THE HISTORY, BEHAVIOR, AND BREEDING BIOLOGY OF THE ST. KILDA WREN

By Edward A. Armstrong

The island group of St. Kilda lies about fifty miles west of the Sound of Harris in the Outer Hebrides and consists of Hirta or St. Kilda proper (1575 acres), Soay (244 acres), and Dún (79 acres), lying close together, with Boreray (190 acres) and huge rock stacks, Stac an Arnim and Stac Lee, some four miles to the northeast. All the islands are precipitous and the sheer cliff of Conachair (1200 feet) on Hirta is the highest in the British Isles. The village on Hirta was inhabited for hundreds of years until 1930 when the few remaining islanders were evacuated. Although the romantic interest of St. Kilda stimulated many visitors to record their impressions, only desultory observations of the St. Kilda Wren (*Troglodytes troglodytes hirtensis*) were made before the evacuation. As transport is difficult to arrange and there are days when landing is impossible, no ornithologist has been able to make a thorough study of the bird. Moreover, the advanced dilapidation of the abandoned cottages in which visiting naturalists used to stay renders conditions more difficult. This situation forms some justification for a review of the main facts of the life history of the St. Kilda Wren, although the writer's stay on Hirta lasted only seven hours.

Appearance and General Behavior

In the field, the upper-parts of St. Kilda Wrens look grayer and their under-parts look paler than those of European Wrens (*Troglodytes t. troglodytes*). St. Kilda Wrens are less ruddy than the latter, though Harrisson and Buchan (1936) remark that dark birds have a more rufous appearance than pale individuals. Commenting on the difference in appearance between birds they say (p. 19) that "evidence for dimorphism similar to that in the mainland wren, is strong." There is a certain amount of variation among European Wrens in Britain, but it could not be called dimorphism. Indeed, to call St. Kilda Wrens dimorphic is rather misleading as there are intermediates, though they can be roughly denominated "light" and "dark." The conspicuous dark barring on the mantle of some birds is particularly distinctive. Dresser (1886: 44) minimized the importance of the stoutness and length of the St. Kilda Wren's bill as diagnostic characters, yet even in the field close observation reveals that the bill of this race is stronger than the bill of the European Wren. Modification of the bill is characteristic of the insular subspecies of the North Atlantic

and North Pacific. Thus, *T. t. islandicus* and *T. t. zetlandicus* have stronger bills than *T. t. troglodytes;* and, in the Pacific, *T. t. tanagaensis* and *T. t. semidiensis* have relatively long bills (Oberholser, 1919: 231, 234).

St. Kilda Wrens constantly work along the walls in the village and pass in and out of chinks in the "cleits"—oval, stone structures in which the villagers used to store carcasses of birds, etc. On cliffs they take *Machilis* and tipulids, and feed among nesting Fulmars (*Fulmarus glacialis*) and Puffins (*Fratercula arctica*).

Like European Wrens, the wrens of St. Kilda occasionally sun-bathe. The molt occurs from early August until well into September (Clarke, 1915; Harrisson and Buchan, 1936).

Most of those who have studied the St. Kilda Wren record that it is tamer than the European Wren in Britain. The St. Kilda birds are more tolerant of observers near the nest. The males of several, if not most, races are apt to seem more timid than their mates, but it is difficult to compare the timidity of the sexes at the nest as it is bound up with the relative strengths of the drive to feed the nestlings, which in some races is weaker in the males. Away from the nest I found that birds, when disturbed, tended to fly out of sight. My impression was that they were not quite so bold as Shetland Wrens (*T. t. zetlandicus*), but were somewhat more tolerant of the presence of a human observer than Hebridean Wrens (*T. t. hebridensis*). There is no reason to think that either the period of "persecution" or the subsequent interval during which the wrens have seldom seen a human being has made any difference to their reactions to mankind.

HISTORY AND POPULATION

T. troglodytes is the only species of wren in Eurasia and is evidently a comparatively recent immigrant from the New World. It may have reached Asia by the Bering Straits land-bridge no earlier than the Pleistocene (Mayr, 1946; and *in litt.*). If it were known that during any phase of the Ice Age, conditions were too extreme on St. Kilda for the wren to survive, it would be possible to infer the approximate period which has been required for subspeciation. Unfortunately the extent to which there may have been refugia in Britain is still in dispute, though the evidence for such in the Western Isles is increasing. The available data suggest that St. Kilda may have remained ice-free. Turrill (1927) says that the flora of St. Kilda is much as it was in late Pliocene times and that it survived the Ice Age *in situ*. The climate has been milder than it is now, for examination

of the peat has disclosed pollen of birch, pine, alder, hazel, and willow (Poore and Robertson, 1949). As a wren habitat it must have approximated country favored by the European Wren more than at present, for trees do not now grow there. Conditions are probably similar to those prevailing on some of the North Pacific islands where wrens are found.

The wren was mentioned as one of the birds of St. Kilda by Martin (1698) and Macaulay (1764). Mackenzie (1905), publishing notes made by his father, who was on the islands from 1829 to 1843, refers to the wrens as resident. Apparently A. G. More was the first to suspect that the wren might be distinctive, but Barrington (1884) failed to obtain specimens and it was left for Dixon to bring back skins from which Seebohm (1884) described the bird as a new species. After Dresser (1886) had criticized its being given this status it was reduced to subspecific rank.

The recognition of the St. Kilda Wren as distinct inaugurated a period during which skins and eggs were sought by museums and collectors. Soon the cry was raised that its extinction was imminent. The outcome was the passing of "The Wild Birds Protection (St. Kilda) Amendment Bill, 1904" providing legislative protection for the St. Kilda Wren and Leach's Petrel (*Oceanodroma leucorhoa*). Thus the St. Kilda Wren played a part in stimulating the campaign which has gradually resulted in the more adequate conservation of British wildlife. It is curious that this should be so, as in the interests of the foraging activities of the islanders, who lived largely on the birds and their eggs, St. Kilda had been expressly omitted from the Wild Birds Protection Act of 1880.

