the foraging organs and is involved both in the primary biomechanics of capturing prey during hunting and in processing this prey during feeding. When working with the images, geometric morphometric methods were used in part (Rohlf and Slice, 1990; Pavlinov and Mikeshina, 2002; Zelditch et al., 2004; Klingenberg, 2011). The images were obtained using a Canon EOS 6000 camera mounted on a tripod at a resolution of 1809 × 1179 pixels. Using the tpsUtil and tpsDig2 pro-



**Fig. 1.** Scheme of the arrangement on the buccal side of the American mink mandible: (a) LM landmarks (1–7), SM semi-landmarks ( $n = 8$ ), and scaling landmarks (8, 9); (b) measurements  $A, B, C, D, E, F$  (after Gálvez-López and Cox, 2022) and angles  $\alpha, \beta, \gamma, \delta$  for calculating the mechanical potential indices of the canine and carnassial teeth (see text for designations and explanations), and (c) method for calculating the force direction angle (FA) (after Cornett et al., 2015). Arrows show directions of bio-mechanical forces of the in-levers.

grams, 7 homologous landmarks (LM), eight semi-landmarks (SM), and two scaling landmarks on the ruler divisions (see Fig. 1a) were placed in the photographs (Rohlf, 2017, 2017a). Using the CoordGen6f program from the IMP package (Zelditch et al., 2004), the centroid sizes (CS) were presented in millimeters.

Figure 1b shows the scheme of the main measurements of the buccal side of the mandibular branch of the American mink for the further calculation of four mandibular indices indirectly characterizing the mechanical potentials in the region of the canine tooth  $c$  (canine) and the first lower molar  $mI$ —the carnassial tooth. The measurements and their abbreviated names (with slight modifications) correspond to the mea-

surements proposed in the study of Gálvez-López and Cox (2022): ( $A$ ) the length from the anterior alveolus of the canine (LM 1) to the upper posterior edge of the condyle of the articular process (LM 5) corresponds to the measurement “ $out.c$ ,” the out-lever in biomechanical analysis; ( $B$ ) the length from the middle of the base of the first molar  $mI$  (lower carnassial tooth) LM 2 to the point LM 5 on the condyle of the articular process corresponds to the measurement “ $out.m$ ,” the short out-lever; ( $C$ ) the length from LM 5 to the third semi-landmark (SM) from LM 3 corresponds to the measurement “ $mata$ ,” an assessment of the mechanical advantage due to the anterior temporal muscle (mechanical advantage of the  $m. temporalis anterior$ ); ( $D$ ) the length from LM 5 to the ventral edge of the mandible

**Table 1.** Mechanical potential (MP) indices of the canine and carnassial teeth and centroid sizes (CS) of the mandible in the compared strains and the Canadian natural population of the American mink, as well as in related species—the European mink and Siberian weasel

Species, strains, gender (specimens)	Mechanical potentials (MPs) of canine and carnassial teeth				Centroid size (CS), mm
	MP $_{madm}$ per canine	MP $_{matp}$ per carnassial tooth	MP $_{mata}$ per canine	MP $_{masm}$ per carnassial tooth	
<i>Neogale vison</i> :					
AM (69)	0.178 ± 0.001	0.539 ± 0.003	0.077 ± 0.001	0.285 ± 0.003	105.25 ± 0.43
AF (51)	0.174 ± 0.002	0.522 ± 0.003	0.076 ± 0.002	0.283 ± 0.003	90.97 ± 0.38
A (120)	0.176 ± 0.001	0.532 ± 0.002	0.076 ± 0.001	0.284 ± 0.002	99.18 ± 0.71
NM (142)	0.173 ± 0.001	0.532 ± 0.002	0.080 ± 0.001	0.270 ± 0.002	104.23 ± 0.30
NF (113)	0.169 ± 0.001	0.528 ± 0.003	0.076 ± 0.001	0.293 ± 0.002	89.88 ± 0.26
N (255)	0.171 ± 0.001	0.530 ± 0.002	0.078 ± 0.001	0.280 ± 0.001	97.87 ± 0.49
TM (30)	0.162 ± 0.002	0.544 ± 0.005	0.088 ± 0.003	0.263 ± 0.004	100.49 ± 0.75
TF (31)	0.159 ± 0.001	0.524 ± 0.005	0.082 ± 0.004	0.271 ± 0.003	86.16 ± 0.52
T (61)	0.160 ± 0.001	0.534 ± 0.004	0.085 ± 0.003	0.267 ± 0.003	93.25 ± 1.03
Can (16)	0.171 ± 0.002	0.548 ± 0.006	0.093 ± 0.003	0.278 ± 0.003	103.53 ± 1.45
<i>M. lutreola</i> (7)	0.155 ± 0.003	0.572 ± 0.008	0.096 ± 0.003	0.269 ± 0.010	90.06 ± 1.94
<i>M. sibirica</i> (9)	0.148 ± 0.003	0.577 ± 0.004	0.108 ± 0.002	0.291 ± 0.005	83.28 ± 1.60

