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Lifespans of Fur Color Morphs in Polymorphic Populations of the Mole Vole and the Hypothesis of Adaptive Polymorphism

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Abstract—Different lifespans were for the first time demonstrated for three (brown, bicolor, and black) fur color morphs in ten mole vole populations of the Volga, Ural, and Trans-Ural regions. With the longest lifespan of 5 years in the species, morphs that numerically dominate in a population can live 1–4 years longer than accompanying morphs. Spearman's correlation coefficient between the longest lifespan of the morphs and their proportion in the population was $R_{sp} = 0.81$ ($p < 0.0001$). A number of morphological and functional features were identified in the color morphs. The findings are of general biological significance, confirming the hypothesis of adaptive polymorphism. Evolutionary and ecological mechanisms whereby selective advantages develop in morphs (as probable ecomorphs) are possible to evaluate using the morphs as a natural model of the initial step of sympatric form development in different parts of the range.

Keywords: adaptive polymorphism, lifespan, geographical variability, fur color, mole vole

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The problem of how adaptive polymorphism originates and is maintained in populations has been discussed for many years after Timofeev-Ressovsky and Svirezhev [1, 2] performed their pioneering studies in color morphs of the two-spotted ladybug *Adalia bipunctata*. Interest in the problem of polymorphic populations was rekindled as color polymorphism was discovered in the European hamster in northern Bashkiria [3], the phenomenon of industrial melanism observed in the peppered moth *Biston betularia* in the United Kingdom [4], and adaptive color polymorphism detected in several tropical mollusks [5, 6]. Molecular genetic methods have recently come to be used with success to study the adaptive processes in populations [7, 8]. However, adaptive polymorphism of phenotypic traits and animal coat color in particular is still is still important to study because such traits may mark the development of new ecomorphs that promote rapid adaptive changes in population structure in changing environmental conditions [8].

The objective of this study was to check the hypothesis of adaptive polymorphism by estimating the lifespan in model polymorphic populations for color morphs of the mole vole *Ellobius talpinus* (Pallas, 1770) from different parts of the species range with due regard to their morphological and functional features.

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Mole voles were collected from different parts of the species range from the Volga region to the southern Trans-Urals. Ten populations were examined: 1, Samara (Samarksaya Luka nature reserve, Samara Oblast, $n = 35$); 2, Totskoe (region of the Totskoe station, Orenburg Oblast, $n = 36$); Kuvandyk (region of the town of Kuvandyk, Orenburg Oblast, $n = 137$); 4, Burangulovo (region of the village of Burangulovo, Bashkortostan Republic, $n = 49$); 5, Troitsk (town of Troitsk, Chelyabinsk Oblast, $n = 51$); 6, Kunashak (village of Kunashak, Chelyabinsk Oblast, $n = 57$); 7, Zverinogolovskoe (village of Zverinogolovskoe, Kurgan Oblast, $n = 26$); 8, Kurtamysh (village of Kurtamysh, Kurgan Oblast, $n = 113$); 9, Naurzum (Naurzum Nature Reserve, Kazakhstan, $n = 50$); and 10, Omsk (village of Moskalenki, Omsk Oblast, $n = 50$). In total 604, mole voles were examined.

The proportion of the three—brown, black (melanistic), and transitional bicolor—morphs was estimated in each population. The mole age was determined according to Evdokimov [9], based on the relative root length of the first cheek tooth of the mandible. The following six age groups were isolated: 0+, current year young; 1+, one-year-olds; 2+, two-year-olds; 3+, three-year-olds; 4+, four-year-olds; and 5+, five-year-olds. The proportion (%) and the greatest individual age were estimated for each morph in each population. The age distributions and proportions of the morphs in the populations are summarized in Table 1. The mole vole lifespan does not exceed 62 months (5 years) according to an earlier study in a breeding facility [10].