So vehemently did the protectionists advocate, and sometimes exaggerate, their case that it has been erroneously assumed, and is still believed, that the St. Kilda Wren narrowly escaped extermination. As long ago as 1884, however, Barrington, who had climbed cliffs on St. Kilda, said of the wren (p. 384): "It would take some of the best cragsmen in the Alpine Club to extirpate it." Two myths became established—that the wren had nearly become extinct and that legislation had saved it. Harrisson and Buchan (1934: 134) remarked that "in 1888 the wren was almost extinct." Apparently they accepted at its face value the statement of Harvie-Brown and Buckley (1888: 56) that the bird "appears to have become almost extinct." They omitted to take account of Harvie-Brown's later admission (1902: 143) that these remarks "were perhaps somewhat premature." The climax was reached when Hudson (1894: 31) exterminated the wren with his pen, remarking that as a result of the

invasion of the islands by collectors "the St. Kilda Wren no longer exists."

Elliott (1895), perhaps influenced by these dismal stories, estimated the total wren population to be fifteen pairs, but as he found three occupied nests—amounting to twenty per cent of the supposed population—the unreliability of his estimate is apparent. Lowe (1934) remarked that the bird nearly became "an interesting memory," and as recently as 1947 an anonymous writer in 'British Birds' referred to the traffic in skins and eggs as having threatened the wren with extinction. Fisher (1948a, 1951: 30) pointed out that such opinions were exaggerated but wrote: "There is no doubt that until well into the present century the wrens were raided, and became rare in the accessible parts of the islands, particularly round the village of Hirta." Even this statement goes beyond the facts.

In 1896 Harvie-Brown (1902) noted wrens close to the village and Dixon (1885a, 1888, 1898) found the bird common in 1884. Kearton (1897) was impressed on landing by their joyous songs. Heathcote (1900), who explored the islands thoroughly in 1898 and 1899, stated that they were to be heard "in all parts." In 1910 and 1911 Clarke (1915) found wrens abundant in the village and elsewhere, and the Duchess of Bedford (1914: 174) noticed several "about the houses and cleits."

Harrisson and Buchan (1934: 134) referred to the legislation of 1904 being "just in time to save the remnant" and Gardiner (*in* Hudson, 1923: vi) thought it gave the bird "a new lease of life," but it may have had the opposite effect by increasing the "black market" value of the eggs and thus stimulating the ardor of collectors and the cupidity of the islanders. Fisher (1948a) mentioned a dealer who took birds and eggs in 1907 and solicited subscribers for another collecting trip in 1908. A collector, Whitaker (*unpubl.*), saw a nest in 1927 which had already been robbed; Lowe (1934), who visited the islands in 1929, remarked that high prices were paid for eggs. Harrisson and Buchan (1934: 135) referred to "a dozen or so nests" being robbed annually and mentioned £5 as the value of a clutch. Evidently the Act of 1904 was honored more in the breach than the observance.

It might seem that human predation on the scale of a dozen nests robbed annually would reduce the population seriously but, although the nest-record cards of the British Trust for Ornithology show that about one-third of the nests of European Wrens come to grief, it remains a common bird. Apparently St. Kilda Wrens re-nest after being robbed (Lowe, 1934:98) so that the loss of a clutch does not mean that the birds will not rear young that season. Harrisson and Buchan

(1934: 137) estimated that about 82 per cent inhabited cliffs. Few nests in such places would be robbed. Moreover St. Kilda must have been inhabited by wrens before the building of the village, which provided additional nesting-places for them, so that we need not suppose that the elimination of the whole village population annually would have extirpated the bird. The ten skins in the Royal Scottish Museum apparently constitute the largest set in any collection. It is highly improbable that as many as 100 were obtained in 50 years.

It has been maintained that "there is no reason to suppose that any significant change in numbers has occurred" (Nicholson and Fisher, 1940: 31) and that the population remains "remarkably constant" (Fisher, 1948a, 1951: 31), but there is evidence that numbers fluctuate.

In 1883 Barrington (1884: 284) "only came across it six times in three weeks." Dixon, as we have noted, found the wren common in 1884, but J. T. Mackenzie who spent a fortnight on St. Kilda in that and the subsequent year reported that in 1885 the birds were "not nearly so numerous" (Dixon, 1885b). This was before they were persecuted. The geologist Cockburn (*in* Harrisson and Buchan, 1934: 135), who was on the islands for some months during 1927 and 1928, roughly assessed the population at under 100 pairs. Later estimates are tabulated below:

TABLE 1

ESTIMATED NUMBERS OF PAIRS OF ST. KILDA WRENS

Island	*(Harrisson and Lack, 1934)*	*(Nicholson and Fisher, 1940)*
Hirta	45	31
Dún	11	12
Soay	9	
Boreray	3 (?)	5 +

Mr. I. J. Ferguson-Lees (*in litt.*) found about 48 pairs on Hirta and 14 or 15 on Dún in 1948. Owing to the difficulties in estimating the number of wrens on the cliffs, all observers admit that allowance has to be made for a margin of error.

Around whatever figure the wren population on St. Kilda may vary, the number of pairs of the Fair Isle Wren (*T. t. fridariensis*), reckoned in 1951 to be between 30 and 40, is probably fewer (Williamson, 1951a, b). In such small populations evolution may be rapid.

Contrary to the situation in most other regions of St. Kilda it is comparatively easy to estimate numbers in the compact area of the village, and the margin of error in most of the estimates is unlikely to be more than one pair.