American mink (*Neogale vison*) strains: A, aggressive (AM, males; AF, females); N, nonselected (NM, males; NF, females); T, tame (TM, males; TF, females); Can, Canadian natural population of *N. vison* (males); *Mustela lutreola*, European mink (males); *M. sibirica*, Siberian weasel (males).

at LM 7 corresponds to the measurement “*madm*,” an assessment of the mechanical advantage due to the lower (deep) masseter muscle (mechanical advantage of the deep m. masseter); (*E*) the length from LM 5 to the apex of the coronoid process (LM 4) corresponds to the measurement “*matp*,” an assessment of the mechanical advantage due to the posterior temporal muscle (mechanical advantage of the m. temporalis posterior); (*F*) the length from LM 5 to the posterior edge of the angular process of LM 6 corresponds to the measurement “*masm*,” an assessment of the mechanical advantage of the superficial masseter.

The specified measurements *A*, *B*, *C*, *D*, *F* and the values of the angles between them  $\alpha$ ,  $\beta$ ,  $\gamma$ ,  $\delta$  (Fig. 1b) were measured based on a specified protocol with the indicated pairs of landmark numbers using the tmorphogen6 module of the IMP software package (Zelditch et al., 2004). Based on the measurements, the morphofunctional mandibular indices were calculated as ratios by analogy with how this was previously done for other mammals (Anderson et al., 2014; Vasil'ev et al., 2016; Gálvez-López and Cox, 2022). Then, the mechanical potential (MP) indices of the canine and carnassial teeth were calculated by multiplying these indices by the cosines of the force direction angles (FA, force angle) in radians (Rad) in accordance with the recommendations of R. Cornett et al. (Cornett et al., 2015) using similar formulas:  $MP_{mata} = (C/A)\cos(\text{Rad}(90 - \alpha))$ ;  $MP_{matp} = (E/B)\cos(\text{Rad}(90 - \beta))$ ;  $MP_{madm} = (D/A)\cos(\text{Rad}(90 - \gamma))$ ;  $MP_{masm} =$

$(F/B)\cos(\text{Rad}(90 - \delta))$ . The method for calculating the force direction angle (FA) as the difference between the subtraction of the crosswise angle ( $\varphi$ ) from the right angle at the point of force application, which was previously proposed by Cornett et al. (2015), is shown in Fig. 1c. Note that algebraic methods for calculating the angle values are also possible (Cornett et al., 2015).

Table 1 shows the estimates of the mechanical potentials (MPs) of the canine for masseter-articular (*madm*) and anterior temporal-articular (*mata*) in-levers in relation to the out-lever of force application (*out.c*), as well as the mechanical potentials of the carnassial teeth for the posterior temporal-articular (*matp*) and angular-articular (*masm*) in-levers in relation to another common biomechanical out-lever (*out.m*) (see Fig. 1b). Let us clarify that the table contains the average values of the corresponding mechanical potentials (MP) taking into account their standard errors ( $\pm$ SE), which were obtained for males and females of the three compared strains of American mink, males of the natural population of this species from Canada, and males of the European mink and the Siberian weasel. Since we used indices—relative values—the influence of age and size of individuals on indices in the sample of natural minks is not expressed (all indices had no significant relationships with the CS value).

The statistical significance of differences in multiple comparison of samples was estimated using two-

way ANOVA. In ANOVA and correlation calculations, the Shapiro–Wilk test was preliminarily used to check the conformity of variables with the normal distribution law. To obtain an integral assessment and to interpret the intergroup variation of several variables, a nonparametric multivariate two-way PERMANOVA based on 10000 repeated permutations was carried out (Anderson, 2001). To remove the probable effect of the influence of different sample sizes on the manifestation of variation in the compared groups, their random alignment was preliminarily performed by the minimum number of observations—in all samples the number of individuals was 30 specimens. Pairwise comparisons were performed using post hoc Tukey–Kramer’s  $Q$ -test. To assess the hierarchical structure of the relationships between samples, cluster analysis was used using the UPGMA method—unweighted pairwise association by mean values. Calculations were performed using the TPS (Rohlf, 2017, 2017a), PAST 4.12 (Hammer et al., 2001), and IMP 6.0 (Zelditch et al., 2004) software packages.

