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SHORT COMMUNICATIONS

Morphological Differentiation of Tits (*Parus* L.) in the Trans-Ural Forest-Steppe and Hutchinson's Rule

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Ecological niche differentiation in cohabitant closely related species is one of the most interesting problems of contemporary ecology [1, 2]. Jointly nesting tits of the genus *Parus* L. have become a popular object of such studies; they form mixed flocks, which can also include other species [3–9].

In terms of ecology, the tit community is, undoubtedly, a guild, i.e., a group of species that use a food resource in a functionally similar way [2]. The guild can consist of related species (as in the case under consideration) or species of different systematic groups [1]. The guild serves as a scene of the most intensive interspecific relationships in the community. Competitive relationships arising in the guild lead to various consequences and are focused on niche separation and competition reduction.

A guild consisting of taxonomically similar species is a particular case. Species of the same genus compete with each other more strongly due to their high morphological and, consequently, functional similarity; accordingly, all the processes in their relations are more clearly defined. In addition, this type of community acts as a kind of unified functional block with respect to other components of the biocenosis.

One of the simplest and most effective ways to differentiate the ecological niches of coexisting species is their morphological differentiation (in particular, size differentiation). As shown by G. Hutchinson (1959, cit. by [2]), the average body size ratio in species of the same genus that belong to the same community and use the same resource is about 1.3 (from 1.1 to 1.4) and the respective body weight ratio is 2. This empirical pattern, termed "Hutchinson's rule," was confirmed by observations on many groups of living organisms. Vivid examples of this rule were obtained from studying birds. Thus, the beak ratio length in cohabiting species of the same genus was tested in representatives of 46 families from temperate and tropical regions: on the average, the rule was met in all areas [2, 10]. At the same time, its use in studies of multispecific communities has been frequently criticized [see 2]. It is currently obvious that this rule does not apply to all organisms and ecological situations [2, 10]. Therefore, it is of particular interest to study the size differentiation of closely related species in different communities and reveal cases meeting Hutchinson's rule.

It is known that the trophic niches of tits were significantly separated, which has now become a classic example: different tit species collect food on different tree species, in different forest layers, and in different parts of the tree crown [3–5, 11–14]. In addition, their size differentiation is also noted: small species collect insects on thin peripheral branches, while larger ones collect insects on thick branches closer to the trunk; however, actual data are usually not given.

The purpose of our research was to analyze the size characteristics of tit species of the genus *Parus* L. in the forest-steppe Trans-Urals and test their correspondence with Hutchinson's rule.

The wing length and body weight of five tit species (willow tit *P. montanus*, coal tit *P. ater*, blue tit *P. caeruleus*, azure tit *P. cyanus*, and great tit *P. major*) were measured during selective catches of small shrub species of birds during autumn migrations. Birds were caught using mist nets with a mesh of 14 mm and a length of 7 and 10 m in August–October 2013 and 2014 and in July–September 2016 in Ketovsky, Shadrinsky, and Chastoozersky districts of the Kurgan oblast, respectively [15–17]. A total of 1475 individuals were caught; the wing length was measured for 1212 individuals and body weight was measured for 630 individuals. The data were statistically processed using analyses of variance (ANOVA and MANOVA) and post-hoc analysis. All calculations were performed in Statistica 6.0 (StatSoft Ink., 1984–2001) and Microsoft Excel 2003.

Figure 1 shows the size characteristics of captured tit individuals. It can be seen that four species (coal tit, willow tit, azure tit, and great tit) are almost on the same line with respect to these characteristics and one species (blue tit) is slightly alongside adjacent species

