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NOTES ON THE BIRD FAMILY PRUNELLIDAE IN SOUTHERN EURASIA¹

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INTRODUCTION

Though a small family, the hedge-sparrows or accentors are a little-known assemblage. Most of the 12 species of the single genus *Prunella* breed in the highlands of central Asia and are inadequately represented in many collections, especially in North American museums. There have been no systematic studies of the biology of these birds. Most of the available information concerns specifically those species that reach western Europe and cannot safely be extrapolated to the Asiatic forms. The few reliable observations concerning the latter are scattered references.

It is therefore particularly gratifying to find that Dr. Walter Koelz has collected almost 350 specimens, including all but three of the species in the genus. To this fine series it has been possible to add the specimens in the collection of the American Museum of Natural History, and through the generous cooperation of Dr. Herbert Friedmann of the United States National Museum, Dr. A. L. Rand of the Chicago Natural History Museum, and Dr. Josselyn Van Tyne of the University of Michigan Museum of Zoology, I have been able to examine specimens

¹ Notes from the Walter Koelz Collections, Number 7. The previous papers in this subseries are: Number 1, American Museum Novitates, no. 1406, 1949; Number 2, American Museum Novitates, no. 1424, 1949; Number 3, American Museum Novitates, no. 1425, 1949; Number 4, American Museum Novitates, no. 1459, 1950; Number 5, Jour. Bombay Nat. Hist. Soc., vol. 49, 1950; Number 6, American Museum Novitates, no. 1472, 1950.

from the collections of those institutions. In all, 575 specimens were available for a study of the distribution and taxonomic status of the forms found in Iran, Afghanistan, and northern India.

During the course of the study several interesting problems connected with the *Prunellidae* became apparent. For this reason the scope of this report has been extended to include a more generalized discussion of certain ecological rules and some factors of evolutionary significance especially as illustrated by, or as they affect, *Prunella*. No attempt was made to monograph the group as a whole, since the present material is not sufficient, but there are enough recognizable trends in the limited south Eurasian material to make some tentative considerations and conclusions possible.

The first part of these notes consists of a systematic report on the specimens collected by Dr. Koelz in India, Iran, and Afghanistan; a discussion of the *Prunellidae* follows in the second part.

All measurements are given in millimeters and are of subadults and adults of the Koelz specimens unless specified otherwise. The length of the wing was taken with the wing pressed flat on the rule; bill length was measured from the base of the bill to the tip of the culmen.

Since many new localities have been added to the known ranges of many forms, a list of the specimens collected by Walter Koelz accompanies each species account. Attention may be called to the fact that Dr. Koelz has established the first authenticated records of *P. himalayana*, *strophciata*, and *fulvescens* breeding in Afghanistan.

If the specimens are not too worn, first-winter birds can be distinguished from adults; where it was possible to make such a distinction I have indicated the fact by use of the term "sub-adult" for birds in first-winter plumage.

SYSTEMATICS

Prunella collaris montana (Hablizl)

IRAN: Northern Iran: Karaj, January 24, 1945, 1 ad. ♂, 1 ad. ♀. Luristan: Durud, March 13, 1941, 1 ad. ♂, October 23-24, 2 ad. ♂, 4 ad. ♀, 1 subad. ♀.

Although breeding birds of this race are to be found in the Taurus, Caucasus, and Elburz Mountains, none seem previously

to have been reported from the Zagros Mountains in western Iran. These first specimens from the Zagros (in Luristan) were taken in March and October, quite probably outside of the breeding season, but the species is not usually migratory and it may well be looked for in the future as a breeding bird in these mountains.

There were available for comparison with the Zagros series four specimens from the Caucasus, three worn and one in fresh plumage, and the two Koelz specimens from Karaj. If the effects of foxing are allowed for, the three series are not very different from one another in color and size, but the sample is quite small.

MEASUREMENTS: Caucasus (Rothschild Collection): Male, wing, 102, 108, tail, 66, 71, bill, 15, 16.5; female, wing, 98, 103, tail, 64, 72, bill, 15.5, 15.5.

Gilan, Pish Kuh (*vide* Stresemann, 1928): Wing, male, 101, 102, 104, 104, 106; female, 96, 98.

Northern Iran, Karaj: Male, wing, 96, tail, 67, bill, 16; female, wing, 100, tail, 66, bill, 16.5.

Luristan, Durud: Male, wing, 98 (very worn), 105, 106, tail, 63 (very worn), 69.5, 70.5, bill, 15.5, 17, 17; female, wing, 97, 97, 98, 103, tail, 63, 63, 65, 66.5, bill, 16, 16, 17.

***Prunella collaris rufilata* (Sewertzoff)**

***Prunella collaris whymperi* (Baker)**

***Prunella collaris nipalensis* (Hodgson)**

In the north Indian Himalayas there are two races of the alpine hedge-sparrow: *whymperi* and *nipalensis*. A Turkestan subspecies, *rufilata*, is sometimes stated to extend into extreme northwestern India, but the Indian material examined by me does not include *rufilata*.

There is a progressive intergroup cline of increasing saturation of the upper parts from west to east. The largest and palest form, *rufilata*, breeds in Turkestan; a slightly smaller and darker race, *whymperi*, is resident in Kashmir, Punjab, and northern United Provinces; and the darkest race, *nipalensis*, ranges from Nepal to western China. Whistler (1944) states that *rufilata* is said to nest on the Safed Koh in Afghanistan, although it had never been collected there. A Koelz specimen from Bulola in the western Safed Koh, identified here as *rufilata*, was perhaps

only a winter visitor from Turkestan, but the species is generally non-migratory and there appears to be no reason why it should not breed in Afghanistan.

The small series from Ladak, Baltistan, and Punjab agrees very well in color with specimens from Kumaon (lying east of Garwhal, the type locality of *whymperi*). On the whole, these birds are exactly intermediate between *rufilata* and *nipalensis*. The steepening of the cline coincident with the transition from *whymperi* to *nipalensis* must occur in Nepal. I have not seen specimens from the region between Kumaon and Sikkim, but

TABLE 1

MEASUREMENTS OF ADULTS OF FOUR ASIATIC SUBSPECIES OF *Prunella collaris*

Subspecies and Region	Sex	Wing	Tail	Bill
<i>rufilata</i> ^a				
Russian Turkestan	♂ ^b	102, 102	68.5, 71	17, 17
<i>whymperi</i>				
Kashmir	♂	97 (molt)	66	16
	♂ ^c	97, 100, 100, 101	65, 66, 68.5, 69.5	15, 15.5, 16, 16
	♀	91, 94	60.5, 61	15.5, 16
	♀ ^c	92	61.5	15
Punjab	♂	93, 94, 97, 98, 98, 102	62, 62, 63, 65, 65, 69	15, 15, 15.5, 15.5, 15.5, 16
	♀	91, ^d 93	56, ^d 62	15, 15.5
United Provinces, Kumaon	♂ ^d	95, 96, 97, 97, 97, 97, 98	63, 63, 64, 65.5, 66, 66.5, 67	14.5, 14.5, 15, 15, 16, 16.5, 16.5
	♀ ^d	88, 90, 91, 91, 93, 94	56, 58, 60.5, 60.5, 62, 62.5	15, 15, 15.5, 16, 16, 16
<i>nipalensis</i>				
Sikkim ^e	♂	96, 100, 100, 100, 101	63, 66, 68, 69, 69	14.5, 14.5, 15, 15.5, 16
	♀	97, 99, 101	65, 66, 67	15, 15, 15
Northwest Yunnan ^a	♂	97 (molt), 102, 102	66, 67, 67	14.5, 15, 16
	♀ ^d	92	61.5	15
<i>talifuensis</i>				
Southwest Szechwan ^a	♂ ^d	103	103	15
	♀	100	100	15

^a Rothschild Collection.^b Subadult.^c United States National Museum.^d Very worn.^e Chicago Natural History Museum.

examples from the latter locality are very much darker than any from the northwest. *P. c. talifuensis* (Rippon) (= *ripponi* Hartert) of Szechwan is a continuation of the cline and is scarcely, if at all, distinguishable from *nipalensis*. Field notes on the specimen labels indicate that these accentors breed at altitudes of 13,000 to 15,000 feet in Baltistan and Lahul, descending in winter as low as 8000 feet.

