THE SYSTEMATIC POSITION OF THE SURFBIRD, *APHRIZA VIRGATA*

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The taxonomic relationships of the Surfbird, *Aphriza virgata*, have long been one of the most controversial problems in shorebird classification. Although the species has been assigned to a monotypic family (Shufeldt 1888; Ridgway 1919), most modern workers agree that it should be placed with the turnstones (*Arenaria* spp.) in the subfamily Arenariinae, even though they have reached no consensus on the affinities of this subfamily. For example, Lowe (1931), Peters (1934), Storer (1960), and Wetmore (1965a) include the Arenariinae in the Scolopacidae (sandpipers), whereas Wetmore (1951) and the American Ornithologists' Union (1957) place it in the Charadriidae (plovers). The reasons for these divergent views have never been stated. However, it seems that those assigning the Arenariinae to the Charadriidae have relied heavily on their views of turnstone relationships, because scholars who have paid particular attention to the Surfbird alone have concluded (1) that it is closely related to the Scolopacidae (Shufeldt 1888), (2) that it is an offshoot of the subfamily Calidridinae* (Lowe 1931), or (3) that there is no evidence against its inclusion in the Scolopacidae (Bock 1958). In this paper I wish to review and extend the evidence that supports the inclusion of the Surfbird in the Scolopacidae.

HISTORY OF SURFBIRD TAXONOMY

Described as *Tringa virgata* by Gmelin in 1789, the Surfbird was placed in a new genus, *Aphriza*, by Audubon (1839), who took no definite stand on its relationships. Yet, he did note (p. 249) that it bore "a considerable resemblance to the Knot" as well as to the turnstones, and that it differed from the latter in bill morphology, tail shape, and tarsal scutellation. Sclater and Salvin (1873:143), without stated reasons, united the Surfbird, turnstones, and *Pluvianellus socialis* as a subfamily of the Charadriidae. Baird, Brewer, and Ridgway (1884) elevated the turnstone-Surfbird unit to family rank. But, although they stated (p. 126) that *Aphriza* "agrees very closely" with *Arenaria*, the only points of similarity mentioned were "robust feet, without trace of web between toes, the well formed hind toe, and the strong claws; the toes with a lateral margin forming a broad flat under surface." These differences are hardly sufficient to support familial differentiation, or even to suggest close generic relationship.

Coues (1884:605) was uncertain about the Surfbird's relationships. He called it "a remarkable isolated form, perhaps a plover and connecting this family with the next [Haematopodidae] by close relationships with *Strepsilas* [*Arenaria*], but with the hind toe as well developed as usual in Sandpipers, and general appearance rather sandpiper-like than plover-like. *Aphriza* might go under Haematopodidae next to *Strepsilas* [he considered the turnstones a subfamily of the oystercatchers] or, perhaps better, *Aphriza* and *Strepsilas* might together constitute a family Aphrizidae, next to, but apart from, Haematopodidae." Although he adopted the latter course (1903), his resulting classification was one of convenience, since he stated (p. 783) "there is probably no better way of arranging these two unconformable genera." Coues also thought these genera had "much in common," but noted only (p. 784) that they "agree in structure of feet, which are 4-toed, with anterior toes cleft to base and tarsi scutellate in front." By these criteria the Aphrizidae has much in common with many families.

Shufeldt (1888) made the first serious attempt to determine the Surfbird's relationships by comparing its skeleton with those of other Charadrii, including *Arenaria*, *Charadrius*, and *Haematopus*. He concluded (p. 337) that the "sum total of skeletal characteristics place . . . [*Aphriza*] nearer the Tringeae [Scolopacidae] . . . than it does to the plovers; less to *Arenaria*, and far less to *Haematopus*." He placed *Aphriza* and *Arenaria* in separate families. Ridgway (1919:57), who followed Shufeldt, characterized these families as follows:

a. Bill distinctly convex terminally and constricted subterminally, neither the maxilla nor mandible depressed terminally; lateral grooves of