TABLE 2

ESTIMATED NUMBER OF PAIRS OF ST. KILDA WRENS IN THE VILLAGE ON HIRTA

Authority	*Year of Census*	*Number*
Harrisson and Lack, 1934	1931	8
Harrisson and Buchan, 1934	1931	12
Atkinson, *in litt.*	1938	12
Nicholson and Fisher, 1940	1939	12
Fisher, 1948b	1947	10
Ferguson-Lees, *in litt.*	1948	11
Fisher, *in litt.*	1949	10
Armstrong and Westall	1951	10

It will be noted that the two estimates for 1931 do not agree. The 1938 figure is based on a count late in the season of the number of nests used or in use and may be slightly over-estimated. Perhaps the count by Armstrong and Westall is one too many. Further details regarding the village wrens and the behavior of the birds will be discussed elsewhere (Ferguson-Lees, Fisher, and Armstrong, *unpubl.*).

Fisher based his opinion that the total population of the St. Kilda Wren remains constant on the stability of the breeding population in the village. He wrote (1948b): "We have found evidence from the village sample that the population has not changed in sixteen years." Unfortunately such generalization is unreliable. In seasons when numbers of the European Wren are low one notices that the birds concentrate on the most favorable localities, leaving untenanted the "marginal" areas which are only occupied in peak years (Armstrong, *in press*). Almost certainly this applies to St. Kilda. Thus a census of the favorable area of the village does not provide an accurate index of the total population. The slopes behind the village constitute a "marginal" area, and as the numbers there vary we have positive evidence of fluctuations in population. Harrisson and Buchan (1934) said they found no wrens on the village slopes or anywhere inland in 1931, though reference is made to a brood fledging from a nest in the glen—which is an inland area (Harrisson and Lack, 1934). Whitaker (*unpubl.*) found an old and a new nest there in 1927. Four male wrens were noted on the slopes in 1947. Fisher (1948b) remarked that this year was apparently their first nesting there and in the glen, but he has since called my attention to a reference mentioning a nest in 1886 "on the shoulder of Connaker" (Newton, 1902: 264). It is unlikely, however, that this refers to the village slopes. Ferguson-Lees observed 14 pairs on the slopes in 1948, but in 1951, Dr. Westall and I found none there. It is improbable that the wrens vacated the

cliffs in favor of the slopes. In 1948 Ferguson-Lees found 14 or 15 pairs on Dún, where numbers are comparatively easy to assess. Only 11 pairs were noted in 1931. These data provide further evidence of fluctuations in total population.

That the St. Kilda Wren population should be variable is not surprising in view of what is known of other races. The European, Shetland and Alaska wrens fluctuate in numbers (Armstrong, *in press*, 1952; Nelson, 1887: 210) and probably also the Iceland Wren (*T. t. islandicus*) (Armstrong, 1950a). Gudmundsson (1951) suggested that this race has become commoner with the amelioration of the climate, but there is insufficient evidence to prove this.

HABITAT

The wren breeds on the major islands, mainly where the vegetation is comparatively lush on steep slopes, cliffs, and the damp area near the village. Barrington (1884) flushed one from a crevice 300–400 feet down the cliff of Conachair, and in 1884 Dixon found wrens on the hills and cliffs as well as in the village. Clarke (1915) was told that the wren occurred on Stac an Arnim, the gaunt, gannet-frequented, 627-foot crag which rises like a huge tooth from the sea off Boreray, but he did not state, as Harrisson and Buchan (1934) said that he did, that it bred there. Like the Hebridean and Shetland wrens, the St. Kilda Wren particularly favors places where moisture and fertile soil stimulate rich vegetation harboring numerous insects. The habitats it prefers resemble those chosen by Faeroe Wrens (*T. t. borealis*) (Williamson, 1948), but differ from the areas favored by Iceland Wrens. These are mainly regions of birch scrub (Timmermann, 1949). There is an interesting relationship, most conspicuous on Dún, between the populations of wrens and Puffins, and estimates indicate a pair of wrens to about every five to seven acres—a density greater than that noted elsewhere in the islands with the exception of Village Bay, where streams, marshy, coarse herbage, and the varied rank vegetation which grows around the houses, cleits, walls, and shore provide excellent foraging for the wrens in spite of grazing by Soay sheep. Dún is one vast puffinry, inhabited by thousands of birds, and the abundant guano fertilizes the soil so that there is a characteristic zooplethismic vegetation and a variety of scatophagous insects (Lack, 1932a, b). Thus, for example, *Rumex acetosus* grows to a height of two to three feet (Petch, 1933; Poore and Robertson, 1949). Harrisson and Buchan's figures show that there were about twice as many wrens on the puffin slopes as on the steep cliffs. These writers

stated that the areas unfavorable to wrens are low or sheer cliffs near sea-level and homogeneous grass slopes. Thus, like other races, the St. Kilda Wren tends to avoid areas with scanty vegetation or where the ground is dominated by a few low-growing species.

TERRITORY

Dixon (1888) stated that year after year the St. Kilda wren is found in favorable localities, and this is borne out by later observers. Harrisson and Buchan (1934) estimated the average distance between pairs in the village as slightly over 90 yards, with a variation between 70 and 200. I found no bird more than 200 yards, or less than 90 yards, from his nearest neighbor. The males were fairly evenly spaced so that if one assumed each bird's territory to consist of a circular area around his singing point the radius of the circle would be some 75 to 100 yards. This would indicate territories of the order of about 17,000 to 30,000 square yards—more than four times larger than the previous highest estimate. Harrisson and Buchan computed that the village territories averaged 3000 to 5000 square yards and Ferguson-Lees' estimate is 3500 square yards. The singing male in the center of the village was surrounded by five neighbors. The distances of their singing stances were respectively, 200, 200, 200, 185, and 150 yards, giving a circular area around the central bird of some 26,000 square yards, if we suppose half the average distance to the stations of the males to represent the radius of the territory. This calculation, and others on a similar basis, would not be seriously erroneous unless there were extensive neutral areas between territories. No doubt small neutral or disputed areas exist and perhaps we may assume that near the peripheries of territories defense tends to diminish in vehemence, but it is improbable that large areas of "no-man's-land" exist in a congested area where a wren is surrounded on all sides by rivals. As the neutral areas established by the European Wren are not very extensive relative to the size of the territory, it is so much the less likely that the St. Kilda Wren differs in this respect. Making allowance for such neutral areas I believe that the wrens I observed in the village area held territories of not less than 15,000 square yards. Some were probably considerably larger.