## RESULTS

It follows from Table 1 that the highest values of the mechanical potential  $MP_{madm}$  per canine that is produced by the lower (deep) masseter (*madm*) were found in the samples of aggressive males and females, with unselected minks of both sexes approaching them in terms of this indicator, as does the natural series from Canada. It is noteworthy that the sex differences in individuals of all three strains are statistically insignificant: in aggressive ones,  $Q = 2.288$  ( $p = 0.6707$ ); in tame ones,  $Q = 1.615$  ( $p = 0.9151$ ); and in nonselected ones,  $Q = 2.509$  ( $p = 0.5655$ ). Meanwhile, male Canadian minks differ significantly from aggressive and tame males (respectively,  $Q = 4.358$  ( $p = 0.0337$ ) and  $Q = 5.368$  ( $p = 0.0028$ )), but are similar to nonselected males ( $Q = 1.471$ ,  $p = 0.9447$ ). Significantly, the lowest values of this indicator were shown by two closely related species—the European mink and the Siberian weasel (see Table 1). With regard to the experimental selected strains of American mink, it can be concluded that in aggressive animals the  $MP_{madm}$  index formally increased somewhat in relation to the original nonselected and natural Canadian minks, although significant confirmation of differences was manifested only between nonselected females and aggressive males ( $Q = 5.396$ ,  $p = 0.0026$ ), but both sexes of tame individuals showed a significant increase in the  $MP_{madm}$  index (from  $Q = 4.330$ ,  $p = 0.0026$  to  $Q = 8.454$ ,  $p = 0.00003$ ).

Another index,  $MP_{mata}$ , also indirectly indicates the forces applied to the canine tooth, but reflects the ability of the longitudinal cutting displacement of the canine tooth in the forward and backward directions, which probably allows partially changing the grip of the prey and holding it, as well as dismembering, scraping, and tearing off parts of the food object.

According to this indicator (see Table 1), the lowest average values were shown in both sexes of the aggressive mink strain and the highest values were expressed in males of the tame strain. It is noteworthy that Canadian natural American minks are distinguished by the highest  $MP_{mata}$  value among the samples considered, approaching only tame males ( $Q = 2.294$ ,  $p = 0.6679$ ). The highest values of this indicator were shown in the European mink and the Siberian weasel, and in the Siberian weasel, the  $MP_{mata}$  index reaches a maximum in the compared group of samples (see Table 1).

The third index,  $MP_{matp}$  (see Table 1), reflecting the efforts of the posterior temporal muscle per carnassial tooth of the mandible (the ability to cut and crush a food object), indicates that this index is expressed to the least degree in the experimental strains of American minks. It is significantly higher only in tame males in relation to females of all strains, but is close to the same index in males from Canada, in which it is also relatively high. However, this index is significantly higher in the European mink and the Siberian weasel.

The fourth index,  $MP_{masm}$  (see Table 1), reflects the efforts applied to the carnassial tooth of the mandible during its transverse movement, i.e., during lateral cutting, crushing, or changing the grip of a food object. When comparing representatives of American minks, the average value of the mechanical potential index  $MP_{masm}$  is highest in nonselected females, which significantly exceed the males of this strain in this index ( $Q = 8.029$ ,  $p = 0.00002$ ). The index level in aggressive minks of both sexes is significantly higher than in tame animals (see Table 1); however, sex differences in both strains in  $MP_{masm}$  are statistically insignificant (respectively,  $Q = 0.489$ ,  $p = 0.9999$  and  $Q = 2.237$ ,  $p = 0.6943$ ). American mink males from the wild population of Canada occupy an intermediate position between nonselected females and tame males. It is noteworthy that this indicator differs between the European mink (it has a low  $MP_{masm}$  value) and the Siberian weasel ( $Q = 4.725$ ,  $p = 0.0236$ ), which is close to nonselected American mink females in terms of a high index value ( $Q = 0.507$ ,  $p = 0.9999$ ).

To assess the influence of the strain (S) and gender (G) factors on the variability of the values of each of the indices, we conducted two-factor ANOVAs (Table 2) of the above-mentioned indices of the mechanical potential (MP) of the canine and the carnassial tooth in the experimental strains of American mink, taking into account the influence of the S and G factors and their interaction (S  $\times$  G). From Table 2 it follows that the  $MP_{madm}$  index shows significant interstrain differences, as well as sex differences that were inferior to them in terms of the intergroup variance, but the interaction of these factors was insignificant. The variability of the  $MP_{mata}$  index value is less pronounced, but, as in the previous case, the variance caused by the

**Table 2.** Two-way ANOVA of the mechanical potential (MP) indices of the canine and carnassial teeth of the mandible in experimental strains of American mink, taking into account the influence of the strain (S) and gender (G) factors and their interaction (S × G)