* The name of this subfamily has been spelled "Calidridiinae" (*e.g.*, A.O.U. 1957) and Calidritinae (*e.g.*, Lowe 1931). According to Brown (1954: 724) the genitive singular of the feminine Greek word *skalidris* (*calidris* L.) is *skalidridos*. Thus, the stem of the word is *skalidrid-*, and the name of the subfamily should become Calidridinae.

bill extending to base of convex terminal portion; legs and feet much more robust, the lateral membrane of anterior toes more strongly developed, distinctly roughened or serrate; transverse scutella of acrotarsium broken into hexagonal scales on upper and lower portions; planta tarsi reticulate; tail emarginate ..... Aphrizidae.

aa. Bill tapering to the acute tip, not constricted subterminally, both maxilla and mandible flattened at tip; lateral grooves of bill extending not more than half way to tip; legs and feet more slender, the lateral margin of anterior toes less developed, smoother; transverse scutella of acrotarsium continuous; planta tarsi scutellate; tail truncate ..... Arenariidae.

Note that the differences that Ridgway used to separate these families include characteristics of foot structure that Baird, Brewer, and Ridgway (1884) and Coues (1884; 1903) had previously used to unite *Aphriza* and *Arenaria* in a single family.

From studies of myology, pterylography, color pattern, and skull morphology, Lowe (1931:747–50) concluded that *Arenaria* and *Aphriza* were closely related, and that both were specialized calidridine sandpipers. However, his myologic and pterylographic studies were inconclusive, and merely showed that both forms were waders. Furthermore, his remark (p. 749) that "the colour-pattern of *Aphriza* and *Arenaria* present points of such obvious resemblance that . . . it can hardly fail to suggest a genetic basis of community" was clearly an overstatement. The only "obvious" resemblance is between the nonbreeding plumages of the Surfbird and Black Turnstone (*Arenaria melanocephala*), and this may be due to convergence, since both species inhabit rocky coasts in winter (cf. also the rather similar nonbreeding plumages of other rock-inhabiting waders, *e.g.*, *Erolia maritima*, *E. ptilocnemis*, *Heteroscelus incanus*, and *Haematopus bachmani*). Skull morphology did support his view. He showed (1925) that the morphology of the quadrate was useful in distinguishing sandpipers from plovers, and (1931) that the structure of the maxillo-palatine strut could be used to separate the major scolopacidine groups. In *Aphriza* and *Arenaria* "the quadrato-tympanic morphology . . . is scolopacidine" and "the morphology of the maxillary-palatine angle is . . . eroliine" (Lowe 1931:748).

Bock (1958:86) confirmed that the palate structure in these genera was like that of the calidridine sandpipers; yet, he considered the Arenariinae "Incertae Sedis."

In summary, although the only substantial evidence that has been presented to date indicates that *Aphriza*, at least, is a sandpiper, taxonomists continue to disagree on the placement of the Arenariinae. It seems obvious from the foregoing review that the cause of this disagreement is the tacit assumption that *Aphriza* is most closely related to *Arenaria* and, therefore, that both genera must be classified together. A consideration of the relationships of the turnstones is beyond the scope of this paper, but it must be emphasized that no evidence yet offered strongly supports the Arenariinae as a natural taxon.

RELATIONSHIP OF THE SURFBIRD TO THE CALIDRIDINE SANDPIPERS

Lowe (1931:747–50) not only claimed that the Surfbird was a sandpiper, but he also postulated that it was most closely related to the Knot (*Calidris canutus*) and the Red-backed Sandpiper (*Erolia alpina*). Skull morphology provided the major support for his position. Other evidence further indicates the Surfbird's affinity to the calidridine sandpipers, and particularly to the Knot and the Great Knot (*C. tenuirostris*).