Along the cliffs Harrisson and Buchan (1934: 138) estimated that 21 out of 33 pairs were between 150 and 300 yards apart. The rest were separated by distances from 300 to 450 yards. Shetland Wrens on low cliffs and Hebridean Wrens on a ridge tend to be about 250 yards from one another (Armstrong, 1952, 1953). Heath's data (1920)

suggest that an Alaska Wren's territory may extend for about a quarter of a mile along the coast. Harrisson and Buchan (1934: 139) stated that the "range" of each pair abutted directly on that of the next, but "there was usually a neutral zone and a certain amount of overlap." This rather inconsistent statement can best be interpreted as indicating that when birds are feeding nestlings the territorial boundaries are not rigidly maintained. Observations by Ferguson-Lees show that at this stage males may defend no more than a radius of 12 yards around the nest. He found an overlap of foraging areas of two pairs nesting 50 yards apart to within about 12 yards of each nest. R. Atkinson (*in litt.*) also noted intrusion to within a few yards of a nest with young. Such diminution of territorialism when nestlings are being fed is frequent among passerines but is modified among European Wrens by various forms of behavior associated with polygamy. Reduction in song and sexual and territorial activity is correlated with increasing concern for the nestlings in all races of *T. troglodytes* which have been studied. In general, sexual and territorial activity are in inverse ratio to domestic activity.

Probably when Harrisson and Buchan, and later, Ferguson-Lees, made their estimates in July and August, territorialism had become subordinated to caring for the young and not only had the area defended diminished, but defensive manifestations had decreased and become less conspicuous. My estimate was made near dawn on June 13 when breeding activity was beginning—the times of day and year when singing and territorialism are at their maximum. Thus it seems that when breeding starts, the territories are comparable in size with those of European Wrens in garden-woodland surroundings (Armstrong, *in press*) or even larger, but as the needs of the nestlings make increasing demands on the energy of the males the territories tend to contract and their boundaries become vague.

THE CONCEPT OF "FOOD TERRITORIES"

On the basis of their study of one pair, Harrisson and Buchan came to the conclusion that the St. Kilda Wren's territory is divided into subterritories where food is obtained. They state (1934: 144): "Food territories are further divided into sex territories, each parent tending to feed in exclusive patches not used by the other." As it is of the essence of territory to be defended (Armstrong, 1947: 271–292), and since no evidence of this was found in regard to these individual foraging areas which Harrisson and Buchan styled "a new type of territory," the term should not be used in connection with them. No

other observer has found evidence of foraging areas peculiar to one or the other of the pair. Shetland Wrens nest in habitats very similar to those chosen by St. Kilda Wrens. The birds of a pair forage independently and are apt to pay a number of successive visits to particular patches of rich vegetation (Armstrong, 1952). Superficial observation might suggest that these were exclusive foraging areas, but persistent study showed that neither bird claimed proprietary rights over the other in any area. Occasionally they could be seen foraging only a few yards from each other. When both male and female European Wrens feed the nestlings, their behavior is very similar, and the male Hebridean Wren seldom forages near the female. Miller (1941: 85) has shown that early in the year the male Bewick Wren (*Thryomanes bewickii spilurus*) feeds in a higher zone of the vegetation than his mate. This is true to some extent of European Wrens and may decrease competition for food, but these feeding zones should not be described as sexual food territories.

Harrisson and Buchan suggested that much of the territory is virtually unused for foraging. They estimate that the pair they watched obtained 95 per cent of the food for themselves and their nestlings in one per cent of the territory. They do not state, however, on how many hours' watching this estimate is based. St. Kilda Wrens, when feeding nestlings, act as do the other races in which such behavior has been studied—spending most of their time foraging in patches of rank vegetation and avoiding areas of short turf and homogeneous herbage. The observations of Harrisson and Buchan, however, raise an important issue which merits comment.

Evidence is accumulating to show that family size in birds is closely related to the expenditure of time and energy in foraging. It is the availability of food and not merely its presence which is relevant. Whatever importance a territory may possess as a foraging area is dependent on the food's being obtainable without an uneconomical expenditure of time and energy. If the feeding areas in a territory were all at the periphery, so much time would be occupied in fetching food that the nestlings might be undernourished. Moreover, a territory might contain adequate food and yet, if prey were difficult to find or the organisms very small, it might be impossible for the birds to rear young. The much-debated question of the food value of nesting territory will not be decided by considering whether or not the birds forage throughout the whole territory. A very large territory might be essential to the successful reproduction of a pair of birds because scattered widely in it were a few comparatively rich areas where food could be obtained expeditiously. Thus Harrisson and

Buchan noted that wrens were never seen feeding in arable grassland. Undoubtedly arthropod prey is to be found there, but its value is apparently sometimes so low that it is not worth the time consumed in foraging for it. Lack (1932a: 262) stated that sweeping for diptera "in the thick vegetation of the formerly cultivated area around the village and in a small marsh just outside this area was particularly remunerative." He also mentioned (1931) that the terrestrial fauna is poor as regards both species and individuals. So far as species are concerned this is borne out by Edwards and Collin (1932).

Referring to the autumn dispersal to non-breeding areas Harrisson and Buchan remarked that, as birds are found in late summer and autumn in these areas, scarcity of food cannot be the primary reason wrens do not choose them for nesting. This is obviously fallacious since transient individuals could subsist for a time where families could not be reared.

