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CHARACTER DISPLACEMENT IN INDIAN NUTHATCHES (*Sitta*).

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In connection with work on the birds of India, I have had occasion to arrange the various nuthatches of the genus *Sitta* occurring in India in a purely linear listing suitable for a checklist. Arrangement of this sort at once reveals that far more is at stake than a mere listing can indicate. Some aspects of the problem are given in the recent comprehensive treatise by Voous and Van Marle (1953) who have attempted to recreate the distributional history of the several species of *Sitta* of Southeast Asia.

It is quite clear from a study of these nuthatches that several species are involved, that they are all closely related and that they tend to replace each other. However, where these species are sympatric they show character displacement as well as a degree of niche specificity, thus a tendency to special adaptations as discussed by Brown (1958). That closely related species of nuthatches exhibit this type of speciation allowing geographical overlap and ecological specificity has been well illustrated by Vaurie (1950, 1951) in his two papers on *Sitta neumayer* and *S. tephronota* of west central Asia. These two species of Rock Nuthatches are admitted to be most closely related to each other. Voous and Van Marle (*ibid*: 54) feel that the Rock Nuthatches are in addition a

central Asian offspring of the common European Tree Nuthatch adapted to a xeric environment. That these forms could have split off from the tree-inhabiting nuthatch at opposite geographically isolated ends of two glacial refugia in the southeastern Mediterranean and central Asia respectively seems conceivable. At a later stage the two populations, almost indistinguishable morphologically and with similar habits and ecological requirements, having spread into contiguous areas have evolved adaptively so that both can coexist in the same range without hybridization. Morphologically the two species differ in the area of overlap by a significant change in bill size. Whereas isolated populations at the ends of the range have similar bills, the overlap populations differ greatly, the Asian *tephronota* possessing a large bill, the Mediterranean *neumayer* a relatively small bill. In addition whereas both species possess a black facial stripe of equivalent size and length, running from the base of the bill through the eye and back to the nape, the overlap populations differ greatly, the eye stripe in Asian *tephronota* being much enlarged and prolonged farther backwards, that of the Mediterranean *neumayer* being greatly reduced to a strip between bill and eye passing backwards to just above the auricular region. Thus two species which are virtually sibling species have developed prominent recognition marks and adaptations for food gathering sufficient to prevent interbreeding and reduce competition.

That competition is a factor seems inevitable from what is known of the habits of these species, both living in xeric areas of cliffs, rocks and low stunted trees. Both occur in the same areas and have been collected together at the same altitude. This biotope would appear to be homogeneously diverse to use Hutchinson's term (1957) and would confirm his supposition that in stable homogeneously diverse biotopes the abundances of different species are arranged as if the realized niches were non-overlapping.

A different series of constants are involved in the Himalayan ranges of India and Pakistan. From the lowlands to the heights of 15,000 feet above sea level, a number of biotopes occur which are essentially heterogeneously diverse, woodland

of different types ranging from cultivation and tropical thorn scrub to tropical, subtropical, pine, temperate and alpine forest. The following species of *Sitta* may be listed, giving such ecological details as are known:

<i>Species</i>	<i>Habitat Preference</i>	<i>Altitudinal Range</i>
1) <i>Sitta castanea castanea</i>	mango groves, orchards, cultivation, tropical deciduous forest	lowlands to 3,500 feet in central India; lowlands to foothills 1,000 ft. in Himalayas
<i>Sitta castanea neglecta</i>	tropical lowland forest, also scrub and cultivation	lowlands to 2,500 ft.
<i>Sitta castanea cinnamoventris</i>	masonry walls, gardens, bamboo clumps, scrub, sub-tropical forest	edge of the plains (winter) to 4,500 ft.
<i>Sitta castanea cashmirensis</i>	mixed forests at all levels, lower parts of trees	4,500-11,500 ft.
2) <i>Sitta europaea</i> , various subspecies	mixed forests at all levels	4,500-8,500 ft.
<i>Sitta europaea montium</i>	mixed alpine and fir forests	4,500-12,000 ft.
3) <i>Sitta himalayensis</i> , various subspecies	heavy mixed forests, usually deciduous, strong preference for oaks; may descend to undergrowth	5,000-10,000 ft.
4) <i>Sitta leucopsis</i>	almost exclusively upper parts of trees in fir and pine forest	7,000-12,000 ft.
5) <i>Sitta victoriae</i>	alpine forest, avoids pines	7,500-9,200 ft.
6) <i>Sitta yunnanensis</i>	barren fir forest association	9,000-15,000 ft.