A single specimen from Kashmir was well advanced in molt on September 14. A female from Poo, Rampur-Bushahr, Punjab, has some white feathers interspersed among the normally colored feathers of the crown, neck, ear coverts, back, and breast; the abnormal feathers are white to the bases.

MEASUREMENTS: The measurements of the four subspecies discussed above are shown in table 1. Although *rufilata* may be slightly larger than the others, more specimens would be needed to show that fact.

***Prunella collaris rufilata* (Sewertzoff)**

AFGHANISTAN: Bulola, December 10, 1937, 1 ad. ♂.

***Prunella collaris whymperi* (Baker)**

INDIA: Kashmir: Baltistan, Burzil, August 6, 1936, 1 ad. ♀; Karzong Pass, September 14, 1 ad. ♂, 1 subad. ♀. Punjab: Lahul, Kolang, August 13, 1933, 1 ad. ♂, 1 ad. ♀; Rampur-Bushahr, Kunawar, Raghi, October 29, 1933, 1 ad. ♂, Rarang, November 16, December 9, 1930, 2 ad. ♂, Pangi, November 17, 1 ad. ♂, Sunam, November 30, 1 ad. ♂, Poo, December 3, 1 ad. ♀. United Provinces: Kumaon, Sumto-Rahlam Pass, June 17, 1948, 2 ad. ♂, 1 ad. ♀, Bedang, July 12-13, 4 ad. ♂, 5 ad. ♀, Janlingkang, July 13, 1 ad. ♂.

***Prunella himalayana* (Blyth)**

AFGHANISTAN: Munjan Pass, July 27-28, 1937, 1 ad. ♀, 1 juv. ♂, 1 juv. ♀. INDIA: Punjab: Kulu, Nandukital, October 31, 1930, 1 ad. ♀, Naggar, December 30, 1931, 1 ad. ♂, Banjar, December 30, 1932-January 4, 1933, 7 ad. ♂; Rampur-Bushahr, Darkali, December 20, 1930, 2 ad. ♂, 2 ad. ♀.

This species, although similar in habits and appearance to *Prunella collaris*, occupies a smaller range. The total range of the alpine accentor extends from western Europe to eastern China; *himalayana* breeds in Mongolia west to Khangai and the Altai, south to Russian Turkestan and eastern Afghanistan, and eastward in the Himalayas to Sikkim. In contrast again with *collaris*, of which many subspecies are known, *himalayana* is monotypic.

Since Whistler (1944) stated that he could find no authority for the occurrence of this accentor in Afghanistan, the three specimens from Munjan Pass constitute the first definite record. This extends the known breeding range of the species southwestward to the Hindu Kush, near Chitral.

The very worn Afghanistan adult does not differ from Russian Turkestan birds which are in similar plumage condition. The measurements of worn adult females (Rothschild Collection) from the Tian Shan Range in Turkestan are: wing, 89, 90, 90, 92, tail, 54, 54, 55, 58. The single Koelz bird measuring wing, 88, tail, 51 is slightly smaller, but more worn.

Other Koelz specimens (northeastern Punjab, October, December, January) measure: 10 males, wing, 92-99 (95.5), tail, 55-61.5 (57.9), bill, 13-14.5 (14.1); females, wing, 89.5, 90, 90, tail, 52, 53.5, 55, bill, 14.5, 15, 15. All these are in comparatively fresh plumage.

The two juvenals from Afghanistan have completed about half of the post-natal molt; the wing, tail, lower back, and rump feathers are already replaced. The adult is in an extremely worn plumage and shows no sign of molt, although specimens from Russian Turkestan taken earlier in July show evidence of having begun the post-nuptial molt, and a specimen taken at the end of August had almost completed its molt.

***Prunella strophciata sirotensis* Koelz**

AFGHANISTAN: Sirotai, June 17-18, 1937, 1 ad. ♂ (type), 1 ad. ♀.

These two specimens are the first record of the rufous-breasted hedge-sparrow in Afghanistan. Since *strophciata* had been first reported from near the Indo-Afghan border (Whitehead, 1911), it was expected eventually to be discovered in Afghanistan. The species' range now extends approximately 60 miles farther southwest, Sirotai being just east of Gardez on the southern slopes of the Safed Koh.

The type and cotype of *sirotensis*, the only known examples of this subspecies, are extremely worn and differ from the Kashmir race, *jerdoni*, in being somewhat grayer above. The birds observed by Whitehead at Kurram, quite naturally referred to *jerdoni*, were most likely of this race, if its distinctness is substantiated by better material.

MEASUREMENTS: Male, wing, 66, tail, 53.5, bill, 12; female, wing, 66, tail, 53, bill, 12.5.

***Prunella strophciata jerdoni* (Brooks)**

INDIA: Kashmir: Baltistan, Tragbal, July 31, 1936, 1 ad. ♀, Burzil Pass, August 5-7, 2 ad. ♂, 1 juv. ♀, 1 unsexed juv., Shigar Nulla, August 22, 1 unsexed juv., Biokdang Nulla, September 4, 1 ad. ♂, 1 ad. ♀, Hundar, September 10, 1 ad. ♀. Punjab: Kangra, Kotla, January 5, 1948, 1 ad. ♂, February 5, 1946, 1 ad. ♂; Chamba, Reling, July 3, 1936, 1 ad. ♀, Kukti, July 31, 1 ad. ♂; Lahul, Kyelang, July 18, 1933, 1 unsexed fledgling, October 16, 1936, 1 ad. ♂, 1 ad. ♀, October 23, 1 ad. ♀; Rampur-Bushahr, Serahan, November 7, 1933, 1 subad. ♀, Darkali, November 17-21, 1931, 2 ad. ♂, Mandali, December 17, 1930, 1 ad. ♂; Kulu, Arsu, November 21, 1933, 1 ad. ♂.

***Prunella strophciata strophciata* (Blyth)**

INDIA: Punjab: Kulu, Banjar, December 30, 1932, 1 ad. ♀, January 4, 1933, 1 ad. ♂; Rampur-Bushahr, Darkali, November 17-21, 1931, 3 ad. ♂, 1 subad. ♂, 1 ad. ♀. United Provinces: Garwhal, Kurumtoli, May 10, 1948, 1 ad. ♀, May 12, 1 ad. ♀ (*jerdoni* ≤ *strophciata*); Tehri, Bhujeka, October 12, 1948, 1 ad. ♂; Kumaon, Sumto-Rahlam Pass, June 16-22, 1948, 6 ad. ♂, 3 ad. ♀.

There is a short break in the known range of *strophciata* between the Safed Koh, where the subspecies *sirotensis* occurs, and the Ladak and Himalayan ranges of Kashmir where the species next appears. From Kashmir it has a more or less continuous distribution eastward through the Himalayas, extending to the mountains of western China.

In Baltistan, Ladak, Chamba, and Kangra the resident subspecies is *jerdoni*; it is replaced in northeastern Punjab (Rampur-Bushahr) by nominate *strophciata* which is the resident race from Kumaon eastward. It would appear from the present material that *jerdoni* and *strophciata* meet rather sharply in northern Punjab near the Sutlej River Valley. In the winter of 1931 Dr. Koelz collected in the region near the Kangra-Bushahr boundary and secured individuals of both races but no evident intergrades. Of 32 specimens from the northwest a single specimen from Garwhal is the only one clearly intermediate. Even well within the range of *jerdoni*, at Banjar in the Kulu Valley, Koelz collected two specimens which appear to be *strophciata*, but at Arsu, also in the Kulu Valley, he collected an example of *jerdoni*. The situation stands in direct contrast with that in *Prunella rubeculoides*, for in the very same geographical area *rubeculoides* has a series of completely intergrading populations between the races *muraria* and *rubeculoides*.

Both *jerdoni* and *strophciata* are easily distinguished; a com-

parison of the two in fresh plumage shows *strophhiata* to be more rufous on the upper parts, with darker stripes on the back extending distinctly onto the crown. In addition, *strophhiata* has a more richly colored pectoral band and supercilium and darker and more distinctly streaked flanks. The two races are also separable in worn plumage, for the nominate form is always more heavily and darkly streaked on the back and crown.

