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Numerous workers have reported that shorebirds are relatively common throughout the boreal summer over a broad expanse of the Pacific. The phenomenon is mentioned in several major sources (Bent 1929; Mayr 1945; Baker 1951; Palmer 1967; Amerson 1969, 1971). An early record (Henshaw 1910) described shorebird migrations in the Hawaiian Islands from 1894 to 1904. Henshaw found the Pacific race of the American Golden Plover (Pluvialis dominica fulva) and the Ruddy Turnstone (Arenaria interpres) in the Islands all summer and commented that "these appear to consist wholly of immature individuals which as a rule are thin and not in good trim." As to plumage, he stated "summer plover and turnstones . . . were without exception in the winter garb." Stickney (1943) included many records from the Galapagos, Hawaiian Islands, Polynesia, northern Melanesia, and the eastern Papuan Islands. Morgan and Morgan (1965) documented a full year of shorebird observations in the Fiji Islands, and Burland (1964) presented data for the boreal summer period in the northern Cook Islands. "Over-wintering" was reported for several species of shorebirds (including the American Golden Plover) in Tasmania, and for the Ruddy Turnstone in northern New Zealand (Thomas 1968, 1970; Edgar et al. 1969).

In addition to records from the Pacific, Ruddy Turnstones and Whimbrels (*Numenius phaeopus*) were found during the boreal summer on various Atlantic islands (Volsoe 1950; Bannerman and Bannerman 1963–68), and at Diego Garcia Atoll in the Indian Ocean (Bourne 1971). McNeil's (1970) extensive observations in northeastern Venezuela revealed 14 species of shorebirds summering far to the south of their breeding ranges. Other references which document this phenomenon throughout the world are reviewed by McNeil (1970).

Although there is no generally accepted explanation for such migratory failure, several of the aforementioned authors have variously postulated immaturity, hormone imbalance, injury, or disease as possible factors. This paper presents data on the reproductive status of individuals from five species of shorebirds which had failed to migrate and were spending the boreal summer on their wintering grounds.

## MATERIALS AND METHODS

The investigation was carried out at Eniwetok Atoll in the northwest Marshall Islands (approximately 11° N, 162° E), during the period from 9 June through 6 July 1970. Most collecting and census work was performed on Eniwetok islet (code-named "Fred" during World War II), the major islet of the atoll. Operations were conducted from a vehicle since this disturbed the birds least. We concentrated our attention on the area surrounding the runway (the latter was especially attractive to American Golden Plovers) and the seaward margin of the islet. Observations of shorebirds on two other islets (Libiron or "James" and Chinimi or "Clyde") were also obtained.

Immediately after collecting a bird, its reproductive organs (plus the bursa of Fabricius if present) were fixed in AFA. Cross sections from a representative sample of testes were cut (paraffin method) at 8  $\mu$ , and stained with Heidenhain's hematoxylin and eosin. The sections were from the mid-region (greatest diameter) of each organ. To delimit relative histologic development within the annual cycle, each testis preparation was assigned to one of the spermatogenic stages described by Johnson (1961). Measurements of ovarian follicles and testis size were made with an ocular micrometer in a dissecting microscope. The mean diameter of the seminiferous tubules in an individual was calculated from measurements (using an ocular micrometer in a compound microscope) of 25 cross-sectioned tubules from both testes. Each specimen was placed in one of three categories descriptive of plumage development: nonbreeding, partial breeding, or breeding.

On 13 and 15 May 1971, a series of American Golden Plovers (*P. d. dominica*) was collected near Moorhead, Minnesota. These birds were in the midst of their northward breeding migration, and it seemed desirable to compare their reproductive status with the materials from Eniwetok.

## **RESULTS AND DISCUSSION**

## REPRODUCTIVE ORGANS

The testes selected for histological examination span the gradient of testicular size encountered in the study, and also represent each plumage class. The first five of seven spermatogenic stages used by Johnson (1961) to describe the annual cycle in Mallards (*Anas platyrhynchos*) were adapted readily to this material. Stages 6 and 7 were not present among the shorebird specimens. A brief review of stages 1 through 5 is as follows:

Stage 1. Inactive condition; tubules contain spermatogonia and a few primary spermatocytes. Occasionally one of the latter is found in synapsis.

Stage 2. Primary spermatocytes are more abundant. Early in this stage, small groups of primary spermatocytes in synapsis are scattered throughout the tissue. Approximately one-half of all primary spermatocytes per given microscope field display synapsis in late stage 2 tissues.