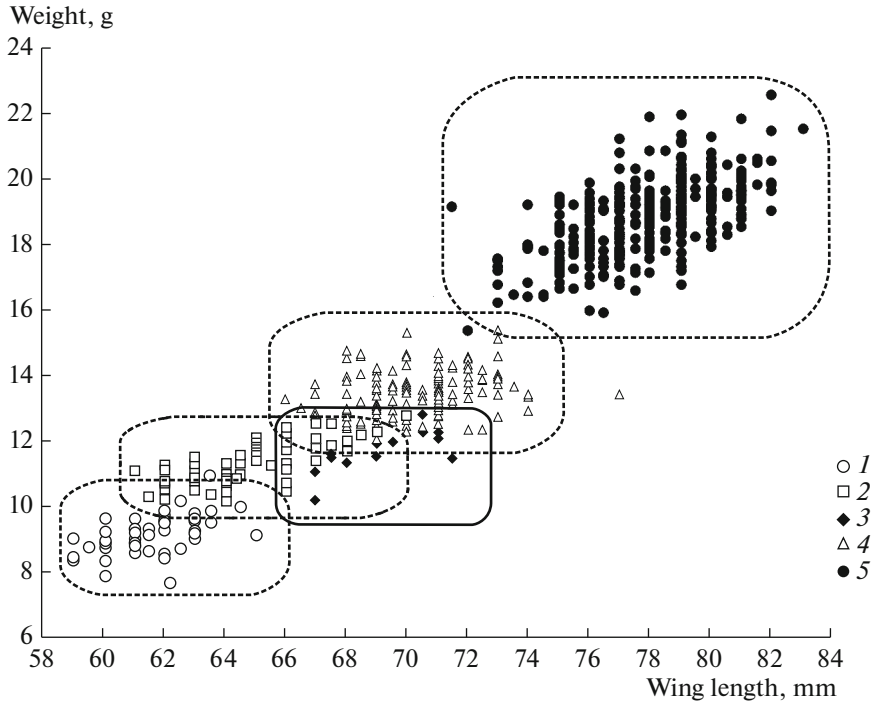

Fig. 1. Size–weight structure of the tit community according to the data for 2013, 2014, and 2016: (*1*) coal tit, (*2*) willow tit, (*3*) blue tit, (*4*) azure tit, and (*5*) great tit. The solid line marks the range of azure tit.

(willow tit and azure tit) rather than between them. The average values of the wing length and body weight of the studied species are given in Table 1 and average values of the size ratio of species pairs are given in Table 2.

Two-way analysis of variance (MANOVA) did not reveal a significant effect of the study year; therefore, we combined samples from different years. One-way analysis of variance (ANOVA) showed a high significance of differences between tits of different species with respect to their wing length ($df = 4$, $F = 2412.4$, $p < 0.001$) and body weight ($df = 4$, $F = 2182.74$, $p < 0.001$). Pairwise (post-hoc) comparison by the Tukey method showed that significant differences between species were absent only in one case: willow tit and blue tit did not differ in their body weight ($p = 0.606$), while the other differences were highly significant ($p < 0.001$).

If we do not consider the blue tit, which penetrated into the Trans-Urals only in the 21st century (see below), the studied guild of tits is quite consistent with Hutchinson's rule. The ratio of the average wing length is 1.05–1.11 for the neighboring pairs of species, which is slightly lower than that predicted by Hutchinson's rule. In our view, this can be explained by the fact that we use the wing length rather than the absolute size of birds (which cannot be easily estimated) or the size of food-procuring structures. The wing length is a variable trait that is allometrically and, possibly, nonlinearly connected with the total body size. In addition, the ratio of this trait is slightly higher for these species in a wider region (Urals, Trans-Urals, and Western Siberia, according to [18]): 1.06–1.13. It should be noted that the beak length ratio in the examples given by P. Giller [2] was also 1.3 times lower for tropical birds (from 1 to 1.7, mean 1.15).

Table 1. Size–weight characteristics of tits, $M \pm m$ (n)

Species	Wing length, mm			Body weight, g	
	2013	2014	2016	2013	2016
Coal tit	61.75 ± 0.32 (16)	60.36 ± 0.36 (11)	61.42 ± 0.20 (45)	9.73 ± 0.20 (9)	9.08 ± 0.07 (45)
Willow tit	64.54 ± 0.54 (13)	64.83 ± 0.23 (54)	64.63 ± 0.23 (67)	11.20 ± 0.18 (12)	11.33 ± 0.10 (51)
Blue tit	69.00 ± 1.05 (5)	68.58 ± 0.24 (72)	68.53 ± 0.35 (19)	11.98 ± 0.29 (5)	11.56 ± 0.19 (15)
Azure tit	70.48 ± 0.59 (21)	70.30 ± 0.21 (56)	70.06 ± 0.11 (242)	13.41 ± 0.13 (13)	13.40 ± 0.06 (143)
Great tit	77.71 ± 0.18 (144)	78.05 ± 0.17 (171)	77.75 ± 0.13 (276)	18.81 ± 0.12 (89)	18.91 ± 0.07 (248)