The diminution in territorialism among birds feeding nestlings is a consequence of the fact that defensive activities are a dissipation of time and energy at this stage. If at the beginning of the breeding season a number of birds so divide up an area that there will subsequently be sufficient food for the family in each domain, it does not matter whether the boundaries later become indefinite and defense of the territories breaks down. What is essential is that the species should be equipped with inherited behavior-patterns, related to the establishment of territory, such that when the time for feeding the nestlings arrives there will be, in normal seasons, an adequate and sufficiently available food supply.

SONG

I was able to hear the songs of St. Kilda, Hebridean, and European wrens (in Scotland and England) on three successive days and was impressed by the points of difference between them. The Hebridean Wren's phrase, with its "reel," is the most distinctive of the songs I have heard. In the St. Kilda Wren's song there is often only one trill, but sometimes in a longer phrase there may be two. Preceding the trill the notes frolic up and down in a brief, pleasant warble. The song is more musical, less mechanical, and less shrill than that of the European Wren. In spite of the statements of several observers, including Mr. James Fisher, to the contrary, Ferguson-Lees, Westall, and the writer are convinced that the song is no louder than that of *T. t. troglodytes*. Possibly it is softer. The rocky background amplifies the sound so that birds can be heard singing at a distance of half a mile and, no doubt, under good conditions considerably further.

Harrisson and Buchan (1936) were incorrect in stating that the average duration of the phrase is 20 seconds. Kearton (1897) reckoned it correctly at five to six seconds. A bird in ardent song, whose mate was at the stage of nest-lining, timed for five successive minutes sang, 6, 5, 4, 5, and 5 songs. This rhythm with songs and intervals of the order of about five seconds approximates that of other European races. Another bird, singing less consistently, uttered phrases lasting 5, 3, and 3 seconds, with pauses of 6, 5, and 11 seconds. Occasional songs of as long as eight seconds were noted. Counter-singing occurs, two birds regularly alternating their phrases; this also occurs in the mainland race (Armstrong, 1944). As with other races the duration of the phrase is modified when the bird is excited by the presence of a female; it may then be either extended or abbreviated.

Probably song begins about civil twilight—when the sun is 6° below the horizon. When the writer landed at 2:42 G. M. T. the birds were in full song. While search was being made for the landing-place in the dim light of a foggy daybreak, the songs of wrens from the deserted village, heard above the crash of the breakers on the cliffs, served as clues to our position. By 4:00 there was a marked diminution of song and several birds seemed to have ceased, or almost ceased, singing; by 9:30 only two or three of the ten males in the village were noticeably vocal. This experience during the season of the year when song is at its peak suggests a source of inaccuracy in censuses, especially on the cliffs, taken later in the season and several hours after dawn when most counts were made. Harrisson and Buchan (1936) heard no birds on the cliffs during the last few days of July; and for several days at the beginning of August, despite careful observation, not a single song was heard in the village. The molt had begun.

Like the European Wren, the St. Kilda Wren sings with his tail cocked when excited, but by no means always. Flight-song is fairly frequent and has been noted in June, July, and August. Probably all races of *T. troglodytes* sing in flight, but flight-song may be particularly characteristic of those inhabiting relatively open habitats (Armstrong, 1953, *in press*).

DISPLAY

The little which has been observed of the epigamic display indicates that it is substantially similar to the displays of other races (Armstrong, *in press*). Ferguson-Lees saw a bird posture with drooping wings and spread tail while singing a snatch. Harrisson and Buchan (1936: 16) noticed alarmed birds "quickly running around on rocks and stones with fluttering wings" and regarded this behavior, probably correctly,

as "a modified sexual attitude." Perhaps it might also be considered an incipient distraction display. Nice and Thomas (1948: 152) noted a form of impeded flight by a Carolina Wren (*Thryothorus ludovicianus*), which they regard as distraction display, but no quite definite form of distraction display has been recorded in the Troglodytidae. Displays of related character by various species reinforce the view that some forms of distraction display are modifications of epigamic posturing originating as displacement activities (Armstrong, 1949, 1950b).

Atkinson (1949: 256 and *in litt.*) noticed that on one occasion when both birds arrived together at the nest, one "greeted the other by spreading and vibrating its wings and making queer little chipping noises." He also saw a single bird, clinging to the nest, display in this way. Judging by analogous displays, this performance probably had a sexual basis but may have been stimulated or accentuated in displacement fashion by the presence of the photographer and his hide. Somewhat similar displays are seen when Hebridean or Shetland wrens are together near the nest, and I have known a European Wren to display while holding food in front of the nest while I was in a hide close by.

PAIR-BOND

About fifty per cent of the European Wren population in garden-woodland areas of Holland and England are polygamous (Kluijver *et al.*, 1940; Armstrong, *in press*), but the St. Kilda race is monogamous. The low development of multiple nest-building is consistent with monogamy and inconsistent with polygamy. Moreover, all observers who have studied the activities at nests with young have noted both parents feeding them; but the female European Wren is often left to tend the nestlings unaided. The evidence suggests that the male St. Kilda Wren may even exceed the assiduous male Shetland Wren in his concern for the nestlings. As there are records of Eastern and Western Winter Wren nestlings (*T. t. hiemalis* and *T. t. pacificus*) being fed by one parent (Stanwood *in* Bent, 1948; Grinnell and Storer, 1924) and multiple nest-building is characteristic of both races (Bent, 1948: 151; Bowles, 1899), it is highly probable that they also tend to be polygamous. Both parents fed the young at a July nest in Maine (Cruickshank, 1951), but the male European Wren frequently helps feed the nestlings late in the season when his sexual drive has weakened; doubtless this is true of the Winter Wren also. On the other hand *T. t. zetlandicus* is predominantly monogamous and so, probably, is *T. t. alascensis*, for Heath (1920) noticed that the male is diligent in

feeding nestlings. Thus it appears that the wrens in bleak, northern insular habitats tend to be monogamous while those of southern "continental" habitats incline to polygamy. The principle involved is discussed later in this paper and also elsewhere (1952, and *in press*).