Table 1. Age distribution of the three color morphs and their proportion (%) in mole vole populations (morphs that numerically dominate in the respective populations are in bold)

Population	Fur color morph	Age group						Total voles (%)
		0+	1+	2+	3+	4+	5+	
Samara (Samara oblast, Russia)	Brown	**14**	**3**	**4**	**2**	**2**	**1**	**26 (74.3)**
	Bicolor	5	2	0	0	0	0	7 (20.0)
	Black	2	0	0	0	0	0	2 (5.7)
Totskoe (Orenburg oblast, Russia)	Brown	0	0	0	0	0	0	0 (0)
	Bicolor	**27**	**7**	**2**	**0**	**0**	**0**	**36 (100.0)**
	Black	0	0	0	0	0	0	0 (0)
Kuvandyk (Orenburg oblast, Russia)	Brown	**52**	**37**	**29**	**10**	**1**	**0**	**129 (94.2)**
	Bicolor	7	0	0	0	0	0	7 (5.1)
	Black	1	0	0	0	0	0	1 (0.7)
Burangulovo (Bashkortostan, Russia)	Brown	1	1	0	0	0	0	2 (4.1)
	Bicolor	5	2	6	1	0	0	14 (28.6)
	Black	**9**	**12**	**10**	**2**	**0**	**0**	**33 (67.3)**
Troitsk (Chelyabinsk oblast, Russia)	Brown	7	0	1	0	0	0	8 (15.4)
	Bicolor	12	1	5	0	0	0	18 (34.6)
	Black	**21**	**3**	**1**	**0**	**1**	**0**	**26 (50.0)**
Kunashak (Chelyabinsk oblast, Russia)	Brown	0	0	0	0	0	0	0 (0)
	Bicolor	0	0	0	0	0	0	0 (0)
	Black	**39**	**8**	**5**	**3**	**1**	**1**	**57 (100.0)**
Zverinogolovskoe (Kurgan oblast, Russia)	Brown	**13**	**1**	**4**	**1**	**0**	**0**	**19 (73.1)**
	Bicolor	0	0	0	0	0	0	0 (0)
	Black	4	2	1	0	0	0	7 (26.9)
Kurtamysh (Kurgan oblast, Russia)	Brown	4	6	13	9	2	0	34 (30.1)
	Bicolor	12	3	2	3	0	0	20 (17.7)
	Black	**28**	**10**	**11**	**7**	**2**	**1**	**59 (52.2)**
Omsk (Omsk oblast, Russia)	Brown	10	1	1	1	0	0	13 (25.5)
	Bicolor	**16**	**2**	**5**	**1**	**1**	0	**25 (49.0)**
	Black	5	2	5	1	0	0	13 (25.5)
Naurzum (Naurzum Nature Reserve, Kazakhstan)	Brown	**19**	**3**	**2**	**7**	**1**	**0**	**32 (100.0)**
	Bicolor	0	0	0	0	0	0	0 (0)
	Black	0	0	0	0	0	0	0 (0)

As is seen from Table 1, the brown morph dominated in two southern (Samara and Kuvandyk) polymorphic populations. Bicolor mole voles were detected among current-year young (0+) and one-year-olds (1+), while black mole voles were found only among current-year young (0+). Brown mole voles usually reached 4–5 years of age in these populations. All mole voles of the Totskoe population represented the transitional bicolor morph and were no older than 3 years. In the Burangulovo population, bicolor and black mole voles prevailed and reached 3 years of age, while mole voles of the accompanying brown morph were rare and lived only to 1 year of age. Only brown and black mole voles were detected in the Zverinogolovskoe population. The lifespan of the former was 1 year longer, reaching 3 years. Bicolor mole voles were not found, suggesting a certain likelihood of assortative matings for brown and black mole voles in the population. In the Kurtamysh population, black mole voles prevailed and reached 5 years of age, brown mole voles reached 4 years of age, and bicolor mole volves were no older than 3 throughout the region. Only melanistic individuals were found and reached 5 years of age in the Kunashak population of Chelyabinsk Oblast, which is in the northern part of the species range. Only brown mole voles were found and reached 4 years of age in the Naurzum population (Naurzum Nature Reserve) in the southern Trans-

Ural region (Kostanai Oblast, Kazakhstan). We think that the northernmost (Kunashak) and southernmost (Naurzum) populations were monomorphic in fur color as a result of fixation of the respective morphs, which are the best fit to the local conditions and have the greatest lifespan.