Outside of India the species is found in the highlands of northern Burma, southeastern Tibet, Yunnan, Szechwan, Kansu, and the Tsin-ling Mountains. At one time all the Chinese populations were referred to *multistriata* (David), but it now appears that *multistriata* is a synonym of *strophhiata* (cf. Stanford and Ticehurst, 1935; Mayr, 1941). On the other hand, Kansu birds are somewhat paler, and more material may show them to be distinct from *strophhiata*.

Only two of the Koelz specimens were in molt: one (Baltistan, August 22) was changing from juvenal to first-winter plumage, and the other (Baltistan, September 4) was just initiating the post-nuptial molt. By October all specimens are in fresh plumage.

MEASUREMENTS: *Jerdoni*: Ten males, wing, 65.5–71 (68.1), tail, 53–58 (55.9), bill, 12–13.5 (12.8); seven females, wing, 64–69 (66.9), tail, 53.5–56.5 (55.2), bill, 12–13 (12.4).

Strophhiata: Wing, 10 males, 62.5–70 (65.4), tail, 11 males, 50.5–59 (54.3), bill, 11 males, 12–13.5 (12.9); five females, wing, 60–65.5 (62.7), tail, 47–54.5 (50.5), bill, 12–13 (12.5).

The western race appears to be slightly larger, and there is some indication that Kashmir birds may be even larger than Punjab specimens of *jerdoni*.

(The wings of very worn adult males from Kashmir measure 67.5, 70, 71; the wing measurements of adult males from Punjab, in fairly fresh plumage, are 66, 66.5, 68, 69, 70.)

***Prunella rubeculoides muraria* (Meinertzhagen)**

INDIA: Kashmir: Baltistan, Karzong, September 13, 1936, 1 subad. ♂, Karzong Pass, September 14, 2 ad. ♂, upper Tale Valley, August 23, 1 juv. ♀, Tale Pass, August 23–24, 1 ad. ♂, 1 ad. ♀, 1 juv. ♀, Deosai Plain, August 8–9, 1 ad. ♂, 1 ad. ♀, 1 juv. ♂, 1 juv. ♀; Ladak, Shushul, July 24, 1931, 1 ad. ♂, Tankse, July 30, 1 ad. ♂, Tsultak, July 31, 1 unsexed juv., Zongrul, August 1, 1 ad. ♂, Gya, August 14, 1933, 1 unsexed juv., Chorten Chen (Tag Nulla), August 19, 1931, 2 ad. ♂, 2 juv. ♂, 1 juv. ♀, Kangi, September 6–7, 1 ad. ♂, 1 subad. ♀, Leh, September 16–17, 1936, 2 subad. ♀, 1 juv. ♀, Miru, September

24-25, 2 ad. ♂, 1 subad. ♂, Shakkar, Purig, July 24, 1933, 1 ad. ♂; Zankskar, Kargiak, July 11-15, 1933, 2 ad. ♂, 1 juv. ♂, Lagong, July 11, 1 juv. ♀, Rangdum, September 11, 1931, 1 ad. ♂, Bok, September 14, 1 subad. ♀, Sarle, September 20-21, 2 ad. ♀, Cha, September 23, 1 ad. ♀, September 28, 1 unsexed ad.; Rupshu, Karzok, July 6-7, 1931, 1 ad. ♂, 2 ad. ♀, 1 juv. ♂, 1 unsexed juv., Da (Tso Kyun-Hanle), July 12, 1 ad. ♂.

***Prunella rubeculoides muraria* (Meinertzhagen) \leq *Prunella rubeculoides rubeculoides* (Moore)**

INDIA: Punjab: Spiti, Chandra Tal, September 1, 1933, 1 ad. ♀, La Drasa, September 5, 1 ad. ♀, 1 unsexed subad.; Rampur-Bushahr, Kunawar, Chala, October 2, 1933, 1 ad. ♀, Nago, October 5, 1 ad. ♀, Sungnaru, October 11, 1 ad. ♀; Lipe, November 21, 1930, 1 ad. ♀, Chiassu, November 27-December 2, 4 ad. ♀; Lahul, Toyuma, October 7, 1936, 1 ad. ♂, Kyelang, October 18, 1 ad. ♂.

The robin accentor breeds in the Himalayas from Kashmir to Kansu; from west to east there is a tendency towards darkening of the head and back. The resident populations of the western end of the range in Kashmir, *muraria*, are palest; south and east of Ladak *muraria* gradually intergrades with nominate *rubeculoides* until in Nepal and Sikkim *rubeculoides* prevails as a somewhat darker form. All Punjab examples have been identified as intergrades, although some are almost as dark as Sikkim specimens.

In Kansu there is a slight increase in paleness, but it is not very marked. The form of north Kansu, *beicki* Mayr, is doubtfully distinct.

In Kashmir, adults and juvenals begin to molt as early as the first weeks in August; the molt period probably terminates at the end of September.

MEASUREMENTS: *Muraria* (worn adults): Wing, nine males, 79-84 (81.1), tail, 10 males, 59-69 (64.2), bill, 20 males, 13-15.5 (14.6); females, wing, 75, 77, 79, tail, 61.5, 63.5, 65, bill, 13.5, 14, 14, 15.

Muraria \leq *rubeculoides*: Two males, wing, 80.5, 84, tail, 63.5, 69, bill, 14.5, 15.

Prunella ocularis*, *Prunella atrogularis*, and *Prunella fulvescens

Prunella ocularis (Radde) has sometimes been treated as a race of *Prunella fulvescens* (Sewertzoff) and at other times has been granted recognition as a full species. Sushkin (1925) was one of the first to suggest that the two forms were not conspecific,

but he did not state why. It was Stresemann (1928), following Sushkin, who pointed out that *ocularis* combines some of the features of both *fulvescens* and *atroregularis* (Brandt) and that more information would be required to determine of which species the intermediate *ocularis* was a race. Hartert (1910), who had originally included *ocularis* in the Formenkreis *fulvescens*, later (Hartert, 1935) adopted Stresemann's arrangement of keeping the two distinct.

A reëxamination of the three forms convinces me that *ocularis* is closer morphologically to *atroregularis* than to *fulvescens*. A comparison of the three is given in tabular form in table 2. Although the dark throat of *atroregularis* is very striking and undoubtedly the chief reason for associating *ocularis* with *fulvescens*, too much importance cannot be attached to that single character. In the winter plumage of *atroregularis*, the throat feathers are tipped with white but soon wear to produce a uniform color. Both *ocularis* and *fulvescens* have the basal third of the whitish throat feathers dark gray; furthermore, whereas *fulvescens* has a clear throat the gular region of *ocularis* is flecked with brown. Ecologically, however, *ocularis* shows affinity with *fulvescens* rather than *atroregularis*. The latter inhabits coniferous forest and the two others subalpine bush zone.

TABLE 2
COMPARISON OF *Prunella fulvescens*, *P. ocularis*, AND *P. atroregularis*

Character	Species		
	<i>fulvescens</i>	<i>ocularis</i>	<i>atroregularis</i>
Supercilium	White/pale buff	White	Ochraceous buff
Throat	White/pale buff	White, flecked with brown	Dark brown
Under parts	Buff, extending to belly and flanks	Buff, restricted to breast and flanks	Buff, restricted to breast and flanks
Flanks	Virtually unstreaked	Indistinctly streaked	Indistinctly streaked
Back	Pale, indistinctly striped	Dark, distinctly striped	Dark, distinctly striped
Crown	Almost concolorous with back, unstriped	Distinctly darker than back, clearly demarked from back, unstriped	Slightly darker than back, striped in fresh plumage

Although very closely related, *fulvescens* and *atroregularis* are distinct species, and their ranges overlap rather broadly in the

region of the Tian Shan. Geographically, *ocularis*, breeding in the Zagros and Elburz Mountains of Iran, is close to *fulvescens*, whose breeding range includes northern Afghanistan. In winter, however, *atrogularis*, but not *fulvescens*, may occur in northern Iran. Again, the range of *atrogularis* is already broadly divided into two discrete sections; the species breeds both in the central Asian mountains and in the subalpine birch forest of the northern Urals, a break in distribution of about 1500 kilometers. In any case, *ocularis* is as fully isolated spatially from *fulvescens* as from *atrogularis*.