Table 2. Wing length to body weight ratio in tit species most similar in size

Pairs of species	Wing length				Body length		
	2013	2014	2016	according to [18]	2013	2016	according to [18]
Willow tit/coal tit	1.05	1.07	1.05	1.13	1.15	1.25	1.28
Blue tit/willow tit	1.07	1.06	1.06	1.06	1.07	1.02	1.0
Azure tit/blue tit	1.02	1.03	1.02	1.01	1.12	1.16	1.13
Azure tit/willow tit	1.09	1.08	1.08	1.06	1.20	1.18	1.13
Great tit/azure tit	1.10	1.11	1.11	1.13	1.40	1.41	1.28

Table 3. Size–weight characteristics, $M \pm m$ (n), and their ratio in males and females of great tit

Species	Wing length, mm			Body weight, g	
	2013	2014	2016	2013	2016
Males	79.49 ± 0.20 (66)	79.77 ± 0.19 (78)	79.28 ± 0.13 (130)	19.42 ± 0.13 (45)	19.39 ± 0.09 (119)
Females	76.21 ± 0.15 (77)	76.62 ± 0.16 (79)	76.26 ± 0.14 (119)	18.15 ± 0.14 (43)	18.27 ± 0.11 (105)
Ratio	1.04	1.04	1.04	1.07	1.06

According to our data, the body weight ratio is 1.15–1.41 for neighboring tit species (1.13–1.28 according to [18]), which is also less than 2, as could be expected according to Hutchinson's rule. In the Giller example [2] with Papuan mountain pigeons, this ratio was 1.33 to 2.73, which is quite close to our values.

However, it should be emphasized that the size characteristics, considering both traits, only partially coincide for the studied tit species or are completely different for some of them, which indicates a clear differentiation between the morphological traits.

There is a view that sexual dimorphism in some species is also determined by the reduction of intraspecific food competition (Schoener, 1977, cit. by [10]). The size distributions proved to be bimodal for all tit species that we studied; however, their sex can be reliably determined only for the great tit. The size characteristics of males and females of this species are given in Table 3. It can be seen that the intersexual differences in great tits are significantly lower than the differences between tit species and considerably lower than those predicted by Hutchinson's rule. Therefore, the sexual dimorphism of great tits is determined by other factors (probably, sexual selection) rather than by food competition.

Hutchinson's rule and closely related ideas of limiting similarity are in line with the problems of ecological niche dimension and differential overlap, which, in turn, is one of the central areas of studying the organization of multispecific communities and principles of ecosystem functioning [1, 2]. Hutchinson's rule is usually associated with a food resource (most often with the size of food items).

One of the most striking illustrations of Hutchinson's rule is the size differentiation of Papuan mountain pigeons. Differences between species of different sizes are noted, firstly, in the preferred size of consumed fruits and, secondly, in the distribution on different parts of branches during feeding [2]. A similar pattern is characteristic of tit species. They can be differentiated with respect to food search areas: on different parts of a crown, along thin/thick branches, and closer or farther from the trunk [3–6, 9, 12]. Several studies also showed the difference between different tit species in their food items, including the size of food items [9, 19–23]. This is an important point, since the differences in the size of preferred food items are closely related to the difference in the size of the species themselves, in particular, their food-procuring structures [2]. At the same time, all authors note that the food spectra of different tit species can significantly overlap. Presumably, the slight deviation of their weight and size ratio from Hutchinson's rule is connected not so much with the size of food items as with differences in preferred sites for food search.

The compliance of a multi-species community with the Hutchinson rule is actually a consequence of competition for one resource, and, therefore, evidence of such competition in the past. In our opinion, the appearance of morphological differences is the slowest and, at the same time, most energy-saving way of niche separation. Other ways of ecological niche separation, namely, spatio-temporal and behavioral differentiation, may prove to be energetically more costly. As can be seen, Hutchinson's rule is fulfilled in mature communities, where the species have passed a certain common evolutionary path and the phase of intense competition has passed [24]. It can be assumed that tits had the same competition in the past, taking into account the facts of their differentiation in foraging layers and methods of searching for insects and their

catching [3–5], as well as the compliance of the size differences with Hutchinson's rule (our data).