As pointed out by Voous and Van Marle (*ibid*:59-61) all these species are roughly similar in size and close to each other in pattern. Some wing and bill measurements can indicate relative size:

	bill (mean length m.m.)	Wing (mean m.m.)
1) <i>castanea castanea</i>	19.1	75.5
" <i>neglecta</i>	19.8	79.9
" <i>cinnamoventris</i>	23.2	83.7
" <i>cashmirensis</i>	21.8	85.2
2) <i>europaea</i> , various subspecies	18.8	78.6
" <i>nagaensis</i>	19.1	78.2
" <i>montium</i>	19.1	80.2
3) <i>himalayensis himalayensis</i>	15.9	72.3
" <i>australis</i>	16.6	73.6
4) <i>leucopsis leucopsis</i>	21.6	79.2
" <i>przewalskii</i>	17	75.1
5) <i>victoriae</i>	14.5	70.2
6) <i>yunnanensis</i>	17	73

Status of Sitta castanea

Sitta castanea with its various allopatric subspecies has often been listed as part of the common Palearctic Tree Nuthatch species, *Sitta europaea*. It is obvious that it is most closely related to *Sitta europaea* and it satisfies a taxonomist's criterion by being strictly allopatric, both geographically and ecologically. However, *Sitta castanea* differs from *europaea* by having pronounced sexual dimorphism and a strikingly different color pattern on the under surface of the males. Its distribution throughout the Gangetic plain and hills of the Indian Peninsula, with the development of a distinct subspecies in the Eastern Ghats, gives strong evidence for a long colonization similar to that of some of the double invasions and relict forms discussed by me previously (1949). I feel that it belongs to an early break-off of *europaea* stock, separated from that species in time and by the imposition of two other old Palearctic invasions into the Himalayan chain, the earliest *Sitta leucopsis*, the second *Sitta himalayensis*. *Contra* Voous and Van Marle (*ibid*:53, 55) I believe that the hill populations of *castanea*, namely *cashmirensis*, *almorae*, *cinnamoventris* and *tonkinensis*, which are all larger in measurements than the lowland populations, *castanea* and *neglecta* (see measurements) have developed from the older lowland stock which has been able to capture and exploit vacant niche space in the adjacent hills in post-pluvial times. That this has been done more than once is shown by the isolated eastern, Indochinese population of *tonkinensis* which has developed a highland form in the same way that the western forms have evolved.

Sitta leucopsis and *Sitta himalayensis*

I would have listed these in my zoogeographic study of the Indian avifauna (1959) except that by ranging into the Indochinese and Chinese subregions, these species did not fit my criteria for such a listing. However, I would include them here along with species I did list (*ibid*:79) such as *Zoothera wardi*, *Parus melanolophus*, *Sitta formosa* and *Pyrrhula erythrocephala* and *P. aurantiaca* as Palearctic relicts.

Sitta victoriae

From the list of measurements it will be noted that this isolated species, confined to the summits of the Chin Hills, Mount Victoria, of western Burma, is relatively small in size. It has been listed in the past as a sub-species of *S. himalayensis*, indicating obvious affinity, (Voous and Van Marle, *ibid*: 58) but they as well as other authors have overlooked the fact that *himalayensis* has been taken on the same mountain.

A view of a map should prove instructive here. Surveying the Himalayan chain from Kashmir east to Sikang and northern Indochina, I have indicated the zones of ecological overlap between the species under discussion. Although the ranges overlap geographically, it can be seen that there is very little overlap among these species:

