

SYSTEMATICS OF SMALL PALEARCTIC SHRIKES OF THE "CRISTATUS GROUP"

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ABSTRACT.—I studied the interactions among several species and forms of Palearctic shrikes. Three zones of overlap and hybridization between *Lanius collurio* and *L. phoenicuroides* are described in detail as well as the analogous zone formed by *L. collurio* and *L. isabellinus speculigerus*. Hybrids are characterized by increased variability in plumage characters but not by reduced fitness. *L. cristatus* forms two large areas of overlap with *L. collurio* and *L. i. speculigerus*. Several temporal mixed pairs were found in these zones and a few hybrid specimens. The differences in mating displays and vocalization seemed to be more important species-isolating factors than those of morphology, habitat preferences, and breeding periods. Finally, the taxonomic status of all species and semi-species of the "cristatus group" is established.

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In the Palearctic Laniidae, the taxonomic status of a series of forms, known as the "cristatus group," was always a stumbling block for many generations of systematists. The interaction of different forms of small shrikes and zones of sympatry of many of them had not been described. Consequently at least eight schemes of taxonomic relationships have been proposed for this group.

METHODS

For over 10 years I studied shrikes in different parts of the USSR, concentrating on their zones of contact. Data were collected on habitat preference, breeding season, reproductive biology, phenotypical composition of pairs, mating and agonistic behavior, and vocalization. Also collections of 13 ornithological museums were studied, where more than 4,000 specimens were examined, and most of them were measured. The birds' karyotypes were studied using the standard technique.

RESULTS

The "cristatus group" encompasses the larger part of the Palearctic (in comparison to other shrike groups) (Fig. 1). I describe the limits of some forms, and in others, their interactions. I will first consider the interactions of forms occupying the zones of sympatry.

The Red-backed Shrike (*Lanius collurio*) and Brown Shrike (*L. cristatus*) are phenotypically well distinguished species, although some systematists treat them as conspecifics (e.g. Dementiev 1954; Voous 1960, 1979). Their zone of

overlap is more extensive than was previously known. The relative number of both species occurring in an area varies from place to place. For example, near Teletskoe Lake, Altai Mountains, the Red-backed Shrike prevails 1.5 times over the Brown Shrike. The two species use the same habitat and their territories sometimes abut. Red-backed Shrikes appear on the nesting grounds one to two weeks earlier in spring than the Brown Shrike, and after the latter arrives redistribution of territories occurs. The period of pair-formation for both species overlaps. These circumstances allow the forming of mixed-species pairs. I observed three attempts at mixed-pair formation. None was successful and they lasted for periods from some minutes up to one day. However, two hybrid specimens exist. One is known in the literature (Johansen 1935), and the second is now in my collection, a male from Kuznetsk Alatau, Siberia, obtained by S. Gureev. Based on my observations and the number of such specimens, it appears that in general hybridization between *collurio* and *cristatus* occurs only occasionally.

I also studied geographical variation of some characteristics of coloration and measurement in the populations of these species from European Russia to Sakhalin Island. Constant interspecific diversity and slight interpopulation differences were revealed, but "character displacement" was not discovered.

Another pair of species, the Brown Shrike and Isabelline Shrike (*L. isabellinus speculigerus*) have a long zone of sympatry in southern Siberia, eastern Mongolia, and central China