EXTERNAL MORPHOLOGY

In a separate study (Jehl 1967) it was shown that downy plumages offer a highly reliable index to relationships in the waders (Suborder Charadrii). The Surfbird chick is typically calidridine in color, pattern, and feather structure, and is completely distinct from chicks of turnstones, plovers, or other groups of waders. An excellent photograph of newly hatched Surfbirds may be found in Wetmore (1965b: 324). The only specimen known to me (U.S. Natl. Mus. no. 286741; description in Bent 1929:273) is of a chick approximately one week old, in which the primaries, scapulars, and some of the flank feathers had begun to erupt. This chick is shown with chicks of *Calidris canutus* and *Arenaria interpres* in figure 1. Although it is not evident in the photograph, owing to the age of the chick and the preparation of the skin, the Surfbird chick is nearly identical to that of the Knot, even to details of face pattern; moreover, it is more similar to Knot chicks than to those of other calidridine sandpipers. Portenko's plate (1933: opp. p. 96) shows that chicks of the Great Knot are like those of the Knot. The turnstone downy plumage is not calidridine, but has probably been derived from that of the tringine sandpipers (Jehl 1967).

The breeding plumage of the Surfbird, which is totally unlike that of the plovers and turnstones, is similar to that of several calidridine sandpipers, but most closely resembles that of the Great Knot. The pattern and coloration on the head, neck, and back of these species are nearly identical. The heart-shaped

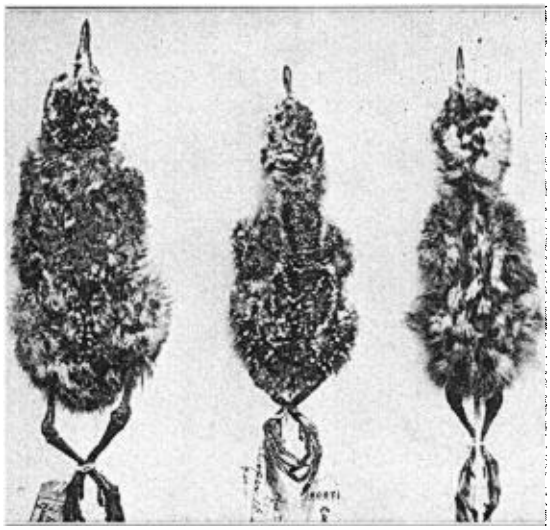

FIGURE 1. Left to right, downy young of *Aphriza virgata*, *Calidris canutus*, and *Arenaria interpres*.

or V-shaped markings at the tips of the breast and flank feathers are also similar; similarly patterned feathers are found in a few other calidridine species (*e.g.*, *E. ptilocnemis*) but not in plovers or turnstones. In size, underwing pattern, and whitish rump, the Surfbird also resembles the Great Knot more closely than any other sandpiper (figs. 2 and 3).

The Surfbird's juvenal plumage is more like that of the Knot than that of any other calidridine, although the resemblance is not particularly close. The nonbreeding plumage is similar to those of other rock-inhabiting sandpipers.

The toes of the Surfbird, which received much attention from early taxonomists, differ from those of the turnstones in having a "strongly developed lateral tumid membrane to the anterior toes" (Ridgway 1919:57). In some calidridines, particularly the knots, this membrane is also prominent.

Unlike the calidridine sandpipers, in which the podotheca is scutellate, the podotheca of

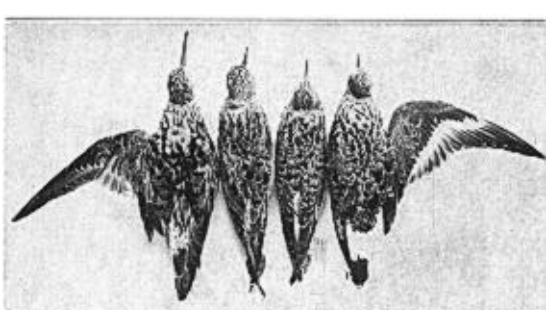

FIGURE 2. Dorsal view of *Calidris tenuirostris* (two left) and *Aphriza virgata* (two right) in breeding plumage. The bill of one knot is broken.