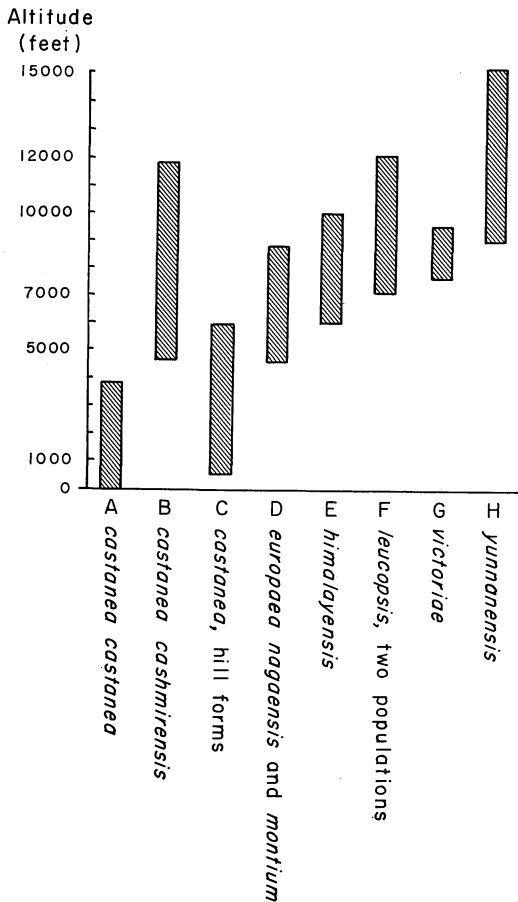


Figure 1. Altitudinal Ranges of Species and subspecies of *Sitta*.

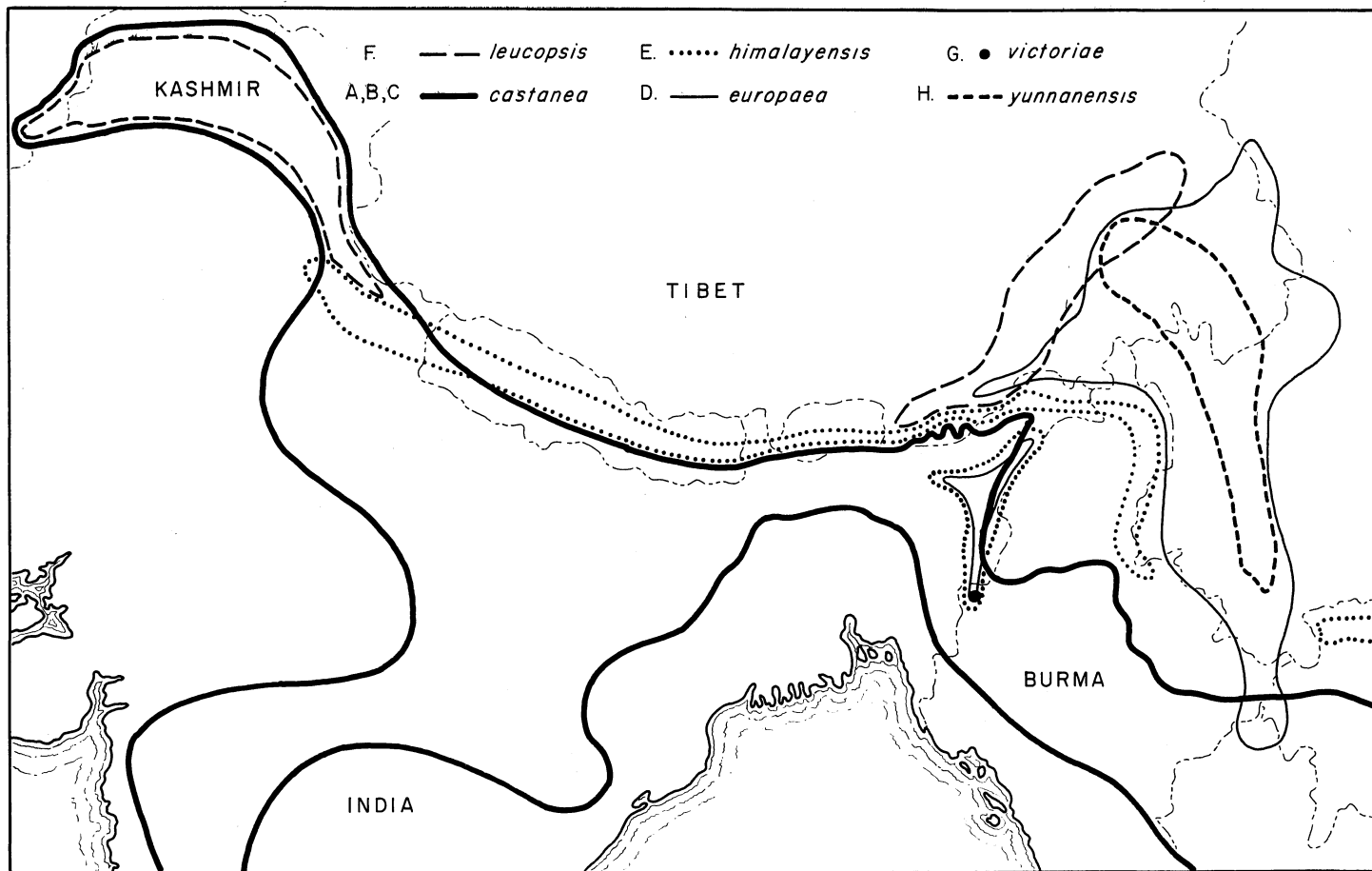


Figure 2. Map showing geographical orientation of species of *Sitia*.