NEST-BUILDING

The nest is built by the male, as in all races which have been studied, although exceptionally female European Wrens may build. Heath (1920) was mistaken in assuming that the female Alaska Wren makes the nest. On the whole, the nest of the St. Kilda Wren is more crudely constructed than the nests of *T. t. islandicus* (Armstrong, 1950c), *T. t. zetlandicus*, *T. t. hebridensis*, and *T. t. troglodytes*. Judging by published descriptions it is also often less well fashioned than the nests of *T. t. mülleri*, *T. t. kabylorum*, *T. t. hiemalis*, *T. t. alascensis*, and other races for which details are available. Many are built rather loosely of coarse grass and tend to be bulkier and to have wider apertures than do nests of European Wrens (Kearton, 1897). Others in cleits or other cramped cavities consist of a shell or cup of vegetable material, mainly moss. They are frequently well concealed. Perhaps the crudity of many nests is due more to the use of recalcitrant materials than to lack of craftsmanship for Dixon (1898) saw nests which he spoke of as being beautifully made of moss with the threshold strengthened with grass stalks.

In the village area the nests are in cleits, dilapidated cottages, and stone byres, many of which were used as dwellings before the cottages were built about the middle of last century. The nesting sites are commonly over, or quite near to, the low entrance of the cleits. The very small area of shingle bank near the beach is also chosen for nesting (Harrisson and Buchan, 1936; Lowe, 1934). Harrisson and Buchan (1936: 11) remark that "the entrance holes seem to have been burrowed in the earth, as was a nest seen by Eagle Clarke," but they have misinterpreted his comment (1915) which is that a nest "was built in a cavity in a mass of dead thrift on the face of a cliff." In spite of Lowe's remark about seeing a nest in a hole such as might have been made by a rat (although, as he points out, there are no rats on St. Kilda) evidence is lacking that the St. Kilda Wren ever enlarges an earth cavity by excavation. Bank nests are often sheltered by tufts of coarse herbage.

The nest is usually constructed of material available quite close at hand. Withered grass is commonly used and is probably collected when damp and most pliable. Nests in cleits are often built of hay found inside the cleit. Like other races, *T. t. hirtensis* adapts the nest

to the site, sometimes shaping grasses into a rough ball and on other occasions packing material into a cavity to create a soft recess to receive the eggs. Old nests are sometimes refurbished and used again, and Lowe reported finding a nest in a cavity from which a nest and eggs had been removed earlier in the season.

The St. Kilda Wren builds fewer nests than the European Wren (Atkinson, 1949) which averages about six and may build ten or a dozen (Kluijver *et al.*, 1940; Armstrong, *in press*). Ferguson-Lees (*in litt.*) estimated that in July, 1948, there were less than three nests to every two pairs. He noticed a male, whose young had fledged, engaged in building. Iceland Wrens build as late as June 28 (L. S. V. Venables, *in litt.*), European Wrens up to the end of July, and Kashmir Wrens (*T. t. neglectus*) in the first week of August (Bates and Lowther, 1952). These late nests can seldom be used for breeding. Harrisson and Buchan's remarks are confused and misleading for they speak of "cock's nests" being used for breeding whereas a "cock's nest" is merely one of a series—often unfinished—which has not been chosen by a female. Fisher's references (1948a; 1951: 30) to some "nests probably made by the cocks" should not be regarded as indicating that others are built by the females.

NEST-LINING

Lining with feathers or other soft material is performed by the female when she has chosen a nest. Most used nests contain some Fulmar feathers and emanate the characteristic musky smell. Puffin, Starling (*Sturnus vulgaris*), Hooded Crow (*Corvus cornix*), and Snipe (*Capella gallinago*) feathers have also been recorded. Dixon (1885a) commented that the nest is abundantly lined with feathers, but European Wrens' nests often contain more, but smaller feathers. Harrisson and Buchan (1936) counted 35 feathers from a St. Kilda nest, whereas Marples (1935) noted that a European Wren's nest contained 498. Dixon (1888) remarked that the wrens used to steal hair from the Puffin snares set by the islanders.

EGGS

The eggs are noticeably larger than those of *T. t. troglodytes*, averaging 18.55 by 13.93 mm. (Jourdain, *in* Witherby *et al.*, 1938: 217), and are marked with rufous spots similar to those on the eggs of the European Wren. Immaculate, or almost immaculate, single eggs and clutches occur (Seebohm, 1885; Dixon, 1888; Elliott, 1895; Whitaker, *unpubl.*). As pointed out elsewhere (Armstrong, 1950a) spotless eggs appear to be commoner among northern insular races than in *T. t.*

troglodytes. Perhaps this is correlated with the presence of fewer mammalian egg-predators. Thus eggs of the Alaska and Aleutian wrens (*T. t. alascensis* and *T. t. meligerus*) are sometimes without markings (Bent, 1948; Turner, 1886: 181). Jourdain stated that the clutch is four to six with seven occasionally, but this maximum must be very rare as the Factor on St. Kilda, who had seen some 50 nests, told Kearton (1897) that none contained more than six. The average clutch-size is evidently smaller than that of the European Wren, and the evidence is consistent with, though insufficient to prove, a reduction in clutch-size late in the season.