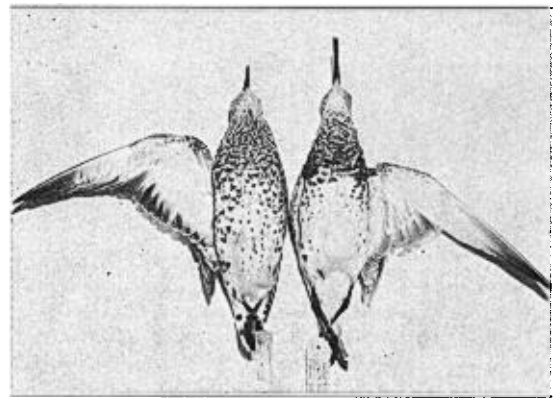

FIGURE 3. Ventral view of *Aphriza virgata* (left) and *Calidris tenuirostris* (right) in breeding plumage.

Aphriza is scutellate to reticulate anteriorly, reticulate posteriorly.

The Surfbird differs most obviously from the calidridine sandpipers in having a superficially plover-like bill. Yet, an approach to a Surfbird-like bill occurs in the Knot, in which the bill is relatively short, the dertrum is slightly inflated, and the premaxilla is slightly broadened distally.

BREEDING BIOLOGY

The breeding habitat utilized by Surfbirds is unlike that of any calidridine sandpiper except the Great Knot. Both apparently nest exclusively in alpine areas, Surfbirds in southern Alaska, Great Knots in Anadyrland (fig. 4). The Knot nests on tundra, although it may also nest on rocky plateaus or on elevated slopes.

Little is known of the Surfbird's breeding behavior. Its courtship is undescribed. Dixon (1927) reported that only one bird, a male,

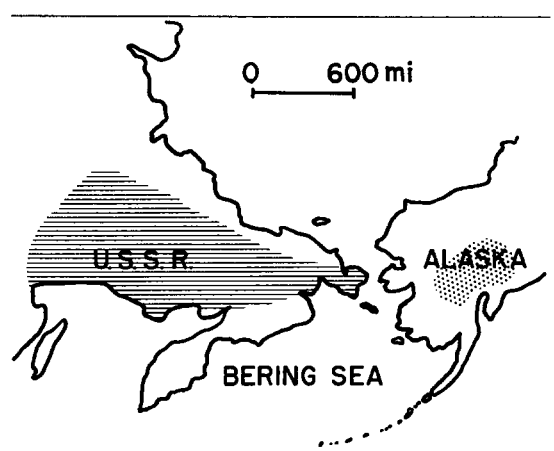

FIGURE 4. Approximate breeding ranges of *Aphriza virgata* (stippled) and *Calidris tenuirostris* (horizontal lines). Data from A.O.U. (1957) and Dementiev and Gladkov (1951).

incubated at the single nest he observed, and that brood patches were present on the five males, but not the two females, that he collected. From this he concluded (p. 14) that "the male does most, perhaps all, of the incubation." His data, however, are not unequivocal. His observations were brief (elapsed period of 16 hours) and were made hourly, not continuously; thus, an undetected changeover could have occurred. Variation in distraction displays indicated to him (p. 13) that a "second bird" was incubating. Furthermore, although he did not find brood patches on the females that he shot, he presented no evidence that these birds were paired, or even had laid eggs. On the other hand, both members of a presumed pair collected by H. Kyllingstad, near Mountain Village, Alaska, have well-developed brood patches (Univ. Mich. Mus. Zool. nos. 123660, 123661). I believe that, as in most other calidridine sandpipers, both sexes of the Surfbird will be found to share in incubation.