From the above it can be seen that there are only a few cases of overlap which need to be explained. Among the subspecies of *castanea* there is no overlap. The apparent range overlap is due to wintering birds of the montane subspecies descending into the range of the lowland form out of the breeding season. In addition A, B and C are allopatric with E, G, and H. The following range overlaps then need some word of explanation.

1. In Kashmir and adjacent areas of West Pakistan and eastern Afghanistan, *Sitta castanea cashmirensis* overlaps with *S. l. leucopsis* but is ecologically separated, the latter preferring the upper branches of firs and pines, the former the lower branches of mixed deciduous and evergreen hardwoods. These two species then occur within the mosaic elements of a heterogeneously diverse biotope. There is no competition, hence no character displacement.

2. In eastern Assam in the hills south of the Brahmaputra River, although *castanea* has a separate population, *koelzi*, it is allopatric with *europaea*, the latter not occurring below 4,500 feet, the former being a lowland and submontane form up to 4,500 feet. However, a population of *himalayensis* overlaps with *europaea* in these hills and occupies the same altitudinal range and much the same biotope. Both inhabit mixed forest. The only known ecological difference is the preference of *himalayensis* for oaks, rhododendrons, and lower areas of trees. Evidently a degree of interspecific competition exists here. In the contact area both have evolved recognizable distinct populations showing character displacement. The character displacement follows the same general pattern as in the case of the Rock nuthatches. (See Fig. 3, Page 8)

As the figure indicates, the overlap population of *europaea*, called *nagaensis*, has become very pale on the under surface with a slimmer bill and a pronounced facial stripe. The overlap population of *himalayensis*, called *australis*, has become richer buff on the under surface with a stouter bill and a shorter facial stripe. Thus morphological differences emphasizing both feeding habits and recognition are involved in this interspecific situation. That characters having recognition

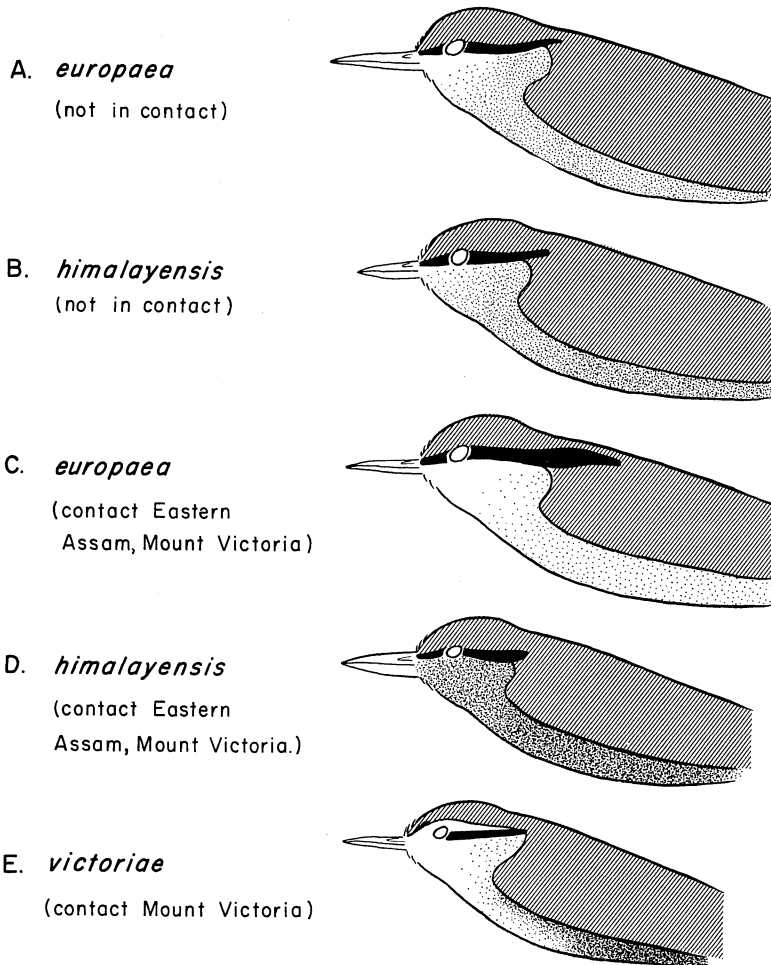


Figure 3. Outline sketch to show differences between sympatric populations of species of *Sitta* (C., D., E.) compared to two populations not in contact (A., B.).

value are developed even between these two fairly distinct species would imply that selection pressure towards plumage pattern differences is heavy. In a similar way North American warblers have evolved marked phenotypic differences as well as behavioral and food gathering adaptations as discussed by Mac Arthur (1958).