Spearman's rank correlation coefficient between the longest lifespan (maximal age in years) of a particular morph and its portion (%) in a population R_{sp} = 0.81 ($p < 0.0001$).

Thus, we observed that mole voles of the predominant morph show not only the greatest portion in a population, but also a greater lifespan as compared with mole voles of the accompanying (rarer) morphs. Their greater lifespan directly indicates that the color morphs and associated phenotypic traits are adaptive in mole voles. The major morph that numerically dominates in a particular population is probably the most fit to the local conditions. The accompanying morphs are probably reserve genotypes, which might be used to maintain the population size in abnormal years with different weather conditions, when the numerically dominant morph is temporally unfit. If the abnormal ecological climatic trend grows stronger or is preserved for a few years, the best-fit color morph will increase in numbers in the population. Thus, the portion and lifespan will increase in the morph that is currently a reserve morph, while decreasing in the currently dominant morph. It is possible to assume that different adaptive properties are characteristic of homonymous morphs from different parts of the species range. Moreover, dominance and adaptive properties of a particular morph may change as local conditions change with time.

A comparison of our original and literature data on the proportions of color morphs in various mole vole populations confirmed that the portion of melanistic individuals increases in the South Urals at the northern boundary of the species range. In good agreement with our finding, Gershenson [3] has detected a similar increase in spreading and portion of melanistic individuals in European hamster populations of the northern forest-steppe zone. Evdokimov et al. [11] have observed that the portion of the black morph increased in a directional manner, while the portion of the brown morph decreased from 1985 to 1999 in the Kurtamysh mole vole population, which is polymorphic in fur color. Spearman' rank correlation coefficient between the portions of the brown and black morphs was $r = -0.90$ ($p < 0.0001$) over that period, while correlation coefficients between the portions of these morphs and the portion of the bicolor morph were low and statistically nonsignificant. An analysis of the time series of observations showed that the portion of the black morph significantly linearly correlates with average October temperature ($r = 0.68$, $p < 0.0049$) and negatively correlates with the portion of the brown morph ($r = -0.71$, $p < 0.0029$) [11]. Similar results were obtained when total June precipitation was tested for correlation with the portions of the black ($r = 0.67$, $p < 0.0064$) and brown ($r = -0.72$, $p < 0.0023$) morphs. Thus, fur color polymorphism in mole vole proved to be associated with total moisture content in the habitat in early summer and air temperature in autumn.

Cheprakov et al. [12] have performed a genetic analysis and demonstrated that expression of color morphs is genetically determined in mole vole, giving grounds to assume that melanistic individuals are positively selected when environmental humidity increases [11]. Genetic and possible epigenetic factors in the phenomenon are still unclear and need further experimental investigation.

An analysis of the morphological and functional specifics of the mandible has been performed in the color morphs from monomorphic and polymorphic mole vole populations. Differences in mandible shape between morphs were clearly detected in both comparisons of different populations and comparisons of individuals within the same polymorphic population [13]. The mandible shapes observed in polymorphic populations fail to ensure the same force in food processing as in specialized monomorphic populations. However, because food processing functions are redistributed between the morphs in polymorphic populations, their joint trophic population potential increases and the development becomes more stable [13].

Our findings agree well with the hypothesis of adaptive polymorphism as far as the fur color morphs in mole vole are concerned. The morphs are therefore possible to consider as models of probable ecomorphs [8] in different parts of the range. Further analysis of the phenomenon by geometric morphometry will help to identify the functional specifics that provide the morphs with selective advantages in local populations and to better understand the evolutionary ecological mechanism of adaptive polymorphism, which is of general biological significance as a special model of the initial step of sympatric speciation.

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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.

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