Stage 3. Majority of primary spermatocytes show synapsis, a few secondary spermatocytes present in some tubules.

Stage 4. Central portions of most tubules contain spermatids and a few immature spermatozoa.

Stage 5. Spermatids are abundant; moderate numbers of spermatozoa many of which are associated with Sertoli cells. The first mature sperm are apparently produced during this period.

The testes of American Golden Plovers (P. d. fulva), Wandering Tattlers (Heteroscelus incanus), and Ruddy Turnstones were typically small and in spermatogenic stages 1 and 2 (table 1, fig. 1a). These findings contrast with the implications of Carpenter et al. (1968), who noted "enlarged gonads" in some plovers and turnstones at Eniwetok. Unfortunately, they provided no relative measurements. In American Golden Plovers collected in Minnesota during northward migration, two of three birds examined histologically were nearing complete spermatogenic maturity. Presumably specimens M2 and M6 (table 1) were also approaching full sperm production based upon testicular weight.

Van Oordt (1928, 1931) studied gonadal development and plumage in Knots (*Calidris canutus*), Dunlins (*Calidris alpina*), and Ruddy Turnstones collected during late June in Holland. These birds were nonbreeders spending the boreal summer far to the south of their nesting grounds. Most individuals displayed partial breeding plumages of varying intensities. Van Oordt's descriptions of testicular histology stress immaturity (comparable to spermatogenic stage 1 as defined earlier). However, in one Knot (of 6 males examined), all the Dunlins (3 males were collected), and two Ruddy Turnstones (of 12



FIGURE 1. (a) Immature testicular tissue (spermatogenic stage 1) which was relatively common among shorebirds collected at Eniwetok. The material photographed is from Ruddy Turnstone no. 66 (table 1). (b) Active spermatogenesis producing moderate numbers of spermatozoa. Tissue from Bristle-thighed Curlew no. 69 (table 1) is shown. Both photographs approximately  $500 \times$ .

males examined), van Oordt found slight testicular recrudescence (early stage 2). Because most of the males in the stage 2 group possessed adult or nearly adult plumage, van Oordt postulated a direct relationship between testicular maturity and plumage development. My data do not support this correlation since plovers and turnstones at Eniwetok displayed similar testis histology in each plumage category (table 1). The physiological basis of these findings rests amidst many variables (Voitkevich 1966; Payne 1972) and warrants further study. Loftin (1962) examined plumage and gonad development in several species of boreal-nesting shorebirds apparently summering (collected during June) in Florida. With the exception of one Semipalmated Plover (Charadrius semipalmatus) and one Black-bellied Plover (Pluvialis squatarola) which were producing sperm, he found immature (comparable to my stages 1 through 3) testes. It is noteworthy that the two plover specimens were in breeding and nonbreeding plumage, respectively.

Spermatogenic activity in one Whimbrel (no. 48) and the Bristle-thighed Curlew (Numenius tahitiensis) varied conspicuously from the other males collected at Eniwetok (table 1). In both cases, testicular recrudescence had progressed such that moderate numbers of immature spermatozoa were present (fig. 1b). No indications of gonadal degeneration were seen, and it is possible that the individuals involved might have proceeded to full reproductive maturity. The situation suggests slow but continuous development at a photoperiod less than that considered by Lofts and Murton (1968) to be associated with