BREEDING SEASON

Many observers have speculated as to the period of breeding and the occurrence of second broods. Analysis of the data available from all sources indicates that the main laying period lies from the last week of May until about mid-June, with the peak probably early in June, but there is seasonal variation of about a fortnight and apparently a greater "spread" of nesting than is usual among insectivorous birds of temperate regions. It is exceptional for young to fledge earlier than the last fortnight in June. Such second brood clutches as occur would therefore appear about the first fortnight of July. As there is so little evidence of nests with eggs during this period, second broods cannot be usual. Nest predation does not seem to be sufficiently severe for more than a few of the late nests to be considered as replacements, so it would seem that the St. Kilda Wren, like the Shetland race, tends to spread its nesting and to rear comparatively few second broods.

NESTLING PERIOD

Neither the incubation nor the nestling period is known. The only records of the feeding rhythm are those of Harrisson and Buchan (1936). They stated that during the first week the young are fed on the average 150 times a day and that this is equivalent to about 40 feedings per chick. They speak of 10 to 13 feedings per hour at nests where both parents were active. Such a tempo may be far exceeded by a single European Wren. A female made just over 360 visits to five young on their fifth day and 560 to four chicks when they were sixteen days old (Whitehouse and Armstrong, *in press*).

Harrisson and Buchan considered that the share of the sexes is about equal though some of their observations suggest that at one nest the male was most active. Atkinson (*in litt.*) noticed that the day before fledging the male did most of the feeding. In any race of

wren this is unusual although it sometimes occurs among tits (Hinde, 1952). Atkinson also observed that both parents brooded a family which fledged four days later. Such brooding of well-grown young is remarkable; that a male should take part is incomprehensible. Perhaps he was taking refuge in the nest rather than brooding. Behavior of this kind has not been recorded of the male of any other race.

Harrisson and Buchan (1936) found that each parent tended to take 2 "rests" per hour, staying away from the nest for from 10 to 20 minutes, and Yeates (1948) recorded interludes of about 20 minutes at a Shetland Wren's nest though I never did. Intermissions of as long as 20 minutes at a European Wren's nest are rare, but I have known a Hebridean Wren's young to remain unvisited for 31 minutes. Theoretically such pauses could be due either to the young being satiated and not stimulating the parents by begging or to the scarcity of food necessitating interludes while the parents satisfied their own hunger. As the feeding tempo is more rapid at nests of European Wrens the latter hypothesis is more probable.

Food Brought to the Nestlings

Noctuid and geometrid larvae are brought to the young, as are crane flies (tipulids) and other diptera, earwigs, spiders, and centipedes (Harrisson and Buchan, 1934). This diet is similar to that of Shetland and Hebridean wrens, except that they have not been known to receive earwigs and are given moths. Atkinson (1949) saw fat, white maggots brought to a brood, and a St. Kilda Wren was seen to give a fragment of an earthworm to the nestlings (Lowe, 1934). A pair which Lowe watched foraging on the beach was noticed chasing sandhoppers (*Talitrus*), but other observers noted that during the breeding season the wrens do not forage to any considerable extent on the shore. Shetland Wrens nesting by the sea-shore do not give molluscans or crustaceans to their nestlings (Armstrong and Thorpe, 1952). Lowe's belief (1934: 101) that St. Kilda Wrens extract molluscs from their shells "in the same way that snails are extracted by thrushes" (*Turdus ericetorum*) is pure speculation.

Adults feed on a variety of arthropods, such as those already mentioned and including beetles (Clarke, 1915). Dixon (1888) saw a bird pursue a flying insect, and Clarke (1915) found remains of seeds and vegetable tissue in the stomachs of birds killed in September and October. Inside many of the cleits where wrens feed lies the more or less desiccated and disintegrated carcass of a Soay sheep, for these animals go to cover to die. In a sheltered spot a sick animal is less

liable to be attacked by rapacious birds. As I saw a wren feeding close around one of these carcasses, it is possible that wrens eat some of the organisms which batten on dead sheep. The maggots which Atkinson saw given to nestlings may have been the larvae of diptera from a carcass.

NEST SANITATION

The feces are removed by both sexes. Harrisson and Buchan (1936) noted the interval between taking sacs as averaging 45 minutes, but they did not mention the age or number of the young. When the young are about a week old the parents no longer enter the nest but receive the extruded sac as they cling to the threshold; Atkinson noted, however, that when one of the young had already left the nest a parent went inside twice to clean it. Harrisson and Buchan watched birds wiping off sacs on old wire clothes lines. Shetland Wrens will make use of a wire fence for the same purpose, and I have seen European and Hebridean wrens wipe off the feces on branches. Feces are usually carried well away from the nest as is customary with other races and many other passerines.

FLEDGING

As with other races, one or more young St. Kilda Wrens are apt to fly out of the nest prematurely if disturbed. Atkinson noticed that after a youngster had flown, one of the parents, apparently the male, fed it while his mate tended the remaining youngsters without assistance. Both parents accompany and feed the fledged young. Atkinson saw juveniles, so fully developed as to be indistinguishable from adults, following and importuning their parents for food. Kearton found fledged young very agile in escaping capture by dodging in and out of crevices. Juvenile Shetland Wrens are equally wary.

DISPERSAL

In September and October, Clarke (1915) found wrens here and there all over Hirta, including the moorland, beach, and glen. Before Harrisson and Buchan left on August 14 they noted the beginnings of this dispersal, and one of the birds observed away from the breeding areas was probably a juvenile. Mr. L. S. V. Venables tells me that the "spread-out" of Shetland Wrens occurs at the beginning of August. Iceland Wrens disperse after breeding, mainly to the coast (Armstrong, 1950a), and juvenile European Wrens also wander widely but apparently begin to do so in July or even to a minor extent at the end of June. There is no evidence that St. Kilda Wrens leave the group of islands.

