

Can Shrews Avoid Competition When Hutchinson's Ecological Rule Is Disobeyed?

A. G. Vasil'ev^{a,*}, Academician V. N. Bol'shakov^a, I. A. Vasil'eva^a, and T. P. Kourova^a

Received January 12, 2023; revised January 20, 2023; accepted January 20, 2023

Abstract—It is established that Hutchinson's ratio of the weights and sizes of the body and foraging organs in similar species is not fully obeyed in shrew species of the genus *Sorex*. Similarity in the centroid size of the mandible was observed in the large species *S. isodon* and *S. araneus*. Differences in the shape of the mandible, which is intensely used in foraging, were detected between the species by geometric morphometrics. Interspecific differences were found in mandibular indices, which reflect trophic specialization and functional features of the mandibles. Shrews can therefore avoid competition even when Hutchinson's rule is violated. The avoidance is due to a transformation and specialization of the mandible and changes in prey capture methods and diet, rather than to changes in size. Hutchinson's ecological rule is thus not mandatory, but is only one of the conditions for reducing competition between closely related species.

Keywords: Hutchinson's ratio, *Sorex*, specialization, mandible, geometric morphometrics

DOI: 10.1134/S0012496623700333

Hutchinson's ecological ratio [1] has been known for taxonomically related species sets (taxocenes according to terminology accepted in our studies [2]) from the mid-20th century. Hutchinson has established empirically that a ratio of approximately 1.28–1.30 is observed between the average sizes of the body and foraging organs in closely related sympatric species that are similar in size and belong to the same genus. The size ratio has been both confirmed and disconfirmed many times (see [3]) and is still of interest to study. Likely mechanisms assumed for the phenomenon are based on the ideas that species are sorted and selected from their regional pool and that a shift in the sizes of the body and foraging organs should reduce competition between sympatric species. In the 21st century, the issue has been studied in Galapagos finches by morphometry [4] and salamanders of the genus *Plethodon* by geometric morphometrics [5]. Hutchinson's rule, that is, the problem of a fixed size ratio between closely related species in a community is still considered unsolved.

Geometric morphometrics methods [6, 7] make it possible to separate the components of size variation (by centroid sizes (CSs)) and shape variation (by Procrustes coordinates of objects) and can be used to check Hutchinson's rule with a model of the mandible as a foraging organ in sympatric species of the shrew

taxocene. Elements of the functional ecology of species can be compared by comparing samples with respect to morphofunctional mandibular indices [8, 9].

The objectives of this work were to check Hutchinson's rule by comparing the size and shape of mandibular arches in sympatric shrew species of the genus *Sorex* from the Visim Nature Reserve (the Central Urals) and to indirectly estimate their trophic specialization with the use of geometric morphometrics methods and morphofunctional mandibular indices.

We examined the collection series of skulls that belonged to current-year young of four sympatric *Sorex* species and were collected in the Visim Nature Reserve (the Central Urals) in the late 20th century (in July and August). The species included the taiga shrew *S. isodon* Turov, 1924 ($n = 28$, 1986), common shrew *S. araneus* Linnaeus, 1758 ($n = 50$, 1986), Laxmann's shrew *S. caecutiens* Laxmann, 1788 ($n = 45$, 1986–1987), and pygmy shrew *S. minutus* Linnaeus, 1766 ($n = 16$, 1986–1987, 1989–1992).

Images of shrew mandibles were taken with a desktop scanner at a magnification of 1200 dpi. To analyze the size and shape variation of the mandible in shrews, 20 landmarks were identified on the buccal side of the right mandible (Fig. 1).