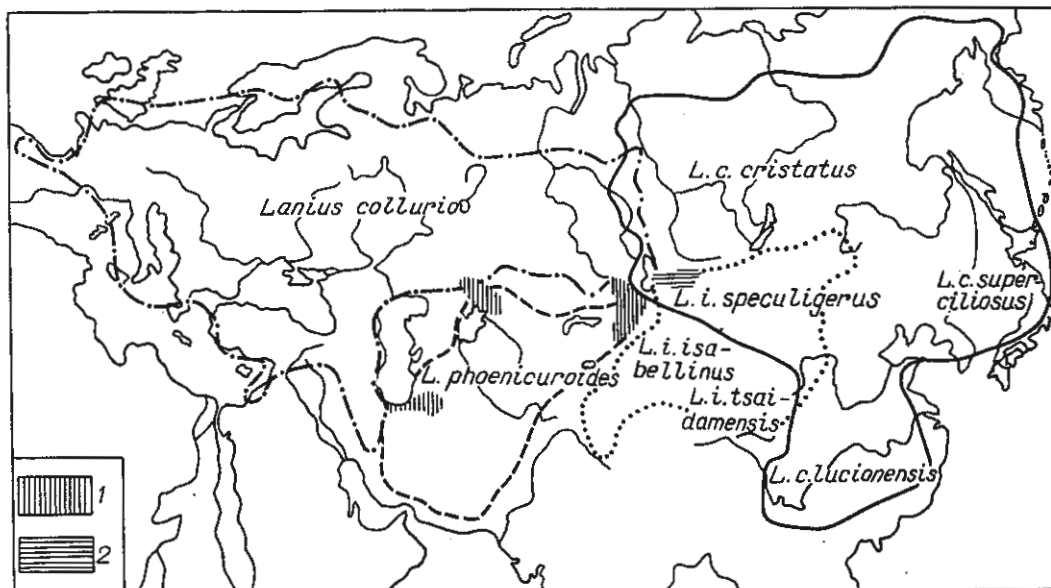


Fig. 1. The distributions of small Palearctic shrikes of the "cristatus group" during the breeding season (according to Mauersberger and Portenko 1971, with corrections). Zones of overlap and hybridization are hatched: 1—*L. collurio* × *L. phoenicuroides*, 2—*L. collurio* × *L. isabellinus speculigerus*.

(Fig. 1). In general, they prefer different habitats, but in some localities of Transbaikalia they nest side by side. Isabelline Shrikes usually form pairs and begin nesting 8–10 days earlier than the Brown Shrike. Although some unmated males of both species occurred, and in spite of their phenotypic similarity, no mixed pairs were observed. We assume that differences in mating displays and vocalizations provide reproductive isolation between these species.

In the zone of overlap of Brown, Tiger (*L. tigrinus*), and Bull-headed (*L. bucephalus*) shrikes in Ussuriland, the only hybrid specimen known is between the first two (Panov 1964). It appears in conditions when one of the species is much more common than the other (*tigrinus* being rare). Only these two species have similar mating displays (Panov 1964). At the same time, we could not provoke mixed-pair formation by removing females or males in two neighboring territories.

In southern Turkmenia, Bay-backed (*L. vittatus*) and Red-tailed (*L. phoenicuroides*) shrikes occupy similar habitats, but the arrival time of the former species coincides with the time of nest building of the latter. These species differ phenotypically and in mating displays

(Kryukov 1978). Thus, the interspecific interactions are limited to territorial struggles.

The principle attraction of the "cristatus group" is the hybridization of several forms. The Red-backed and Red-tailed shrikes form three zones of overlap and hybridization in eastern Kazakhstan, north of the Aral Sea, and southeast of Caspian Sea (Fig. 1). The first of these is the largest. The portion of phenotypically intermediate birds reaches maximum (68%) in the foothills of the Saur Mountains, and decreases to the north and south (Fig. 2). It is important to note that single intermediate shrikes occur throughout the whole area of the Red-tailed Shrike, far from the real hybrid zone (Panov and Kryukov 1973).

Color variation in the hybrid zones is great. One can observe both parental forms and many different hybrids. Most of them have a set of intermediate plumage characters, some have a combination of pure characteristics of parental species; or even, new characters absent in both parents. Some of these hybrid forms were described species or subspecies under remarkable names (e.g. *Otomela p. karelini* Bogdanow, 1881; *O. varia* Zarudny, 1896; *L. p. pseudocollurio* Sushkin, 1906) and 13 such names occur in lit-