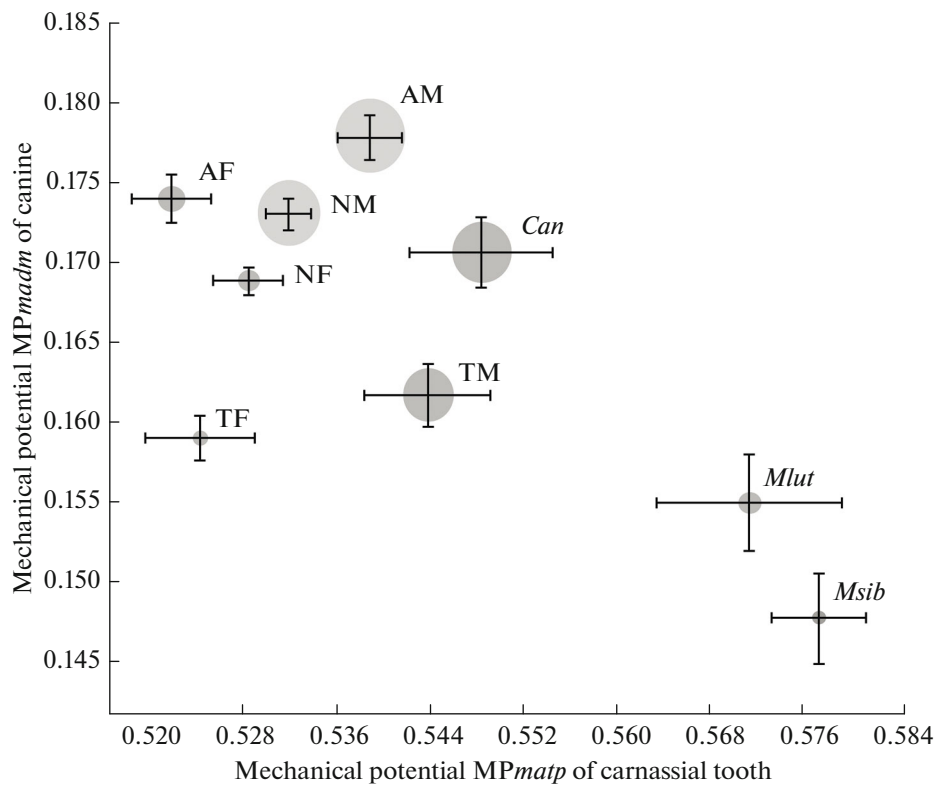
Source of variability (Factor)	Sum of squares (SS)	Number of degrees of freedom (d.f.)	Mean square (MS)	F	Level of significance (p)
<i>MP<sub>madm</sub></i> , masseter-articular mechanical potential of the canine					
Strain (S)	0.01039	2	0.00519	46.76	<0.00001
Gender (G)	0.00207	1	0.00207	18.60	<0.00001
Interaction (S × G)	0.00006	2	0.00003	0.27	0.76600 (ns)
Intergroup	0.04776	430	0.00011		
Total	0.06028	435			
<i>MP<sub>mata</sub></i> , anterior temporal-articular mechanical potential of the canine					
Strain (S)	0.00329	2	0.00165	8.76	0.00019
Gender (G)	0.00136	1	0.00136	7.24	0.00741
Interaction (S × G)	0.00051	2	0.00026	1.36	0.25710 (ns)
Intergroup	0.08075	430	0.00019		
Total	0.08591	435			
<i>MP<sub>matp</sub></i> , posterior temporal-articular mechanical potential of carnassial teeth					
Strain (S)	0.00063	2	0.00032	0.46	0.63310 (ns)
Gender (G)	0.00949	1	0.00949	13.71	0.00024
Interaction (S × G)	0.00544	2	0.00272	3.94	0.02026
Intergroup	0.29750	430	0.00069		
Total	0.31306	435			
<i>MP<sub>masm</sub></i> , angular-articular mechanical potential of carnassial teeth					
Strain (S)	0.01202	2	0.00601	13.31	<0.00001
Gender (G)	0.02079	1	0.02079	46.06	<0.00001
Interaction (S × G)	0.01377	2	0.00689	15.26	<0.00001
Intergroup	0.19410	430	0.00045		
Total	0.24068	435			

strain (S) factor is several times higher than the variance due to the gender (G) factor, and the interaction of the factors (S × G) is also statistically insignificant. Therefore, in addition to the fact that the *MP<sub>mata</sub>* and *MP<sub>madm</sub>* indices reflect interstrain differences, they also reflect manifestations of sexual dimorphism in the values of these mechanical potentials of the canine.

The temporal-articular mechanical potential of the carnassial tooth—*MP<sub>matp</sub>*—did not show significant interstrain differences (see Table 2), but statistically significantly reflects sexual differences and their interaction with the strain factor. In other words, between males and females of different strains, sexual differences in this indicator are manifested differently. Meanwhile, the angular-articular mechanical potential of the carnassial tooth—*MP<sub>masm</sub>*—statistically significantly reflects both interstrain and sexual differences, as well as their interaction. Thus, only three

biomechanical indices showed a direct significant relationship with the results of selection for behavioral traits and the domestication process, reflecting inter-strain differences.