Superimposition of landmark configurations was performed via generalized Procrustes analysis (GPA) [6] with calculation of the Procrustes coordinates. Mandible size comparisons were carried out with respect to CS (mm) [6]. The Procrustes coordinates were used to perform canonical sample analysis with calculation of the matrix of generalized Mahalanobis

^aInstitute of Plant and Animal Ecology, Ural Branch, Russian Academy of Sciences, Yekaterinburg, Russia

*e-mail: vag@ipae.uran.ru

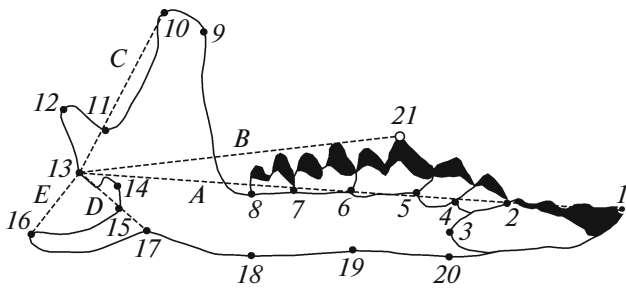


Fig. 1. Scheme of the main landmarks (1–20) and lengths (A, B, C, D, and E) used to calculate the mandibular indices on the buccal side of the *S. araneus* mandible. Additional landmark 21 was used only to calculate length B.

distances (D). Pairwise differences were evaluated by Tukey's pairwise post-hoc *Q*-test.

Mandibular lengths A, B, C, D, and E (Fig. 1) were used to calculate the following morphofunctional mandibular indices according to published equations [8]: temporal-incisor $TI = C/A$, temporal-molar $TM = C/B$, masseter-incisor $MI = D/A$, masseter-molar $MM = D/B$, and angular-masseter $AM = E/D$.

Gender differences in CS were low and nonsignificant in current-year youths of each of the species, and the gender was consequently disregarded in further comparisons. Table 1 summarizes the results of comparisons of mean CSs, which indirectly characterize the mandible sizes in the four sympatric shrew species. The mean mandible CSs of the two larger species, *S. isodon* and *S. araneus*, were similar to each other and showed no significant difference ($Q = 1.197$; $p = 0.832$). However, these CSs were significantly higher than the CSs of *S. caecutiens* and *S. minutus* ($p < 0.0001$). The mandible CSs *S. caecutiens* and *S. minutus* also significantly differed from each other ($Q = 9.088$; $p < 0.0001$). Levene's test did not detect a violation of conditions for equality of variances in CS. Multiple comparisons by one-way ANOVA showed significant interspecific differences in CS ($F = 243.8$; d.f. = 3, 135; $p < 0.0001$).

Hutchinson's ratio was obtained as a ratio between mean CS values and was 1.01 between *S. isodon* and

S. araneus and 1.11 between *S. caecutiens* and *S. minutus*, suggesting a high likelihood of competition in the species pairs (Table 1). However, Hutchinson's rule was obeyed in comparisons between the larger and smaller shrews (Table 1). Thus, Hutchinson's rule was not uniformly confirmed in all cases, but was obeyed only between the larger and smaller species.

MacArthur and Levins [10] have proposed a well-known model, where the degree ρ of niche differentiation between two species is obtained as a ratio of the difference d in mean common resource to the common standard deviation w and should be $\rho = d/w > 1$ for the species to coexist. A minimal allowable ratio d/w between the species corresponds to the limiting similarity ratio $\rho = 1.56$, at which the species are theoretically capable of coexistence. Competition is assumed to occur at $d/w < 1$ and is unlikely at $d/w > 3$ according to Hutchinson's rule.

As follows from Table 1, both Hutchinson's rule and niche similarity ratio (ρ) with respect to CSs and their variation are not obeyed between the two larger species (*S. isodon* and *S. araneus*) and between the two smaller species (*S. caecutiens* and *S. minutus*), indicating indirectly that competition is possible within each species pair. However, both of the conditions are well obeyed between the larger and smaller species (Table 1).

The results of the canonical analysis are summarized in Fig. 2. As is seen, all interspecific differences in mandible shape are great and arranged along the first canonical variate (CV1) axis from an ordinate scatter ellipse of the smallest species *S. minutus*, which is in a region of negative CV1 values, to ellipses of the largest species *S. araneus* and *S. isodon*. The *S. araneus* sample is displaced to the greatest extent along the second canonical variate (CV2) axis, deviating from *S. isodon* and the other species. The *S. caecutiens* sample deviates from the other species into a region of positive values along the CV3 axis.