The situation seems best handled by retaining all three forms as distinct species pending new material or information. The Iranian bird, *ocularis*, appears more nearly allied to *atrogularis*, the two perhaps constituting a superspecies.

Prunella ocularis ocularis (Radde)

IRAN: Luristan: Durud, February 23, 1941, 1 ad. ♂, March 9–31, 5 ad. ♂, 1 ad. ♀, April 16–28, 2 ad. ♀, 1 unsexed ad., October 22–25, 1 ad. ♂, 1 subad. ♀, November 5, 1 subad. ♂. Bakhtiari: Ti, February 3, 1941, 1 ad. ♂, Chamchid, February 22, 1 ad. ♂, Gahar, June 1, 2 ad. ♂, 1 unsexed ad. Fars: Persepolis, March 11, 1940, 1 ad. ♂, Jahrum, March 20, 1 ad. ♀, Niriz, March 29, 1 ad. ♂, 2 ad. ♀. Kirman: Pushte, January 16, 1940, 1 ad. ♀, Dehibakri Pass, January 30, 2 ad. ♂, Khatumabad, January 30–31, 1 ad. ♂, 1 ad. ♀, Guragon, February 9–11, 5 ad. ♂, 1 ad. ♀, 1 unsexed ad., Masghun, February 11, 1 ad. ♂. Yezd: Dehibala, Shir Kuh, February 22, 1940, 1 ad. ♀. Northern Iran: Karaj, December 28, 1944, 1 ad. ♂. Kondor, Kuh Pansar, October 5, 1944, 1 ad. ♀.

Much individual variation is evident in this series. Although in comparative plumage, examples from the same locality may have a dark or light brown crown and a buffy or grayish back with broad or narrow stripes. On the whole, the series of specimens from the mountains of Luristan and Bakhtiari are very slightly lighter crowned and less richly colored on the back than the specimens from the hills of Kirman and Yezd. The latter are all birds killed in winter but represent what must be the first record of this species for central Iran.

The single specimen from Karaj, on the southern side of the Elburz, is darker than the others but is in fresher plumage.

The Luristan specimens were collected near the snow line at about 8000 feet as indicated on the specimen labels.

In the mountains of Yemen, Arabia, there is an endemic accentor, *fagani* (Ogilvie-Grant), generally considered to be a

subspecies of *ocularis* although occasionally referred to *fulvescens*. The latter treatment would result from including *ocularis* itself as a race of *fulvescens*.

MEASUREMENTS: Northern Iran, Karaj: One male, wing, 77, tail, 68.5, bill, 15.

Luristan and Bakhtiari: Twelve males, wing, 74.5–80 (76.1), 11 males, tail, 63–69.5 (65.8), 12 males, bill, 13–15 (13.7); four females, wing, 71–75 (73.6), tail, 61–65 (63.6), bill, 12–13.5 (12.8).

Kirman and Yezd: Nine males, wing, 75–80 (77.7), tail, 64.5–73 (69.0), bill, 13–14 (13.6); four females, wing, 74–78 (75.4), tail, 64–71.5 (66.4), bill, 13.5–14 (13.9).

Fars: Two males, wing, 74, 76, tail, 62.5, 67, bill, 14, 14; two females, wing, 72, 73, tail, 61, 63, bill, 13, 13.

The slightly larger Kirman specimens are a little less worn than the others.

***Prunella atrogularis atrogularis* (Brandt)**

IRAN: Tomogaon, February 3, 1940, 1 unsexed ad. Karaj, March 21, 1943, 1 ad. ♀.

AFGHANISTAN: Girishk, October 28, 1937, 5 ad. ♂, 1 ad. ♀, 1 subad. ♀, Pul i Komri, November 4–7, 1939, 2 ad. ♂, 1 subad. ♂, 3 ad. ♀, 2 unsexed ad., Maimana, November 16, 1937, 1 ad. ♀, Andkhui, November 20–23, 2 ad. ♂, 2 ad. ♀, Balkh, November 28, 1937, 1 ad. ♀, October 28–31, 1939, 1 ad. ♂, 1 ad. ♀.

***Prunella atrogularis huttoni* (Moore)**

AFGHANISTAN: Pul i Komri, November 4, 1939, 1 ad. ♂, Balkh, November 29, 1937, 1 ad. ♂, Jalalabad, December 18–19, 1 ad. ♂, 4 ad. ♀, 1 unsexed ad.

INDIA: Punjab: Lahul, Kyelang, October 18–23, 1936, 1 ad. ♂, 1 subad. ♀, Jalma, October 21, 1 ad. ♂, Tirtsing, October 22, 1 ad. ♂; Kangra, Kotla, January 6, 1948, 1 unsexed ad., January 29, 1946, 1 ad. ♀; Kulu, Kulu, December 12, 1933, 1 ad. ♂, December 23–24, 1932, 2 ad. ♂, January 10, 1933, 1 ad. ♀, Arsu, November 16–22, 5 ad. ♂, 1 ad. ♀; Rawalsar, Mandi, January 3, 1933, 1 ad. ♂; Rampur-Bushahr, Darkali, November 16–21, 1931, 2 ad. ♂, 3 ad. ♀, Lipe, November 20, 1930, 1 ad. ♀, Chiassu, December 2, 1 ad. ♂, Kuki, December 18, 1 ad. ♂.

These winter visitors to the Indo-Afghan-Iranian region belong to two subspecies. Over the greater part of this winter territory only one or the other form is found; in northwestern India and immediately adjacent areas in northeastern Afghanistan *huttoni* is found, and over the rest of Afghanistan and Iran *atrogularis* occurs. In the Koelz series there are one or two speci-

mens of *huttoni* from parts of Afghanistan where *atrogularis* normally winters, but in general the two races tend to keep apart. In the Tian Shan, *huttoni* is commoner, but as many as five out of 15 winter specimens from that range in the Rothschild Collection are clearly referable to the nominate form. Hutton's accentor breeds in Russian Turkestan; nominate *atrogularis* nests in the northern Urals.

Nearly all specimens of *atrogularis* can be separated from *huttoni* by the somewhat smaller size, especially shorter bill and tail, of the former, and by the absence in *huttoni* of a pale buff narrow line between the gular patch and pectoral band.

The nuptial plumage is acquired by a process of wear similar to that which takes place in the starling (*Sturnus vulgaris*) and the house sparrow (*Passer domesticus*), but the transformation is not so marked as occurs in those species. After the post-nuptial molt, which seems to take place in August, the plumage is generally pale. The brown throat and chin feathers are tipped with white, the back is indistinctly streaked, the streaks extending fully onto the crown, and a dark brown line extends along the dorsal border of the buffy supercilium. As the season progresses the white-tipped throat feathers wear until the throat is of a uniform chocolate-brown color, the stripes on the back darken and become more distinct, and the entire crown darkens somewhat, obscuring the stripes. In over-all appearance, a spring bird is darker than an autumn bird in fresh plumage.

MEASUREMENTS: *Huttoni*: Seventeen males, wing, [70] 74–79 (75.9), tail, [60] 65–71 [74.5] (67.1), bill, 13–15 (13.8); 11 females, wing, 71–77 (74.5), 11 females, tail, 59–68 (63.8), 10 females, bill, 12–15 (13.5).

Atrogularis: Eleven males, wing, 71–77 (74.6), tail, 60–66.5 (61.7), bill, 11–14 (12.1); 10 females, wing, 70–74 (71.5), tail, 56.5–62.5 (60.0), bill, 11–13 (12.2).