On Mount Victoria south of the Assam Hills, a third sympatric species is introduced, *Sitta victoriae*. This species with a range of 7,500-9,200 feet overlaps altitudinally on the mountain stopes with *europaea*, which reaches 8,500 feet, and with *himalayensis*, with which it is assumed to be most closely related, which also reaches 9,200 feet. It would appear from a biogeographical point of view that *victoriae* is an old relict species, first to arrive of a double invasion by *himalayensis* stock. It has a known ecological preference for alpine forest and avoids pines. *Himalayensis* also avoids pines and co-occurs with *victoriae* in mixed and alpine forest. *Europaea* may occur in alpine as well as mixed forest. In this case *europaea* and *himalayensis* have a wide range in eastern Assam of co-occurrence and their morphological characters have been described. The third species *victoriae* differs by being noticeably smaller with a more weak and slender bill and different facial pattern.

3. Eastwards in Tibet, Burma, Thailand, Indochina and Yunnan there is little actual overlap. Wherever *europaea* has invaded the mountains of southeast Asia, *castanea* keeps at lower altitudes. In the single instance where *castanea* invades the mountains, *europaea* is absent. *Himalayensis* occurs at predominantly higher altitudes.

4. The single instance of co-occurrence is in the case of three species in Sikang or eastern Tibet. Here are found a population of *europaea*, one of *leucopsis*, and *Sitta yunnanensis*. *Leucopsis* has developed rich bright color on the underparts in contrast to the population of *leucopsis* found in the Himalayas. The population of *europaea*, known as *montium* is intermediate in color of underparts, while the palest of the three is *yunnanensis*. *Leucopsis* lacks an eye stripe, possessed by the other two of differing lengths, longer in *europaea*, and has a short bill, the shortest of the three. In this instance *yunnanensis* has a relatively long needlelike bill, and *europaea* an intermediate, stouter bill. From the table of measurements it will be seen that *europaea montium* differs from other populations of the species by being larger with a larger bill, thus showing character displacement in the presence of the other two species. Schäfer (1938) reports that *europaea* and *yun-*

nanensis were found together, although the latter was found only in rather barren, fir forest. He found *leucopsis* less often, in more open parkland. In the presence of *yunnanensis* the population of *europaea* found with it appears to have developed a shorter, stouter bill, larger size, and a longer eye stripe, as well as somewhat more richly colored underparts, all tending towards character displacement. Even *leucopsis*, not apparently in close competition, would appear to have been affected, so markedly does it differ from the other population of the species.

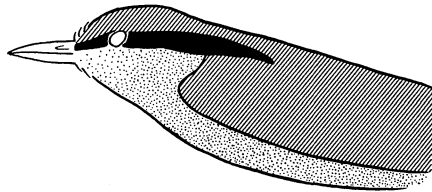
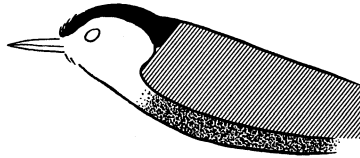
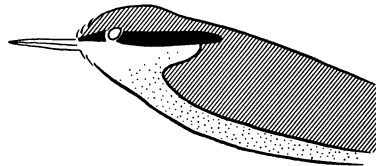
D. *europaea*F. *leucopsis*H. *yunnanensis*

Figure 4. Outline sketch showing differences between sympatric populations of three species of *Sitta* located on the map, Fig. 2.

Summary

Character displacement including external features of recognition value has been shown to occur among nuthatches in the heterogeneously diverse biotope of the mountains of the eastern Himalayan chain. Species of nuthatches which are allopatric elsewhere, replacing each other at various altitudes or in differing forest associations, here come together and dem-

onstrate adaptive characters indicating the presence of interspecific competition, and a lessened degree of niche specificity. As would be anticipated, the biotope of the eastern Himalayas appears to be more rich, more diverse, capable in at least two cases of supporting a greater number of potentially competing species. The more boreal biotope in the western Himalayas exhibits an expected mosaic pattern of distribution of potentially competing species. This pattern with the phenomenon of character displacement would seem to agree with the niche model postulated by Hutchinson and Mac Arthur (1959).

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