A comparison of generalized Mahalanobis distances between the samples of the shrew species (Table 2) makes it possible to conclude that the *S. isodon* and *S. araneus* mandibles are similar in size, but substantially distant in shape ($D = 10.26$; $p < 0.0001$). The *S. araneus* and *S. caecutiens* mandibles are somewhat

Table 1. Mean centroid size (CS) of the mandible and its standard error (SE) in the four *Sorex* species, Hutchinson's ratios by mandible CS (triangular matrix below the diagonal), and degree ρ of niche differentiation in species pairs (triangular matrix above the diagonal, ρ is a ratio of the difference d in CS to the common standard deviation w)

<i>Sorex</i> species	Centroid size CS \pm SE (n)	<i>isodon</i>	<i>araneus</i>	<i>caecutiens</i>	<i>minutus</i>
<i>isodon</i>	17.39 \pm 0.15 (28)	—	0.18*	2.62	5.18
<i>araneus</i>	17.21 \pm 0.09 (50)	1.01*	—	2.63	5.65
<i>caecutiens</i>	14.01 \pm 0.15 (45)	1.24	1.23	—	1.20*
<i>minutus</i>	12.64 \pm 0.12 (16)	1.38	1.36	1.11*	—

* Competition between species is highly likely because Hutchinson's rule is not obeyed or the degree of differentiation of the species niches (ρ) is not high enough.