Prunella fulvescens fulvescens (Sewertzoff)

AFGHANISTAN: Sanglech, July 26–27, 1937, 1 ad. ♂, 1 juv. ♂, 1 juv. ♀, 1 fledgling ♀, Munjan Pass, July 27–28, 2 ad. ♂, 1 ad. ♀, 1 juv. ♂, 2 juv. ♀, Sabz Pass, August 28, 1939, 1 ad. ♂, Safedsang, September 20–25, 6 ad. ♂, 1 subad. ♂, 3 ad. ♀, 3 subad. ♀, Burchao Pass, October 10–15, 2 ad. ♂, 3 subad. ♂, 2 subad. ♀, 1 unsexed ad., 2 unsexed subad.

INDIA: Kashmir: Ladak, Muglib, July 29, 1931, 1 ad. ♂, 2 juv. ♂, 1 juv. ♀, Leh, September 16, 1936, 1 subad. ♀, Kangi, September 7, 1931, 1 ad. ♂, 1 ad. ♀, 1 juv. ♂, Miru, September 25, 1936, 1 subad. ♂, Shakrot, September

26, 1 subad. ♂; Baltistan, Sdongfar, September 4, 1936, 1 ad. ♂, Karzong, September 13, 1 ad. ♂, 1 subad. ♂; Rupshu, Rachogba, June 23, 1931, 1 ad. ♀, October 6, 1936, 1 subad. ♀, Rachogba-Serchu Road near Lahul-Rupshu boundary, October 6, 3 ad. ♂, Ganajil, June 25, 1931, 1 ad. ♀, Korzok, July 7, 1 ad. ♀, Da (Tso Kyun-Hanle), July 12, 1 juv. ♂, 1 unsexed juv., Lachulung, August 22, 1933, 1 ad. ♂, 2 ad. ♀, Rogchin, September 28, 1936, 2 ad. ♀, Tso Kar, September 29, 1 subad. ♀, Tozeri, October 3, 1 ad. ♂, 2 subad. ♀; Punjab: Lahul, Dartse, October 10, 1936, 1 subad. ♀.

With Sushkin (1925) admitting no fewer than 10 subspecies and describing seven new ones himself, this little accentor has the dubious distinction of having been one of the most finely discriminated species in the genus. The recent trend has been to reduce the number of named forms. Hartert in 1935 recognized only four races, and Dementiev (1935) considered that there were but three forms (exclusive of *P. ocularis*) in the Russian avifauna. Baker (1924) felt that Indian ornithologists had to deal with only one race, the nominate one, and he rejected Hartert's *dresseri* as a synonym of *fulvescens*. Singularly, Hellmayr (1929), Hartert, and Dementiev accept *dresseri* as one of the best-marked subspecies.

Some workers, for instance, Dementiev (*op. cit.*), extended the range of *dresseri* from Turkestan through Ferghana into Kashmir. Baker (1924) demurred, and none of the material that I have seen confirms the presence of *dresseri* in India. Indeed, every one of the examples collected by Koelz in Afghanistan and northwest India is representative of the nominate race. If the Turkestan race *dresseri*, reputed to be very pale, ever occurs in India it must do so only as a migrant. There is an old specimen taken at Gilgit in December, 1879 (Rothschild Collection), which matches the only example of *dresseri* available, a May specimen from the Chotan Tagh in eastern Turkestan (Rothschild Collection). The age of these skins renders them of questionable value for color comparison. Baker was probably correct; Kashmir and Punjab birds should be referred to nominate *fulvescens*, although *dresseri* might possibly be found in winter.

The first and only previously recorded observation of *fulvescens* in Afghanistan was made by Meinertzhagen (1938) who saw several near Paghman and Ghorband and collected two. Koelz has found them as far west as the Burchao Pass in the Bend i Turkestan Range, and also at Safedsang, farther east in the same range. Since a number of specimens from both locali-

ties were in molt, it is quite likely that they may have bred locally and were not migrants. The species seems certainly to have bred at Sanglech and at Munjan Pass, and perhaps also at Sabz Pass.

In northwestern India it is said to be not uncommon and to nest eastward as far as Rupshu and Lahul.

The first signs of molt appear at the end of August, and molting birds may be found well into October.

MEASUREMENTS: Afghanistan: Twelve males, wing, 73–79 (76.5), tail, 61–66 (63.8), bill, 13.5–15 (14.0); eight females, wing, 73–77 (74.6), tail, 62–66.5 (64.2), bill, 13–14 (13.6).

Northwest India: Eight males, wing, 73–80 (76.9), tail, 61.5–68.5 (64.7), bill, 12.5–15 (13.8); eight females, wing, 72–77 (74.6), eight females, tail, 59–65 (62.0), five females, bill, 13.5–14.5 (13.8).

***Prunella modularis obscura* (Hablizl)**

SYNONYM: *Prunella modularis blanfordi* (Sarudny).

IRAN: Azerbaijan: Tabriz, October 31, 1940, 3 ad. ♂, Ardebil, November 3–4, 1 ad. ♂, 1 ad. ♀, Rezaieh, December 6, 1 ad. ♂. Northern Iran: Karaj, November 14, 29, 1945, 1 ad. ♂, 1 unsexed ad. Mazenderan (region of Gurgan): Dimalu, July 22, 1940, 1 ad. ♂, 1 ad. ♀, 1 juv. ♂, 1 juv. ♀, 1 unsexed juv. Kermanshah: Qasr i Shirin, December 28, 1940–January 6, 1941, 1 ad. ♂, 2 ad. ♀, 3 unsexed ad., Bisitun, January 15, 1941, 1 ad. ♀. Bakhtiari: Chamchid, February 21–22, 1941, 3 ad. ♀. Luristan: Durud, March 2–4, 1941, 1 ad. ♂, 1 ad. ♀.

Two races of *Prunella modularis* are supposed to breed in Iran, *obscura* in the Elburz Range and *blanfordi* in the Zagros Mountains. Paludan (1938) has already shown that this hedge-sparrow does not nest in the Zagros and that the few specimens that have been collected there were quite possibly migrants or winter visitors from the Elburz or farther north. I am inclined to agree with this interpretation, for the small series from Kermanshah, Luristan, and Bakhtiari, all winter specimens, cannot be distinguished from comparable examples from northern Iran.

The differences that Sarudny (1904) observed between nominate *modularis*, *obscura*, and *blanfordi* were undoubtedly due to wear. By January or February the crown streaking is lost; this can be seen in both *obscura* and nominate *modularis* and thus the absence of dark centers to the feathers of the crown cannot be used to separate Zagros and Elburz birds. I find the color of the throat and breast to vary considerably from gray

brown to gray, and I am unable to detect any differences in the character of the flank striping. The subspecies *blanfordi*, based as it is upon two specimens not certainly known to have been breeding, cannot be recognized, and the name must be considered as a synonym of *obscura*.

Even *obscura* is a poorly differentiated race. The breast appears browner and more mottled, the back perhaps a little less rufous and more darkly streaked in *obscura* as compared with the nominate race, but I was unable to make a fair comparison because some of the older specimens examined were badly foxed. However, the breeding populations of the mountains along the southern border of the Caspian Sea and birds wintering both there and in the Zagros Mountains may be referred to *obscura*. The same race is also said to occur in the Crimea, Asia Minor, and the Caucasus (Hartert, 1935). Two January specimens (Rothschild Collection) from the mountains of Lebanon appear also to belong to *obscura*.

The post-nuptial molt was well advanced in a specimen from Dilamu, July 22; a second specimen taken the same day and place is extremely worn but shows no sign of molt.

MEASUREMENTS: Eight males, wing, 67–73 (69.9), tail, 55.5–60 (58.4), bill, 12.5–14 (13.5); eight females, wing, 67–69 (68.1), eight females, tail, 54–61 (57.8), nine females, bill, 13–14 (13.4).

***Prunella immaculata* (Hodgson)**

INDIA: Northern Bengal: Darjeeling District, Tiger Hill, December 23, 1936, 2 ad. ♀.

This species occurs locally from Nepal and Sikkim eastward to northern Burma, Yunnan, and Szechwan. It is quite uniform throughout this range, and no subspecies have been described.

MEASUREMENTS: Wing, 80, 80.5, tail, 56, 58, bill, 13.5, 14.

Other specimens, in the Rothschild Collection, measure:

Northern Bengal, Darjeeling District: One female, wing, 80, tail, 59, bill, 14.