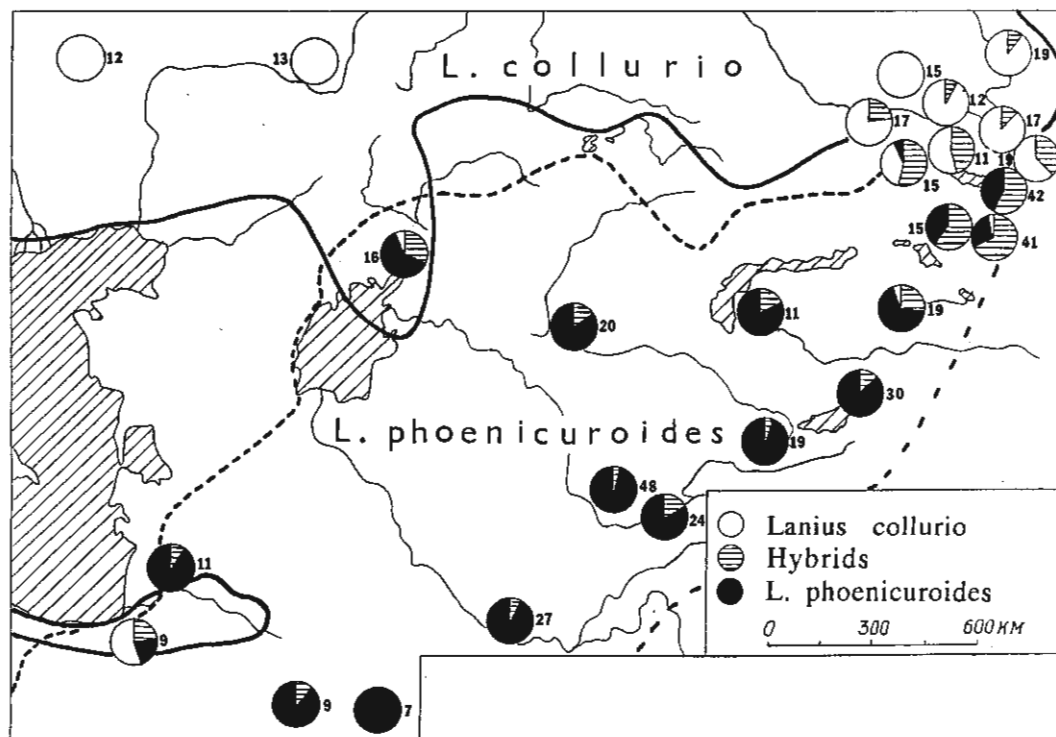


Fig. 2. Population structure in three zones of overlap and hybridization in the region east of the Caspian Sea. Numbers = sample sizes of nesting males.

erature, but all of them are now considered invalid.

In semi-deserts, north of the Aral Sea, the intrapopulation variability and the population density is small. Birds in general are similar to *phoenicuroides*, but the tail is darker, they have a more grayish colored upper plumage, and some size characteristics (e.g. distance between tips of 2nd and 5th primaries) indicate their hybrid nature.

To the east of the Caspian Sea, a large zone of overlap occurs. Some parts of this zone are inhabited mostly by hybrids, but in other places they are rare. Mayr (1942), based on the data of K. Paludan, mentioned the hybrid flock of shrikes in Astrabad, Iran. In Kopetdag Mountains, hybrids are uncommon.

Thus, it is possible to specify the phenotypical appearance and structure of each "zone of overlap and hybridization" (Short 1969), which may be determined by their own peculiar history.

Let us now consider the interactions between the other pair of species: *L. collurio* and *L. i. spe-*

culigerus. During an expedition with E. N. Panov through the Altai Region, we discovered for the first time, that in the southeastern Altai-Chua Steppe, the Red-backed Shrike not only nests together with the Isabelline Shrike, but also hybridizes with it (Fig. 1). In the center of this steppe, 44% of shrikes are hybrids, the rest are Isabelline Shrikes. Only in the northern part of the steppe does a small population of Red-backs occur. In the south and east of the described hybrid zone, the portion of intermediates gradually decreases. The introgression of *collurio* genes is found in a considerable part of the range of *L. i. speculigerus*.