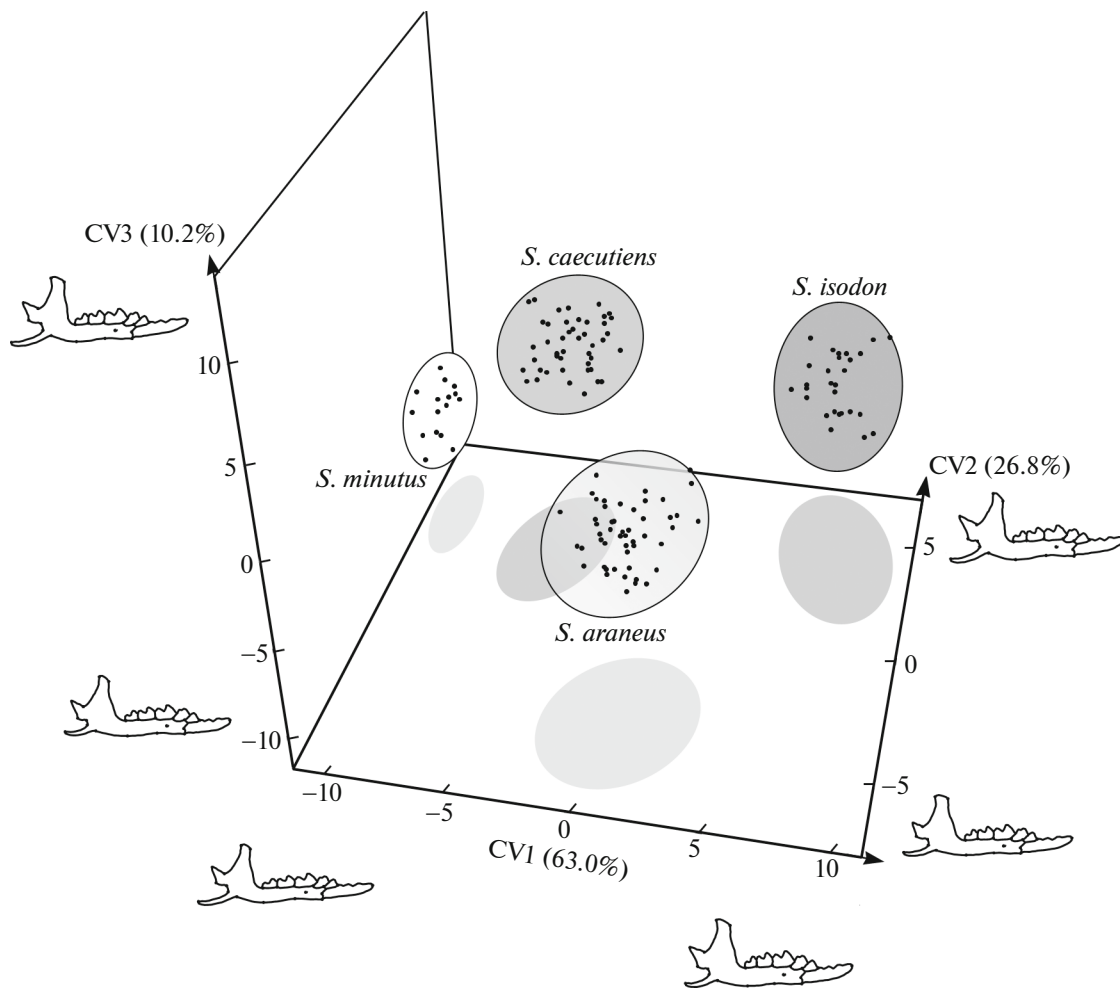


Fig. 2. Canonical analysis of the Procrustes coordinates of the mandible in the four sympatric species of the *Sorex* shrew taxocene of the Visim Nature Reserve. The samples are shown in the morphospace of canonical variates (CV1–CV3). Ellipses characterize the variation of mandible shape in the shrew samples and characterize 95% of the ordinate variance in individuals. The portion (%) of between-group variance is indicated for each canonical variate, and mandible outlines corresponding to maximal and minimal values are shown along the respective axes.

closer in shape ($D = 7.49$; $p < 0.0001$), but significantly differ in size without violating Hutchinson's rule. Thus, the similarity of the species in mandible size is compensated for by their differences in mandible configuration. The samples of all species are substantially separated in the morphospace, and their separation reflects the species specificity of the mandible shape, which is associated with trophic specialization.

Because differences in the function of the mandibular osteomuscular system must accompany differences in mandible shape, the morphofunctional indices were estimated for the species (Table 3). Interspecific differences in mandibular indices were great and, in the majority of cases, significant. While the mandible size was similar in *S. isodon* and *S. araneus*, two indices, TI and TM , were found to differ significantly;

Table 2. Generalized Mahalanobis distances (D) calculated from the Procrustes coordinates to characterize the variation in mandible shape between the sympatric *Sorex* shrew species from the Visim Nature Reserve (significance level p values are shown in the upper triangular matrix)

Species	<i>S. isodon</i>	<i>S. araneus</i>	<i>S. caecutiens</i>	<i>S. minutus</i>
<i>S. isodon</i>	0	$p < 0.0001$	$p < 0.0001$	$p < 0.0001$
<i>S. araneus</i>	10.26	0	$p < 0.0001$	$p < 0.0001$
<i>S. caecutiens</i>	11.30	7.49	0	$p < 0.0001$
<i>S. minutus</i>	17.29	13.06	9.24	0

Table 3. Comparison of the mean mandibular indices (\pm SE) for the four sympatric *Sorex* shrew species from the Visim Nature Reserve (Central Urals)

Mandibular index	<i>Sorex</i> species			
	<i>isodon</i> (<i>n</i> = 28)	<i>araneus</i> (<i>n</i> = 50)	<i>caecutiens</i> (<i>n</i> = 45)	<i>minutus</i> (<i>n</i> = 16)
<i>TI</i>	0.328 \pm 0.002	0.312 \pm 0.001	0.305 \pm 0.001	0.296 \pm 0.002
<i>TM</i>	0.565 \pm 0.003	0.538 \pm 0.002	0.524 \pm 0.002	0.498 \pm 0.004
<i>MI</i>	0.159 \pm 0.001	0.162 \pm 0.001	0.165 \pm 0.001	0.157 \pm 0.001
<i>MM</i>	0.274 \pm 0.002	0.279 \pm 0.001	0.284 \pm 0.002	0.264 \pm 0.002
<i>AM</i>	0.894 \pm 0.011	0.882 \pm 0.007	0.995 \pm 0.008	1.013 \pm 0.014

i.e., the longitudinal force exerted during prey cutting significantly differs between the species. However, the species did not differ in gnawing (the *MM* index) and horizontal swinging of the left and right mandible arches (according to Zazhigin and Voyta [11]) when grabbing their prey anew (the *AM* index). The latter is associated with a special type of capturing prey during foraging and is distinct in the smaller shrews *S. caecutiens* and *S. minutus* (Table 3). Interestingly, the large species *S. isodon* is similar in *MI* to the smallest species *S. minutus* ($t = 1.4$; $p > 0.05$); i.e., incisors are employed to a minor extent in gnawing the two species, unlike in *S. caecutiens* and *S. araneus*.