It is also interesting to note that the divergence of traits of tits increases with growth in their size (see Table 2). Thus, coal tits and willow tits differ by 1.05–1.07 times in their wing length and by 1.15–1.25 times in their weight and azure tits and great tits differ by 1.10–1.11 times in their wing length and 1.40–1.41 in their weight. This pattern was noted by many researchers (see the review in [10]); however, in our opinion, it supplements rather than rejects Hutchinson's rule. Larger species feed on larger prey, the relative abundance of which is lower than that of small prey; therefore, the competition is stronger between them and their differentiation is higher [10]. It should be particularly emphasized that both Hutchinson and his followers had a rather wide spread of ratios and the average value was 1.3 [2].

The only species that does not fit into the pattern that we revealed is the blue tit (perhaps for now), which inhabited only the European part of Russia until the late 20th century [25]. In the Trans-Urals, it was found for the first time in a nesting site in June 1993, when three pairs occupied bird boxes in outliers in the Kamensky district, Sverdlovsk oblast [26]. In June 2000, birds feeding nestlings were recorded for the first time in Dalmatovsky district, Kurgan oblast [27]; in May 2008, they were observed occupying a tree hollow in the Tobol valley [28]; in August 2016, two young individuals in nestling plumage were caught at the eastern boundary of the region [17]. As a result, after penetrating into the Trans-Ural area three decades ago, blue tits soon colonized the entire area of Kurgan oblast. Today, it continues to intensively advance to the east through the forest-steppe zone and has probably already reached the Irtysh [29, 30]. The expansion of blue tits to the Trans-Urals has led to more frequent cases of its hybridization with azure tits [29]; their wing lengths are almost the same; however, the body weight of blue tits is much lower (see Tables 1 and 2). The latter presumably contributes to the reduction of competition between these species.

With respect to size–weight characteristics, the blue tit is slightly alongside of the adjacent species (willow tit and azure tit) rather than being between them (see Fig. 1). It would seem that its morphological niche is now sufficiently isolated. However, that is not quite the case: Fig. 1 shows that the size niche of blue tits is closely adjacent to the niches of willow tits and azure tits, with some blue tit individuals being among the longest-winged willow tit individuals and others being among the lightest azure tit individuals. This case is of interest as an example of the currently observed transformation of the multispecific community due to the introduction of a new species. The previous structure of the community has not yet undergone significant changes; however, the new species has not yet found a new niche and only time will tell how the situation will develop. Therefore, it is of interest to study the size differentiation of tit communities in the European part of Russia, where the azure tit is hardly recorded and the second largest species after the great tit is the blue tit. It is possible that the blue tit is larger in this area than in the Trans-Urals and occupies the size niche of the azure tit.

A similar shift in the tit size in the presence/absence of larger competitors has also been noted by other authors. Thus, coal tits on Scandinavian islands morphologically developed in the same direction as two other species, the willow tit and crested tit *P. cristatus*, which, however, were absent on the islands; as a result, its linear size has become significantly (up to 10%) larger than that of coal tits in mainland Sweden, where these three species coexist [31].

In South Korea, the Far Eastern subspecies of great tit, *P. m. minor*, has become significantly smaller than the European subspecies, *P. m. major*, due to the competition with a larger varied tit, *P. varius*, and has occupied the niche of blue tits, which is absent there [32].

As a result, the studied tit community proves to be clearly differentiated in terms of size and weight characteristics and this differentiation generally meets Hutchinson's rule with only a few indices being slightly lower. The decisive factor in the tit community is the divergence of the ecological niche (food niche in the case under consideration) along one axis; in turn, lower values of the indices than those of Hutchinson indices may indicate that a significant role is also played by the divergence along other axes. On the whole, the presence of a clearly defined size differentiation opens up a new aspect of the study of the organization and functioning of multispecific communities of small passerines in the temperate zone.

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