It was of interest to compare the coupled intergroup variation of the average values of the two main indicators of the mechanical potential of both the canine tooth (*MP<sub>madm</sub>*) and the carnassial tooth (*MP<sub>matp</sub>*) in the strains and the natural Canadian population of the American mink, as well as two closely related species—the European mink and the Siberian weasel. The results of this comparison are presented in Fig. 2. It follows from the figure that, indeed, the mechanical potential *MP<sub>madm</sub>* of the canine is higher in aggressive, nonselected, and natural Canadian American minks, but significantly lower in tame individuals of this species and even lower in the European mink and the Siberian weasel. Meanwhile, representatives of the invader species (the



**Fig. 2.** Comparison of the average mechanical potentials (with standard error  $\pm$  SE) of the canine ( $MP_{madm}$ ) and carnassial teeth ( $MP_{matp}$ ) of males of the natural Canadian population (*Can*), experimental strains of American mink (aggressive: males, AM; females, AF; tame: males, TM; females, TF; nonselected: males, NM; females, NF), males of the European mink (*Mlut*) and the Siberian weasel (*Msib*). The sizes of the shadow spots correspond to the centroid sizes (CS) minus their minimum value.

American mink) and autochthonous species (the European mink and the Siberian weasel) clearly differ from each other in the values of the mechanical potential of the carnassial tooth  $MP_{matp}$ . This indicator reflects not only the specifics of their diet, but also the features of feeding and hunting behavior.

The diameters of the darkened spots-circles presented in this figure for each sample are proportional to the values of the centroid sizes (CSs) of the mandibles minus the minimum value. Figure 2 shows that the average centroid size of the mandibles is positively associated with the values of the mechanical potential  $MP_{madm}$  of the canine: in larger animals, the mechanical potential associated with the bite force of the canine is more pronounced (Spearman correlation coefficient  $R_s = 0.80$ ,  $p = 0.0108$ ). However, this trend is not expressed in the value of the mechanical potential of the carnassial tooth  $MP_{matp}$ —there is no relationship ( $R_s = -0.07$ ,  $p = 0.8432$ ), but sexual dimorphism is manifested in the average values of this indicator ( $R_s = 0.82$ ,  $p = 0.0238$ ). Sexual dimorphism was most clearly manifested in the selected strains: aggressive and tame American minks. Meanwhile, the samples of males and females of the experimental strains, as well as nonselected minks and males of the natural population of the species, showed no significant rela-

tionship between the indices and the centroid sizes of the mandibles.

For the integral assessment of the conjugate variability of all biomechanical indices, multivariate non-parametric two-way PERMANOVA was performed for the values of four mechanical potential indices ( $MP_{mata}$ ,  $MP_{matp}$ ,  $MP_{madm}$ ,  $MP_{masm}$ ) for two factors, strain (S) and gender (G), taking into account their interaction ( $S \times G$ ). The PERMANOVA results are presented in Table 3. It follows from this table that the effects of the influence of both factors and their interaction on the variability of the mechanical potential indices of the canine and carnassial tooth of the mandible are statistically highly significant. However, the total factorial variance in this case was relatively small—16.47%. Meanwhile, the largest share of the intergroup variance of the biomechanical indices was manifested by the strain factor—7.82%, and the gender factor accounted for 6.28%. It is noteworthy that the effect of interaction of these factors explains 2.38% of the variance, which is about 15% of the factorial variance. In other words, sex differences in biomechanical indices in different strains are manifested differently. The latter was partly visible in Fig. 2 by the average values of the mechanical potentials of the canine and carnassial teeth. Linear differences in the

**Table 3.** Results of nonparametric multivariate two-way analysis of variance (PERMANOVA) based on random permutations of individual values of mechanical potential indices (MP<sub>mata</sub>, MP<sub>matp</sub>, MP<sub>madm</sub>, MP<sub>masm</sub>) of females and males of strains of aggressive, nonselected, and tame American minks, taking into account the strain (S) and gender (G) factors and their interaction (S × G) for randomly matched sample sizes ( $n = 30$ )

Source of variability (Factor)	Sum of squares (SS)	Number of degrees of freedom (d.f.)	Mean square (MS)	F	Level of significance ( $p$ )
Strain (S)	0.0227	2	0.0114	8.19	0.0001
Gender (G)	0.0183	1	0.0183	13.15	0.0001
Interaction (S × G)	0.0069	2	0.0035	2.50	0.0118
Residual	0.2429	175	0.0014		
Total	0.2908	180			