Sikkim: One male, wing, 76.5, tail, 55, bill, 14.5.

North Burma: Four males, wing, 80, 81, 81, 82, tail, 56, 57, 57.5, 59, bill, 14, 14, 14, 14; nine females, wing, 76, 77, 77, 77.5, 78, 78, 78, 79, 81, tail, 55, 55, 56, 56.5, 57, 57, 58, 58, 59; bill, 13, 13.5, 13.5, 13.5, 14, 14, 14, 14.5.

Western China (Yunnan and Szechwan): Four males, wing,

76, 78, 80, 80, tail, 52, 52, 56, 59, bill, 14, 14, 14, 14; two females, wing, 78, 80.5, tail, 55.5, 58, bill, 13.5, 14.

DISCUSSION

CHARACTERS AND SYSTEMATIC POSITION OF *Prunella*

The family Prunellidae consists of 12 species of small passerine birds referred to the single genus *Prunella*. The upper parts of all the species are of various shades of rufous- or brownish-gray and with one exception always streaked or striped. There is usually some expression of a rufous band on the breast or abdomen and/or rufous streaking on the flanks; in one species group the under parts are uniformly buffy, with the flanks slightly streaked. The bill is pointed and depressed, the feet moderate in length, the tarsi weakly scutellate in front, booted behind. Males are frequently slightly larger than females, but otherwise the sexes are similar.

A comparative and graphic representation of the size of each of the 12 species is presented in figure 1. Since weights were not available, the length of the culmen and the length of the wing were chosen as approximate indices of body size, and for every series of measurements the observed range, mean, and twice the standard deviation are shown. Except for the four species that do not occur in the region, measurements were made on adult male specimens from Russian Turkestan, Afghanistan, and northern India where there is the greatest overlap of species' ranges. For *montanella*, *koslowi*, and *rubida*, of which I had no adequate samples, the data are from Hartert (1910) who gave only the observed range of variation. In table 3 are grouped the measurements from which figure 1 was drawn.

It will be seen upon comparison of figures 1 and 3 that there is fair agreement of larger size with greater altitude, but Bergmann's rule is not correctly applied to groups other than populations or races within a single species.

In all the species the annual molt takes place immediately following the breeding season. The adults have a complete molt; birds of the year have only a body molt and can be recognized, from August to November, by the worn rectrices and remiges in combination with the fresh body plumage. Otherwise, first-winter birds resemble adults. Juvenals are streaked and somewhat resemble young finches.

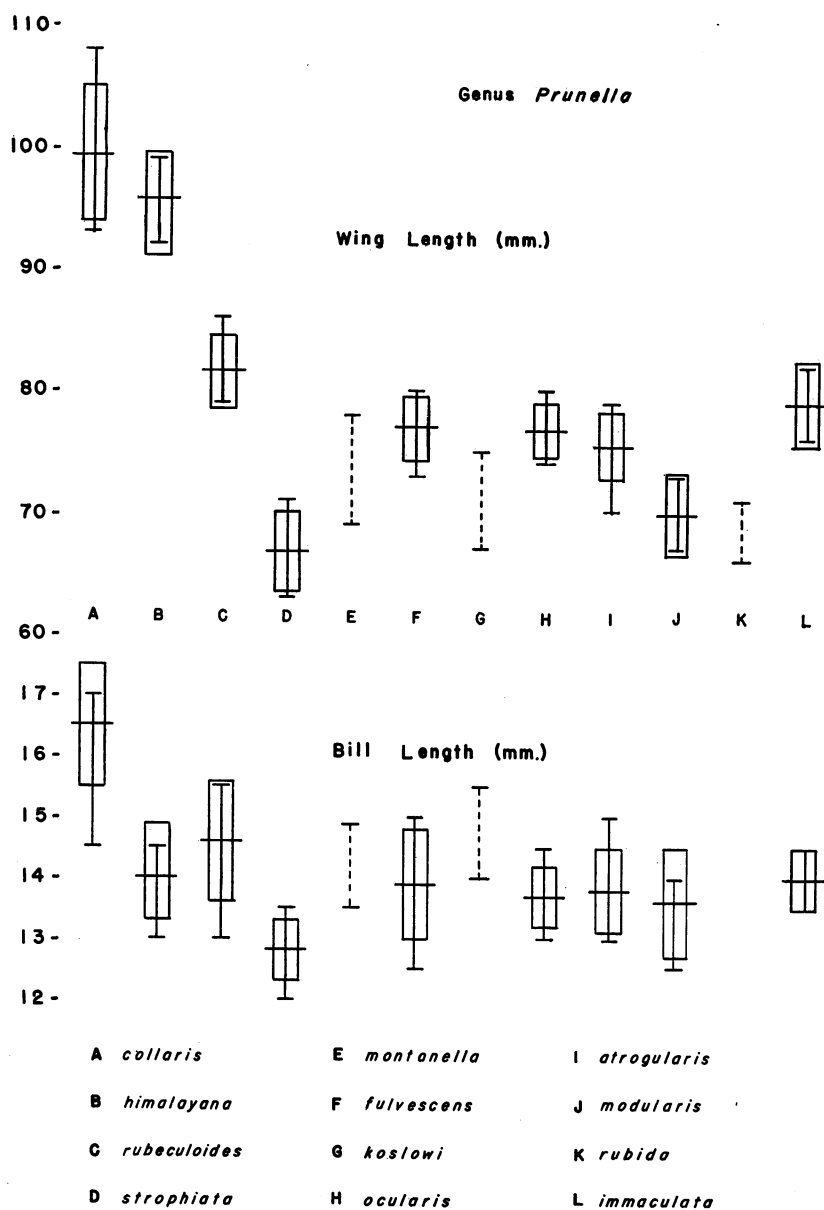


FIG. 1. Size comparison of the species of *Prunella* based upon wing length and culmen length of adult males. Vertical lines: observed range of measurements; horizontal lines: mean of measurements; rectangles: twice the standard deviation on each side of the mean.

TABLE 3
SIZE COMPARISON OF ADULT MALES OF THE GENUS *Prunella*

Species ^a	Wing				Culmen			
	N	Range	Mean	S.D.	N	Range	Mean	S.D.
<i>collaris</i>	36	93-108	99.3	2.75	35	14.5-17.0	16.5	.477
<i>himalayana</i>	13	92-99	95.7	1.88	10	13.0-14.5	14.1	.387
<i>rubeculoides</i>	21	79-86	81.6	1.56	22	13.0-15.5	14.6	.493
<i>strophhiata</i>	23	63-71	66.7	1.66	24	12.0-13.5	12.8	.234
<i>montanella</i>	—	75-78	—	—	—	13.5-15.0	—	—
<i>fulvescens</i>	26	73-80	76.9	1.32	26	12.5-15.0	13.9	.180
<i>koslowi</i>	—	67-75	—	—	—	14.0-15.5	—	—
<i>ocularis</i>	24	74-80	76.7	2.22	23	13.0-14.5	13.7	.237
<i>atrogularis</i>	25	70-79	75.5	1.42	24	13.0-15.0	13.8	.345
<i>modularis</i>	9	67-73	69.8	1.71	9	12.5-14.0	13.6	.465
<i>rubida</i>	—	66-71	—	—	—	—	—	—
<i>immaculata</i>	10	76-82	79.1	1.72	10	13.5-14.5	14.0	.235

^a Included races for purpose of measurement are: *collaris montana*, *c. rufilata*, *c. whymperi*, *c. nipalensis*; *rubeculoides muraria*, *r. muraria* \geq *r. rubeculoides*; *strophhiata jerdoni*, *s. strophhiata*; *fulvescens fulvescens*; *ocularis ocularis*; *atrogularis huttoni*; *modularis obscura*.

The Prunellidae are exclusively Palearctic and chiefly montane. The majority of the species breed in central Asia, but the total range of the family extends from Scandinavia, the British Isles, France, and Spain to Japan, and from Siberia to Burma, India, Iran, and Arabia. Some of the forms are migratory, chiefly the five species of the *fulvescens-montanella* group, but even these migrants do not pass beyond the southern limits of the total breeding range.

Insects compose a large part of the diet in spring and summer; in winter, accentors feed chiefly upon seeds and berries.