In all hybrid zones the clinal variation in a set of measurements and a "hybrid index" (Meise 1936) of coloration was calculated. Intrapopulation variability of the color characters, as noted above, increases greatly in mixed populations whereas variability of all morphological characters remain stable (Kryukov 1982).

In each hybrid zone one can find several mated pairs formed both by pure parental forms and by different types of hybrids. It is impor-

tant to note, that the reproductive success in different types of pairs is similar (Panov and Kryukov 1973). Density in hybrid populations is rather high, and their general fitness is quite normal (Kryukov 1982).

The only unusual property of hybrid population was the sex ratio. The proportion of males in them varies from 60–73%, whereas in "pure" populations it is 54–58% (Kryukov 1982). This observation is in accordance with Haldane's rule of the oppression of the heterogametic sex among hybrid progeny. The unmated males may compete with conspecifics occupying territories. Besides, they may emigrate, enlarging areas of hybrid populations. This is the supposed way of occupying the unusual, for small shrikes, desert habitats by pale-colored hybrids named *karelini*.

We also attempted to examine the temporal dynamics of hybrid zones. I compared two series of skins collected 55 years apart in eastern Kazakhstan, where the hybrid population *collurio* × *phoenicuroides* occurs. The proportion of hybrids and mean values of all studied characters was not changed (Kryukov 1982). The same result was demonstrated in the comparison of series and observations in southeastern Altai (*collurio* × *speculigerus*) during 1914–1990s (Kryukov unpubl. data). Thus, changes in hybrid populations occur quite slowly.

Interrelationships of *phoenicuroides* and *isabellinus* are poorly studied. Our observations in south Turkmenia indicate the possibility of their joint nesting. They differ in plumage characters, some sizes (e.g. wing length), and period of nesting (almost by one month). On the other hand, appearance of a number of intermediates in Turkmenia, Iran, and Dzungaria, as well as our observations of attempts to form mixed pairs, testify to the possibility of their hybridization (Kryukov and Panov 1980). In any case, they do meet somewhere in Afghanistan or China. Until this zone is studied and the variation evaluated, we cannot decide if we are dealing with a situation of primary or secondary contact.

CONCLUSIONS

The revision of allopatric forms is as follows. *L. collurio* is monotypic. *L. cristatus* is divided into *L. c. cristatus* L., *L. c. superciliosus* Lath., and *L. c. lucionensis* L. The Isabelline Shrike has the most "capricious taxonomic history" (Voous 1979). We recognize the following subspecies; *L. i. isabellinus* Hempr. et Ehrenb., *L. i. speculigerus* Tacz., and *L. i. tsaidamensis* Stegm. These forms have some distinct characters and allopatric distribution. We consider *L. phoenicuroides* provisionally as a separate, monotypic species. Its significant variation is due to hybridization with *L. collurio* and *L. i. isabellinus*.

Finally, I present our taxonomic scheme of small Palearctic shrikes of the "*cristatus* group." This name has page-priority over *L. collurio*, both described by K. Linney in 1758. *L. cristatus* is undoubtedly a separate species, isolated in zones of overlap from *L. collurio* and *L. i. speculigerus*. Further, *L. collurio*, *L. isabellinus*, and *L. phoenicuroides*, connected by the described zones of secondary intergradation, are "semispecies" (Short 1969). They satisfy some properties of species and others of subspecies because of incompleting process of speciation. In nomenclatural aspects, all mentioned semispecies must maintain species names. All of them form the superspecies *L. cristatus* together with *L. souzae*, and *L. gubernator* (Hall and Moreau 1970), or perhaps with *L. collurioides* and *L. vittatus* (Eck 1973).

Besides the difficult taxonomic problems, Palearctic shrikes provide an extremely convenient model for the study of species isolating mechanisms. I studied the isolation of each pair of forms in habitats, breeding seasons, mating and agonistic displays, vocalization, and karyotypes. The most important factor for maintenance of reproductive isolation in these shrikes is behavioral differences. I conclude that small Palearctic shrikes are not only pretty, wonderful birds, requiring protection, but also important models for solving modern problems of the theory of systematics and evolution.