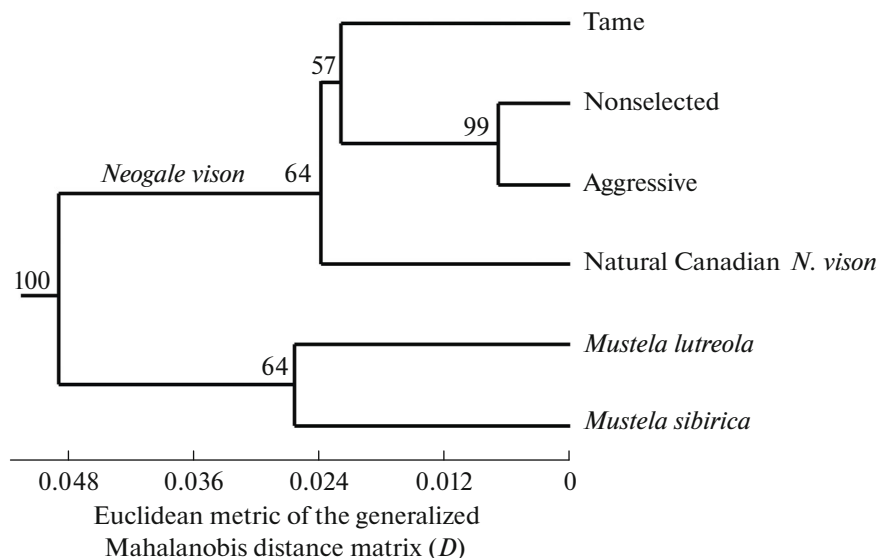
total intergroup variability in biomechanical indices generally slightly exceeded the sex differences, i.e., the results of selection were generally reflected in the change in a number of morphofunctional features associated with the nutritional characteristics and hunting and defensive behavior of American minks.

As a result of cluster analysis (UPGMA) of the hierarchy of relationships of samples of three American mink strains combined by sex, including samples of natural individuals of this species and related species, the European mink and the Siberian weasel, two clusters were identified based on the average values of four indices of the mechanical potential (MP<sub>mata</sub>, MP<sub>madm</sub>, MP<sub>matp</sub>, and MP<sub>masm</sub>) of the canine and carnassial teeth of the mandibles (Fig. 3). The first of them included all samples of American mink, and the second included samples of European mink and Siberian weasel. Within the American mink cluster, a more

differentiated branch of natural Canadian individuals was distinguished. The closest to each other were the branches of aggressive and nonselected minks, and the tame clade occupied an intermediate position between them and the Canadian natural minks. As a result, the structure of this cluster revealed the degree of morphofunctional differences in the biomechanical characteristics of the mandible between the linear and natural samples, also reflecting their taxonomic relationships with related species.

## DISCUSSION

When discussing the results of long-term selection of the American mink in the conditions of the experimental fur farm of the Institute of Cytology and Genetics, Siberian Branch, Russian Academy of Sciences, based on signs of defensive behavior, it is necessary to recall the general idea of D.K. Belyaev on



**Fig. 3.** Results of cluster analysis (UPGMA) of the average indices of mechanical potential of the canine and carnassial teeth of the mandible in individuals of the Canadian population, strains of aggressive, tame, and nonselected American minks (*Neogale vison*) and two closely related species—the European mink (*Mustela lutreola*) and Siberian weasel (*M. sibirica*).

destabilizing selection (Belyaev, 1979a) leading to an increase in variability, destabilization of historically established patterns of morphogenesis, reorganization, and formation of new adaptive traits. All these aspects were observed by us during the analysis of the variability of the mandibular shape in American minks as a result of their selection for defensive behavior traits. Previously, we already noted the emergence of new atypical morphs of fur coloration in American minks that arose during selection (Trapezov, 1997, 2012) under the action of destabilizing selection. As shown by the previously conducted analysis (Kharlamova et al., 2000), changes in the skull and mandible after oppositely directed selection for defensive behavior traits significantly affected the strains of aggressive and tame minks. In the present study, the range of biomechanical functional differences achieved in the mandibles between the strains of aggressive and tame minks slightly exceeded the level of their sexual differences. Meanwhile, it is well known that sexual dimorphism is largely a characteristic attribute of the development of most mustelid species (Abramov and Tumanov, 2003; Loy et al., 2004; Thom et al., 2004; Romaniuk, 2018; Law, 2020). Our results are fundamentally important, since they show that the excess of the range of interstrain differences over sexual ones reflects significant morphogenetic transformations of the mandible, as well as the associated biomechanical characteristics that arose in aggressive and especially in tame minks as a manifestation of new phenotype properties in response to selection for defensive behavior traits. Therefore, it can be stated that such significant changes in the morphogenesis of the mandible and the associated biomechanical features, in particular in the strain of tame minks, approach the phenotypic state “de novo” in relation to the “control” strain of nonselected minks.

We found that the mechanical potential of the canine tooth as a result of selection for an enhanced defensive reaction increased in the strain of aggressive minks, and this is observed to a somewhat greater extent in males of this strain based on the *MP<sub>madm</sub>* index. It can be concluded that, as a result of selection for defensive behavior traits, the mechanical potential of the canine tooth *MP<sub>madm</sub>* (the ability to bite strongly, grasp firmly, hold, and kill prey) increased somewhat in aggressive males and decreased sharply in both sexes of tame American minks. The latter indicates a general connection between the functional capabilities of the mandible of animals and their defensive and feeding behavior.