MORTALITY

In two of four nests from which the young had fledged Ferguson-Lees found a dead chick aged three to four days. He also discovered a whole brood dead in the nest. No ticks were found on any young, although in a recently vacated nest there were numerous flea larvae, probably *Dasypsyllus gallinulae*, which has been recorded from a wren on St. Kilda (M. Rothschild, 1952). The cause of this mortality is uncertain, but it is most plausibly attributed to an inadequate food supply. Elliott (1895) and Atkinson (*in litt.*) reported infertile eggs in nests. In this connection it may be noted that in 1951 the writer examined three recently vacated nests of European Wrens in succession, finding a dead chick in each of two of them and an infertile egg in the third. The spring of 1951 was wet, the breeding season late, and the incidence of infertile eggs and nest mortality in some species high (Campbell, 1951). Human mortality in Britain was also high and butterflies were scarce. So far as nest mortality among birds is concerned, the lack of adequate food appears to have been a major factor. The most plausible hypothesis to explain the high mortality in 1948 among the village wrens of St. Kilda is that the population was too dense for the food supply available. It will be remembered that this was the only year on record when the village slopes as well as the village held a considerable number of wrens. Ferguson-Lees' observations of extensive territorial trespass by birds foraging for nestlings are consistent with this hypothesis. If it be valid, the situation on St. Kilda provides evidence in support of the thesis which I have advocated elsewhere (1952, and *in press*), that food-supply is fundamental in determining the nature of the pair-bond in *T. troglodytes* and probably other species.

In one nest Harrisson and Buchan found four chicks, but no broods of more than three fledged young were seen. They estimated that approximately one young left the nest for every two eggs laid. If this is correct, mortality for which predators are not responsible is at this stage considerably higher than among European Wrens. However, Ferguson-Lees reckoned the average number of fledged young in the families he saw to be four.

PREDATION

Lowe regards cats as having contributed largely to the alleged decline in the number of wrens. He refers to them as having been recently introduced but does not further substantiate this rather surprising statement. It is difficult to believe that primitive folk on

an island supporting two species of mice did not keep cats. About a dozen cats were left behind in 1930, but by 1931 there were only three survivors. Two females, one with kittens, were shot, leaving only the male (Harrisson and Moy-Thomas, 1933). No cat has been seen since. Although cats destroy wrens and their nests, and no doubt ate St. Kilda Wrens, there is no evidence that either cats or mice seriously affected the numbers of wrens. There were not many more than 12 individuals of the apparently now extinct house mouse (*Mus musculus muralis*) in 1931 (Harrisson and Moy-Thomas, 1933). This mouse was restricted to the houses and dependent on man. As the St. Kilda yellow-necked mouse (*Apodemus flavicollis hirtensis*) is apparently almost entirely vegetarian (Waterston, 1905) it cannot be a serious menace to the wren. Attempts to trap it with cheese were a failure. No mice are found on Boreray, so that on this island the wrens are certainly free from all mammalian predation. Although Harrisson and Buchan's statement that natural enemies of the wren are absent from St. Kilda seems somewhat rash, it is unlikely that mammalian or avian predation has a significant effect on the wren population.

Harrisson and Buchan justifiably dismiss Seebohm's notion that the peculiarities of the St. Kilda Wren's coloration enable it to escape the attacks of "hungry hawks." The St. Kilda Peregrines (*Falco peregrinus*) have worthier quarry to pursue than wrens. Population control must be mainly effected by environmental factors other than predation and probably the most important is the availability of food.

DISCUSSION

Although our knowledge of the St. Kilda Wren is based on scattered observations and several observers have drawn incorrect inferences from the data, it is evident that the behavior of this race diverges in some respects from that of *T. t. troglodytes*. The latter's adaptations include polygamy, multiple nest-building, regular second broods, and highly functional song; but the St. Kilda Wren is monogamous, builds few nests, is probably often single-brooded, and song seems to play a somewhat lesser rôle in its life. In these respects the behavior of the St. Kilda Wren approximates that of other northern insular races. Although little has been recorded of the Asian and North American subspecies, it seems that the races of *T. troglodytes* tend towards one of two types, "northern insular" or "continental," the former being characterized by monogamy, the latter by polygamy and a high development of multiple nest-building.

Probably these distinctions in pair-bond and behavior are determined by the availability of food for the nestlings, since the wrens of the bleakest habitats are the least polygamous. The St. Kilda Wren belongs to this type, and we have noted various indications that, at least in some seasons, it suffers from food stringency, territorial trespassing, slow feeding tempo at the nest, and nest mortality. Taken separately each of these might be explained as due to some other factor, but together the hypothesis of lack of available food is most plausible. On the other hand, the polygamy of the European Wren is correlated with a relatively highly available food supply. To what extent these differences in behavior are environmentally determined or have become innate and genetically fixed is debatable. In regard to song there are strong grounds for believing that the racial differences have a genetic basis, and it may well be found that in some other respects divergence in behavior is more than a merely environmental adaptation. One is impressed by the fact that wren accommodation to a new type of environment is attained by the integration of a group of adaptations. Such integrative adaptation may play an important part in speciation.

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SUMMARY

1. The literature dealing with the St. Kilda Wren is critically examined, and it is argued that, contrary to the opinion of a number of writers, the bird was never near extermination. It is also suggested that legislation designed to preserve it was not only ineffective but may have increased its jeopardy.

2. Evidence is adduced indicating that numbers fluctuate considerably.

3. The sexual food territory concept is shown to be unproven.

4. Information in regard to the breeding cycle is reviewed and comparisons made with other races.

5. The St. Kilda Wren's behavior and breeding biology are shown to be more closely akin to those of other northern insular races than to those of *T. t. troglodytes*.

6. It is suggested that in *T. troglodytes* two types of integrated adaptations are apparent: the "continental," characterized by a polygamous pair-bond; and the "northern insular," characterized by monogamy.

7. The thesis is advanced that the availability of food in the breeding season determines to which of these types wrens belong.

8. Attention is called to the significance of integrated groups of ethological adaptations in speciation.

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