In the Knot, both sexes incubate (Parmelee and MacDonald 1960), and the same is probably true of the Great Knot, for Schaanning (1929:38–39) collected a pair at a nest containing fresh eggs. Apparently only one Surfbird (Murie 1924) and one Great Knot (Portenko 1933) have been collected with chicks; both were males. Male Knots (and probably males of most calidridine species) remain with their chicks longer than do females (Parmelee and MacDonald 1960). In the Ruddy Turnstone (*A. interpres*) females do a major share of incubation, and both parents remain with the chicks until they are fledged (Parmelee and MacDonald 1960).

The distraction display of the Surfbird has been described by Dixon (1927:13). When flushed from the nest, the bird runs off "with wings half spread and tail spread out fan-like and dragging on the ground." This type of display is typical of many calidridine species and has been reported for both the Knot (Parmelee and MacDonald 1960) and Great Knot (Portenko 1933). Dixon (1927) observed another distraction display in which the Surfbird, when flushed from the nest, leaps directly toward the head of the intruder; this behavior has not been reported for other sandpipers. Parmelee and MacDonald (1960: 37) described "broken-wing" distraction behavior in the Ruddy Turnstone.

DISCUSSION

The available data confirm that the Surfbird is a calidridine sandpiper and generally support Lowe's view that it is closely related to the knots. In size, plumage pattern, and foot structure, the Surfbird is more similar to knots than to other calidridines. Its downy plumage is most like that of the knots, and its breeding plumage is extremely similar to that of the Great Knot. Data on the breeding biology of the Surfbird are too incomplete to give much support to a Surfbird-knot relationship, but they do not argue against that possibility.

In nonbreeding and juvenal plumages the Surfbird differs somewhat from the knots but, as suggested above, the color and pattern of the nonbreeding plumage may indicate selection for cryptic coloration on rocky backgrounds; the juvenal plumage, which is much like the nonbreeding plumage, probably reflects similar selection. The greatest differences between the knots and the Surfbird are in bill shape and tarsal scutellation, but even in bill shape the Surfbird is most like the knots; the significance of the latter difference is unknown.

The similarities discussed above allow some speculation on the evolutionary history of the Surfbird. As a working hypothesis I would suggest that the Surfbird is most closely related to the Great Knot. The breeding habitats of the two species are similar, are geographically close, and are separated by a major natural barrier, the Bering Sea (fig. 4). Possibly a population of knot-like sandpipers became restricted (during an early glacial advance?; cf. Larson 1957) to mountains on one side of the Bering Sea and subsequently colonized the mountains of the opposite coast. The Alaskan population became adapted to feeding along rocky shores, the Asiatic population to feeding on mudflats. Because of the distance between the populations (the distance between known breeding localities of these species is approximately 1200 miles), there was little, if any, subsequent gene flow, and the populations diverged rapidly. According to this hypothesis the differences in bill morphology would result from selection on the wintering grounds, but data on the feeding behavior of both species on the nesting and wintering grounds are needed to test this suggestion.

TAXONOMIC CONCLUSIONS

The establishment of relationship between the Surfbird and the calidridine sandpipers necessitates its removal from the Arenariinae and its inclusion in the Calidridinae, where it is probably best placed next to *Calidris tenuirostris*. The affinities of the turnstones require further study. I believe that they are most closely related to the tringine sandpipers. But, even if they are offshoots of the Calidridinae,

there is no reason to postulate that they are more closely related to the Surfbird than to any other species. Until further data are available, the turnstones should be retained as the sole members of the Arenariinae.

SUMMARY

The Surfbird (*Aphriza virgata*) has traditionally been grouped with the turnstones (*Arenaria*) in a subfamily of either the Charadriidae or the Scolopacidae. Evidence reviewed in this paper confirms Lowe's (1931) view that the Surfbird is a calidridine sandpiper, and supports the view that it is closely related to the knots, particularly *Calidris tenuirostris*. No evidence has yet been presented that strongly supports a close relationship between *Aphriza* and *Arenaria*. It is recommended that *Aphriza* be removed from the Arenariinae and placed next to *Calidris tenuirostris* in the Calidridinae.

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