The mandible configuration of the aggressive mink strain probably prevents them from effectively exploiting the biomechanical property reflected by the *MP<sub>mata</sub>* index, which is found in wild and tame American minks and is typical of two closely related indigenous mustelid species. It can be assumed that the biomechanical features due to *MP<sub>mata</sub>* reflect the features of hunting behavior and nutrition of wild

American minks in the province of Alberta in Canada and the European mink and the Siberian weasel in the Urals and Siberia. Meanwhile, the tame minks showed a significant decrease in the *MP<sub>madm</sub>* index after selection, which generally also reflects the relationship between differences in behavior and the morphofunctional capabilities and biomechanical properties of the mandibles in the experimental strains of minks.

The mechanical potential of the canine tooth turned out to be proportional to the size of the animals: the largest aggressive minks had a greater potential “bite force” than the relatively smaller tame individuals. The data obtained in this regard are in good agreement with the estimates of other authors who have shown a relationship between the “bite force” of the canine tooth and its size in different species (Van Valkenburgh and Ruff, 1987; Gittleman and Van Valkenburgh, 1997; Law, 2019). Therefore, we emphasize that, in our case, such a dependence was also manifested, but at the intraspecific level—between males and females of different strains. Similar facts are noted by other authors using the example of American and European minks (Gálvez-López and Cox, 2022), as well as other species of mustelids (Carnivora, Mustelidae)—American marten (*Martes americana*) and fisher (*Pekania pennant*) (Law, 2020), river otter (*Lutra lutra*) (Timm-Davis et al., 2015), and sea otter (*Enhydra lutris*) (Law et al., 2017). On the other hand, we found that the mechanical potential of the carnassial tooth does not correlate with the size of the animals, but may be related to their sex. This dependence was also found by other authors when comparing male and female American minks (Gálvez-López and Cox, 2022), as well as other species of predatory mammals (Greaves, 1983; Van Valkenburgh and Ruff, 1987). This dependence may be due to the peculiarities of hunting and feeding behavior of different sexes, as well as the peculiarities of their choice of a specific diet (Law, 2020). Thus, the effort characterized by the *MP<sub>matp</sub>* index and falling on the carnassial tooth of the autochthonous competitor species—the European mink—is higher than the same effort in wild and caged American minks, which also indirectly reflects differences in both the feeding method and the diet of the species.

It is noteworthy that, in our comparison, both experimental strains—aggressive and tame minks—showed a smaller range of sex differences in the biomechanical indices of the mandibles than nonselected ones. Thus, the morphofunctional differences between males and females in nonselected minks that we established were large in the mechanical potential of the *MP<sub>masm</sub>* of the carnassial teeth, but were absent in aggressive and tame minks. It can be assumed that the multidirectional selective process led to the leveling of the existing sexual differences in this trait. Therefore, it can be assumed that selection to one degree or another influenced the manifestation of

some sexual differences in the biomechanics of the mandibles in representatives of different strains.

When analyzing the variability of the *MA<sub>asm</sub>* indicator that characterizes the possibility of transverse movement of the carnassial teeth, it should be noted that such swinging movements of the mandible regularly occur during chewing in mustelids, but are significantly limited in amplitude. This phenomenon was previously discovered by Devis (2014) based on X-ray imaging of radioactive labels and tracking the trajectories of their displacement. We use the term “swinging” following Zazhigin and Voyta (2019) who described this phenomenon in shrews (Mammalia, Lipotyphla, Soricidae). However, unlike shrews, the American mink has a fairly rigid symphyseal connection of the mandibles, which does not allow the animals to use them in the same way as insectivorous mammals do when changing the grip of caught prey. It can be assumed from the *MP<sub>asm</sub>* values that the weasel, like nonselected females, as well as representatives of the strain of aggressive individuals of the American mink, are able to change their grip on prey, move, and/or tear it with a low-amplitude transverse displacement of the mandible. Meanwhile, this function is expressed less strongly in nonselected males and representatives of the strain of tame individuals of the American mink, as well as in males of the European mink. The differences between the European mink and the Siberian weasel in the value of the mechanical potential index *MP<sub>asm</sub>* of the carnassial teeth indirectly indicate the specificity of the process of their primarily processing food objects, as well as the peculiarities of their hunting and holding of caught prey. The most remarkable, but still unexplainable, is the manifestation of sharp sex differences in the index in nonselected American minks and at the same time the absence of such differences in the minks of the aggressive and tame strains. Meanwhile, as a result of selection for behavioral traits as a whole for a complex of biomechanical characteristics, the strain of tame animals acquired a significant functional specificity of the mandibles which is not typical for nonselected and Canadian natural minks and which can be considered as a new phenotypic feature reflected in the process of their feeding and defensive behavior.