Thus, the differences in mandible shape and mandibular indices make it possible to explain how competition is avoided between similarly sized shrews, that is, between the larger species *S. isodon* and *S. araneus* and between the smaller species *S. caecutiens* and *S. minutus*. The avoidance is due to trophic specialization based on transformation of the osteomuscular system of the mandible. The results indirectly point to a specificity in preferable diet with respect to prey size and the method to capture prey during foraging; this specificity also helps to avoid competition. Biotope selectivity further reduces competition between *S. isodon* and *S. araneus* [12].

To summarize, competition can be avoided in shrews even when Hutchinson's rule is disobeyed. Rather than being related to differences in size, this is due to differentiation in mandible shape, functional specialization of the mandible, methods to capture prey, and mechanical composition of the diet. Hutchinson's ecological rule is therefore not a universal mandatory condition, but rather one of the conditions that help to reduce competition between close species, because structural and functional features of the species play a greater role in determining their successful syntopy as compared with their size differences.

ACKNOWLEDGMENTS

We are grateful to staff of the Museum at the Institute of Plant and Animal Ecology for kindly providing material for the study.

FUNDING

This work was supported by a state contract with the Institute of Plant and Animal Ecology (project no. 122021000091-2).

COMPLIANCE WITH ETHICAL STANDARDS

Conflict of interests. The authors declare that they have no conflicts of interest.

This article does not contain any experimental studies involving animals or human subjects performed by any of the authors.

REFERENCES

- Hutchinson, G.E., Homage to Santa Rosalia, or why are there so many kinds of animals?, *Am. Nat.*, 1959, vol. 93, pp. 145–159.
- Hutchinson, G.E., *Treatise on Limnology*, vol. II: *Introduction to lake biology and the limnoplankton*, New York: Wiley, 1967.
- Lewin, R., Santa Rosalia was a goat, *Science*, 1983, vol. 221, pp. 636–639.
- Grant, P.R. and Grant, B.R., Evolution of character displacement in Darwin's finches, *Science*, 2006, vol. 313, pp. 224–226.
- Adams, D.C., Parallel evolution of character displacement driven by competitive selection in terrestrial salamanders, *BMC Evol. Biol.*, 2010, vol. 10, no. 72, pp. 1–10.
- Rohlf, F.J. and Slice, D., Extension of the Procrustes method for the optimal superimposition of landmarks, *Syst. Zool.*, 1990, vol. 39, no. 1, pp. 40–59.
- Zelditch, M.L., Swiderski, D.L., Sheets, H.D., et al., *Geometric Morphometrics for Biologists: A Primer*, New York: Elsevier Acad. Press, 2004.
- Anderson, Ph.S.L., Renaud, S., and Rayfield, E.J., Adaptive plasticity in the mouse mandible, *BMC Evol. Biol.*, 2014, vol. 14, pp. 85–93.

9. Vasil'ev, A.G., Vasil'eva, I.A., Kourova, T.P., et al., Outpost population of the white-bellied shrew at the northern border of the range in the Orenburg region, *Fauna Urala Sib.*, 2022, no. 2, pp. 87–108.
10. MacArthur, R. and Levins, R., The limiting similarity, convergence, and divergence of coexisting species, *Am. Nat.*, 1967, vol. 101, no. 921, pp. 377–385.
11. Zazhigin, V.S. and Voyta, L.L., Northern Asian Pliocene–Pleistocene beremendiin shrews (Mammalia, Lipotyphla, Soricidae): a description of material from Russia (Siberia), Kazakhstan, and Mongolia and the paleobiology of *Beremendia*, *J. Paleontol.*, 2019, vol. 93, no. 6, pp. 1234–1257.
12. Shvarts, E.A., Demin, D.V., and Zamolodchikov, D.G., *Ekologiya soobshchestv melkikh mlekopitayushchikh lesov umerennogo poyasa (na primere Valdaiskoi vozvyshechnosti)* (The Ecology of Small Mammal Communities in Temperate Forests: The Example of the Valdai Upland), Moscow: Nauka, 1992.

Translated by T. Tkacheva