No satisfactory determination of the systematic position of *Prunella* has yet been made. Sharpe (1883) included *Prunella* in a group Accentores of the Timaliidae, but the most widely adopted usage has been to refer the genus directly to the Turdidae (cf. Sharpe, 1903; Baker, 1924) or to recognize a family Prunellidae closely related to the thrushes. The Fringillidae have also been suggested as possible allies (Mayr, 1946), chiefly because of a similarity of the color pattern and habits of *Prunella* to certain of the Emberizinae. The muscular crop, common to both the fringillids and accentors, lends some support to

this argument, but the possibility of convergence cannot be eliminated.

SPECIATION IN *Prunella*

At present, the actual or structural phylogeny and the distributional history of the genus cannot be established. The external appearance of each one of the species is a modification of some single plumage pattern, but there is no evidence for considering any one species as more primitive than any other species in either morphology or ecology. However, it is possible to indicate briefly some of the historical and geographical agents influencing the course of speciation.

The Eurasian mountain systems are complexes of high ranges which are more or less discontinuous and which support discontinuous vegetational zones. These conditions might be expected to favor the isolation and divergence of montane populations such as are encountered in *Prunella*. (Two species breed at elevations of over 15,000 feet; in Asia, accentors are seldom met with below 5000 feet, even in winter.) However, isolation does not seem to have been sufficient to produce more than a few morphologically poorly differentiated races since the present distribution was effected. *P. ocularis*, which by now probably has reached the species level, provides the lone exception, but even this form may be older than the last glacial age. Either habitat selection or valleys have not been as efficient barriers to dispersal and gene flow as these factors have been to some other high mountain groups (e.g., *Leucosticte*, *Carpodacus*), or else the elapsed time has not been sufficient for divergence to become evident.

Clearly, the effects of glaciation should also be taken into account in considering the present distribution, but in view of the fact that our knowledge of the Pleistocene of Asia is far from satisfactory and that there exists considerable disagreement over the effects of the ice ages on Asiatic faunas, discussion of glaciation in reference to the Prunellidae is omitted since it could consist only of the most tenuous sort of speculation. When the geological facts are better known and their zoogeographical consequences generally agreed upon, it should be worth while to reinvestigate *Prunella*.

The origin of new species through extinction of intermediate populations of a species appears to have occurred in one species

group. Although now widely separated geographically (see map, fig. 2), *Prunella modularis*, *P. immaculata*, and *P. rubida* are almost surely derived from a common stock. Similar in general appearance, the three species are found in similar, though not identical, habitats. In Japan, *rubida* lives in the high mountains, breeding in the zone of dwarfed trees (mostly birch and pine) at the upper tree limit, 2000 meters and higher. It winters in southern Japan, frequenting the undergrowth in dense

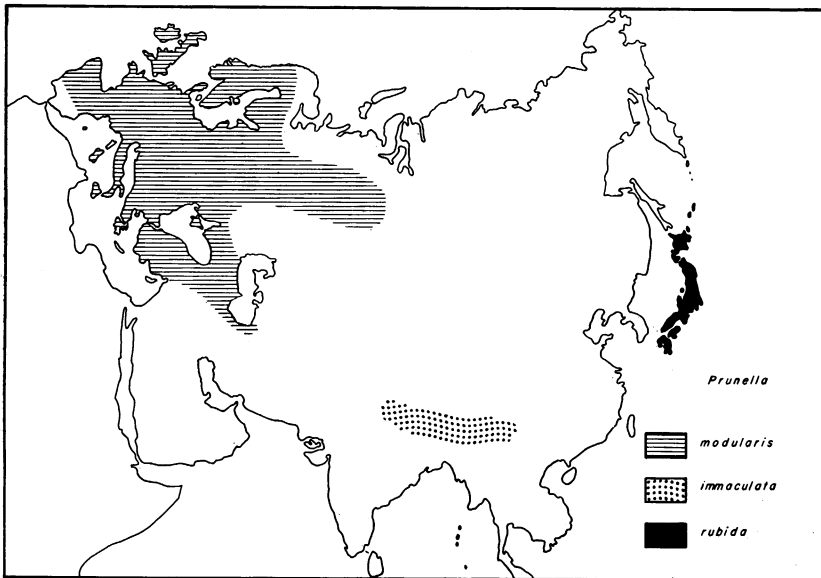


FIG. 2. Breeding ranges of *Prunella modularis*, *P. immaculata*, and *P. rubida*. Horizontal lines: *modularis*; dots: *immaculata*; solid black: *rubida*.

forest. Its song is like that of *modularis* (Jahn, 1942). In the Sikkim and Burmese Himalaya, *immaculata* is characteristically found in the dense forest undergrowth. In the Elburz Mountains of Iran, a race of *modularis* occurs in the bush zone just above the tree line; throughout western Europe, *modularis* is typically a bird of the coniferous forest; in England, *modularis* frequents the hedgerows, which replace the original English forest.

Seemingly, the three forms represent the surviving populations, at one time probably subspecies (cf. Hartert, 1910; Steg-

mann, 1938), of a formerly widespread species, the other races of which have been extirpated by large-scale climatic disturbances of the habitat and by their inability to cross barriers as freely as species such as *Prunella collaris*.

ECOLOGY

The importance of ecological compatability for the persistence of species is well known; a good review is given by Crombie (1947). Since over the greater part of the Palearctic two or more of the very similar species of *Prunella* occur together, it seemed worth while to discover the factors that prevent them from competing. A survey of the literature showed that, with one apparent exception, wherever two or more species are sympatric during the breeding season they do not occupy the same habitat, and because of the distinct zonation of the flora on mountain slopes, habitat isolation is often reflected as altitudinal segregation.

Schäfer (1938), reporting on five species in eastern Tibet, noted the following distributions:

Collaris: Breeding in rocky alpine meadows, especially among calcareous outcrops, at 4500 to 5000 meters and higher; non-migratory.

Rubeculoides: Dwarf willow and rhododendron scrub, especially in damp, rockless, open meadows during summer, at 3900 to 4800 meters; in winter, descends vertically in valleys, keeping to wet areas.

Fulvescens: Nests in same scrub zone as *rubeculoides*, but prefers rocky, arid portion of habitat; in winter, descends farther into valleys than *rubeculoides*, keeping to rockier and drier areas.

Strophiata: In summer, is found in open woodland near the upper limit of the forest, at 3900 to 5000 meters depending upon height of tree line; descends in winter into the valleys and cultivated fields, preferring hedges and bushes.

Immaculata: Breeds in deep coniferous forest, prefers damp situations and seeping water, and noted as a quiet, shy skulker, moving about like a small mammal on the forest floor; descends somewhat in winter but never leaves the woods. [Baker's (1924) account of this bird is so conspicuously different from that of Schäfer and other observers, and contradicted by the appearance of the bird itself, the color of which Schäfer took

pains to point out is beautifully adapted to its mode of existence, that Baker's statement requires confirmation before it should be accepted. Baker states that *immaculata* is a bird of bleak, bare hillsides covered with furze and thorny bushes; such a radical change of habitat over so limited a range scarcely seems possible.]

With certain exceptions, the ecological preferences of these five species appear to be much the same over the remainder of their ranges (see, for instance, Baker, 1924, 1933; Rensch, 1923; Whistler, 1923, 1925; Hartert, 1935; Ludlow and Kinnear, 1933).

The distribution of *Prunella* in the Elburz Mountains of Iran is also instructive. Three species breed on the northern slopes of this range: *collaris*, *ocularis*, and *modularis*. The former, as in Tibet, is confined to the highest alpine meadows. The two latter share the bush zone, but from the accounts of Heinrich, reported by Stresemann (1928), *ocularis* occurs at higher altitudes near the alpine zone, while *modularis* is found at somewhat lower elevations near the edge of the forest. In western Europe, *modularis* gradually descends lower to the hedgerows of Britain, making the transition through the coniferous forest of Germany.