The differences in the biomechanical potential of the mandibles of the invasive species (the American mink) and the closely related European autochthonous species (the European mink and Siberian weasel) that we identified are very large. Our data are in good agreement with similar quantitative estimates obtained earlier for a pair of the most competitive species—the American and European minks (Gálvez-López et al., 2021; Gálvez-López and Cox, 2022). The authors of this study also found that, according to the indices of mechanical advantage of the canine, the American mink has an advantage in “bite force” over the European mink, but according to the indices of the carnassial teeth, the indicators are on the contrary higher for

the European mink. Moreover, the biomechanical features of the mandible, which differ in these species, indirectly indicate a certain specificity of their diet: the European mink shows a specialization in feeding on aquatic and semi-aquatic animals, while the American mink's prey is mainly terrestrial species. According to the results of dietary studies of these two species conducted in natural conditions in Europe (Sidorovich et al., 2010; Põdra et al., 2013; Law et al., 2018), the validity of the conclusions about their different preferred foods is fully supported by factual data.

We agree with the arguments of the above-mentioned authors about the differences in the diet of American and European minks associated with the shape and function of the mandibles. Based on the data we have presented, it can also be argued that there are a number of common biomechanical characteristics distinguishing the Siberian weasel from the American mink, but bringing it closer to the European mink (see Table 1). Nevertheless, the Siberian weasel also differs significantly from the latter in the biomechanics of mandible functioning (see the *MP<sub>mata</sub>* and *MP<sub>asm</sub>* indices in Table 1), which allows us to talk about the specifics of their hunting and trophic behavior. The American mink is able to win the struggle for existence in most shared biotopes due to exploitative and interference forms of competition, and currently many authors (Maran et al., 2017; Korablyov et al., 2018; Croose et al., 2023) are convinced that, in this regard, the European mink is on the verge of extinction.

## CONCLUSIONS

Our results show that, in a short period of time, i.e., in just 16–17 generations of selection for defensive behavior in American minks under the conditions of the experimental fur farm of the Institute of Cytology and Genetics, there was a significant restructuring of not only the behavior, but also the biomechanical characteristics of the mandibles and dentition in the strains of aggressive and tame animals. The data obtained largely confirm the ideas of Academician Belyaev (Belyaev, 1979a). During selection for defensive behavior, a destabilizing effect occurs, leading to increased variability and general destabilization of the system of correlative connections that have historically formed between developing structures and organs in morphogenesis. This yields new properties and features of animals subjected to selection for behavioral features in the direction of domestication. Analysis of the biomechanical indices of the mandible showed that as a result of selection for defensive behavior the strain of tame minks differs significantly from the strains of nonselected and aggressive individuals not only in skull size (Kharlamova et al., 2000), but also in the morphofunctional indices of the mandibles. In other words, biomechanical functional features were closely related to defensive behavior features and changed in parallel with them. The biomechanical dif-

ferences between males of the strains of aggressive and tame minks were greater in scope than between each of them and the males of the conditionally “ancestral” natural Canadian population. Therefore, the change in the biomechanical characteristics of the mandible of the American mink during long-term (more than 100 years) cage maintenance on fur farms compared to individuals of the conditionally ancestral natural Canadian population of the species turned out to be expressed to a lesser extent than as a result of selection for behavioral traits on the fur farm of the Institute of Cytology and Genetics, Siberian Branch, Russian Academy of Sciences. All this indicates a high rate of reorganization of the morphogenesis and biomechanics of the mandible during selection of American minks for defensive behavior traits.

Of particular interest is the fact of differences between the American mink as an invasive species for Europe and Asia and the autochthonous European mink according to the complex of biomechanical indices we used. As follows from our results of cluster analysis, the interspecific differences in biomechanical characteristics exceed the intraspecific ones. In the process of selection for behavioral traits, the strain of tame minks acquired the greatest biomechanical uniqueness compared to the strains of aggressive and nonselected minks. The obtained data allow us to conclude that the American mink as an invasive species with high phenotypic (morphological and ethological) plasticity, as well as greater bite force and mechanical potential of the canine, is quite capable of displacing some of the autochthonous mustelid species in competition. Nevertheless, judging by the biomechanics of the mandible, the vulnerable autochthonous species—the European mink and Siberian weasel—are still potentially capable of reducing trophic competition with the American mink due to the advantage in using the mechanical potential of the canine and carnassial teeth (MP*adm*, MP*asm*, and MP*ata*), as well as differences in trophic niches and hunting behavior.

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#### ETHICS APPROVAL AND CONSENT TO PARTICIPATE

This study was carried out exclusively on museum collection material originally obtained at the experimental fur farm at the Federal Research Center of the Institute of Cytology and Genetics, Siberian Branch, Russian Academy of Sciences, Novosibirsk. The studies were previously approved by the Ethics Committee of the Institute of Cytology and Genetics, Novosibirsk, and were performed in compliance with the rules for conducting scientific research using experimental animals, which were approved by the order of the Presidium of the USSR Academy of Sciences dated April 2, 1980, no. 12000-496, and the order of the USSR Ministry of Higher Education dated September 13, 1984, no. 2, as well as in accordance with the protocol for the humane treatment of laboratory animals accepted in international practice (Fitzhugh et al., 2008).

#### CONFLICT OF INTEREST

The authors of this work declare that they have no conflicts of interest.

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