In the large area of central Asia extending from eastern and southern Siberia to Mongolia, Sinkiang, and Russian Turkestan, there are six sympatric species. Four of these, *fulvescens*, *atroregularis*, *koslowi*, and *montanella*, comprise a group of exceedingly similar species. The last-named species has a more northern distribution than the others and overlaps them only in southern Siberia and northern Mongolia. In north Siberia, *montanella* breeds near the tree line; in the Sajan Mountains, it is a resident of the subalpine zone (Hartert, 1935). *P. koslowi* is a resident of mountain deserts and semi-deserts where there are rocky outcrops, sparse grass, and growths of *Caragana* bushes (Koslova, 1933; Hartert, 1935). The coniferous forest zone, occupied by *strophiatea* in northern India, is taken over by *atroregularis* elsewhere (Hartert, 1935), although in the north Urals this species breeds in birch forest (Portenko, 1937). The fourth species of this group, *fulvescens*, apparently occupies the same habitat that it does in Tibet—scrub and dwarf bush zone. It may subdivide the habitat with *montanella* where the two overlap, as *fulvescens* does where it overlaps with *rubeculoides*.

A pair of very similar species, *collaris* and *himalayana*, share

the alpine zone in central Asia. As a matter of fact, most of the range of *himalayana* is coëxtensive with part of the range of *collaris*. Both species breed in rocky alpine meadows at the same altitude, and no one seems to have observed any differences in their ecologies (cf. Koslova, 1933). They may truly be competing and one driving the other out, but there is no direct evidence for this. Perhaps their ecological segregation is so subtle as to have been overlooked, as Schäfer (1938) indicates was once the case with *fulvescens* and *rubeculoides*. A special study seems called for to determine if *himalayana* and *collaris* are, in fact, competing, and, if not, what is preventing competition.

The Japanese *rubida* is ecologically similar to both *modularis* and *rubeculoides*, but all three species are completely allopatric.

On the whole, the species-habitat associations are fairly clear cut, but since the typological concept is as inapplicable to ecology as it is to morphology, not unexpectedly some variation is met with. The ecological and altitudinal distributions are diagrammed in figure 3; in table 4 an attempt is made to show the

TABLE 4

ECOLOGICAL DISTRIBUTION OF SPECIES OF *Prunella*, SHOWING VARIATION IN HABITAT PREFERENCE

(The most euryzonal species tend to be those having least geographical overlap with similar species.)

Species	Alpine Meadow and Rocky Slopes	Dwarf Pine, Caragana Bush, Shrub	Coniferous Forest and Taiga	Deciduous Forest
<i>collaris</i>	X ^a			
<i>himalayana</i>	X			
<i>rubeculoides</i>		X		
<i>strophiatea</i>		x	X	
<i>fulvescens</i>		X		
<i>montanella</i>		X	X	
<i>koslowi</i>		X		
<i>atroregularis</i>		x	X	x
<i>ocularis</i>		X		
<i>modularis</i>		X	X	X
<i>rubida</i>		X	x	
<i>immaculata</i>		?	X	?

^a Capital letter indicates most common habitat associations; small letter indicates an occurrence, but not the usual association.

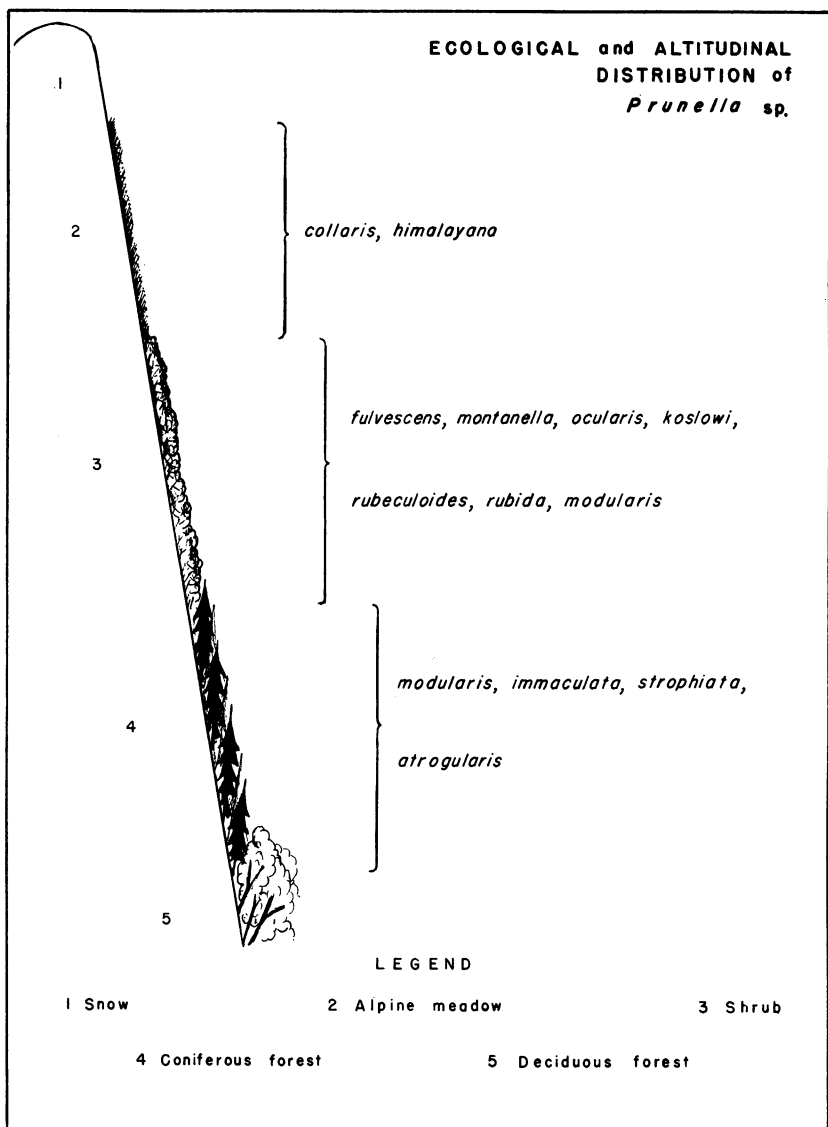


FIG. 3. Ecological and altitudinal distribution of the species of *Prunella*. Variation of this broad pattern is shown in table 4; restriction of several species to lesser habitats included within the larger zones is discussed in the text.

total range of occupied niches, but the chart is quite probably incomplete.

In summary, of the 12 species of the genus *Prunella*, nine species were found to replace one another ecologically where sympatric. One species, *immaculata*, because of its more specialized habitat, was found to be separated both ecologically and geographically. Seven species, having the same ecological requirements, replace one another geographically (*ocularis-fulvescens*, *atrogularis-strophiiata*, *modularis-rubeculoides-rubida*). Two species, *collaris* and *himalayana*, were found to be partially sympatric, with no evidence of an ecological differential in the area of overlap, and further study is suggested.

It may sometimes happen that isolated populations will have achieved complete reproductive isolation but only partial ecological compatability, or that two species have just slightly dissimilar ecologies. In the zone of overlap, natural selection will operate to increase ecological divergence; the selective effects of competition will tend to draw the species farther apart until each occupies a more restricted niche in the environment to which one is better adapted than the other. Selection resulting from competition between closely related species occupying the same general ecological zone seems possibly to have occurred at least twice in *Prunella*. As stated above, where they are sympatric, *fulvescens* and *rubeculoides* share the same bush zone, although each is limited to slightly different habitats within the larger zone. A similar situation is seen in Iran, where *modularis* and *ocularis* occupy the bush zone but appear to subdivide the included habitats. There may be such a slight differential in the ecologies of *himalayana* and *collaris*, a difference that has so far escaped detection. However, inspection of figure 1 suggests one possible means by which competition may be avoided. The alpine accentor has a larger bill than *himalayana*, but the size difference is so slight, of the order of 2 mm., that I hesitate to attach any biological significance to it. Lack (1944) includes size differences between pairs of similar bird species as one common method of securing ecological compatability, the assumption being that sufficiently different types of food are utilized to prevent critical overlap of diet. The beak differences in Darwin's finches (Geospizinae) provide an excellent illustration of this point, but it is not known if the inequality of bill size is a factor in the ecological adjustments of the alpine and Altai accentors.

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