TABLE 1.	Records	of the	breeding	condition	of	male	shorebirds.
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				Testis par				
	Specimen no.ª	Plumage	wt. both testes (mg)	length × width of largest testis (mm)	sperma- togenic stage <sup>b</sup>	mean diameter seminif- erous tubules $(\mu)^c$	Bursa wt. (mg) <sup>d</sup>	Date collected
American	39	breeding	12	$(3.5 \times 2.0)$				6-12-70
Golden Plover	72	breeding	40	$(6.0 \times 3.0)$	2	97	_	6-18-70
	75(100)	breeding	10	$(3.8 \times 1.8)$	1	58	_	6-21-70
	120(121)	breeding	17	$(3.7 \times 2.3)$				6-30-70
	121(116)	partial	9	$(3.2 \times 1.7)$	2	73		7- 1-70
	40	nonbreeding	7	$(3.8 \times 1.5)$	2	63	123	6-12-70
	41	nonbreeding	5	$(3.0 \times 1.7)$			69	6-12-70
	43	nonbreeding	8	$(3.2 \times 1.4)$	2	59	58	6-12-70
	50	nonbreeding	7	$(3.3 \times 1.2)$			_	6-15-70
	118(139)	nonbreeding	20	$(4.3 \times 2.5)$	2	81	_	6-28-70
	M2(188)°	breeding	185	$(8.6 \times 5.1)$				5-15-71
	M6(180)	breeding	201	$(11.0 \times 5.0)$			25	5-15-71
	M7(176)	breeding	74	$(8.1 \times 3.3)$	3	145	19	5-15-71
	M9(171)	breeding	222	$(9.0 \times 5.6)$	<b>5</b>	192		5-15-71
	M10(149)	breeding	162	$(8.9 \times 4.7)$	5	187	—	5-15-71
Whimbrel <sup>t</sup>	47		23	(5.5  imes 2.2)	2	71	405	6-13-70
	48		45	$(6.0 \times 3.0)$	4	109	855	6–13–70
Bristle-thighed								
Curlew <sup>r</sup>	69		63	(7.0  imes 2.8)	4	114		6–16–70
Wandering	71	nonbreeding	4	$(2.8 \times 1.5)$			93	61870
Tattler	115(83)	nonbreeding	6	$(3.0 \times 1.6)$	2	55	29	6–26–70
Ruddy	35	partial	7	(3.5  imes 1.6)	2	74	38	6-12-70
Turnstone	44	partial	4	$(3.5 \times 1.2)$			130	6-12-70
	46	partial	4	(3.5  imes 1.2)			lamaged	6-13-70
	66	partial	3	$(3.3 \times 1.0)$	1	51	87	6-16-70
	116(105)	partial	2	(2.5  imes 1.2)			72	6-26-70
	123(105)	partial	2	(2.8 imes 0.9)	1	50	34	7- 5-70
	125(98)	breeding	12	$(3.9 \times 2.9)$	2	89		7- 6-70

\* Where available, body weights (g) are shown in parentheses.

Where available, body increase (a), the base text.
Corrected for shrinkage by comparison of testis width before and after sectioning.
If no weight is shown, the bursa was absent.
Numbers prefixed by M are American Golden Plovers (P. d. dominica) collected in Minnesota.
No plumage description has been given since basic and alternate plumages are not readily separable.

complete spermatogenic development in these species.

Lofts (1962) described testis histology in two groups of Whimbrels: one sample was killed on the wintering grounds in Africa (Gambia River, 13° N); the other in England during northward migration of the birds to breeding areas. The wintering bird collections ranged from early January to early May, and relative to the histological stages used herein, spermatogenesis progressed from stage 1 to stage 2 during this period. The northward migrating birds were collected in early May and had testes which were histologically mature or nearly so. Lofts did not comment on the considerable disparity between gonadal development of some birds still on the winter range as opposed to the migrants. In fact,

the findings probably reflect a nonmigratory group in Africa similar to that found at Eniwetok. Mackworth-Praed and Grant (1952, 1962, 1970) note the presence of a variety of boreal-nesting shorebirds throughout the year in Africa, including the Whimbrel in eastern Africa.

The length-width values for the largest testis (table 1) obscure the fact that asymmetry of testicular size was marked in many individuals. Often one testis (typically the left) was considerably bigger (half again or more) than the other. In each histological evaluation, both testes were sectioned and mounted in opposing rows on the same slide. Despite this frequent asymmetry, no variation in histological development or tubule diameter was found between testes from the same bird.

			Ovary	and oviduct para			
	Specimen no.ª	Plumage	ovary wt. (mg)	diameter of 5 follicles (mm) <sup>b</sup>	oviduct wt. (mg)	Bursa wt. (mg)°	Date collected
American	74(154)	partial	80	(1.8–1.5)	21	_	6-21-70
Golden Plover	119(127)	nonbreeding	36	(1.4 - 1.2)	13	<u> </u>	6-28-70
	$M1(186)^{d}$	breeding	129	(2.4-1.7)	91		5 - 13 - 71
	M3(189)	breeding	321	(4.2 - 3.2)	201	43	5-15-71
	M4(183)	breeding	282	(3.9 - 2.9)	140		5-15-71
	M5(178)	breeding	278	(3.3-2.7)	160	63	5-15-71
	M8	breeding	365	(3.9–2.8)	144		5-15-71
	M11(190)	breeding	599	(4.3-3.2)	166	<u> </u>	5 - 15 - 71
Whimbrel*	49		102	(1.3-1.1)	damaged	599	6–15–70
Wandering	45	breeding	65	(1.7 - 1.5)	38		6-12-70
Tattler	73	nonbreeding	72	(1.3 - 1.2)	22	79	6-18-70
	114(106)	nonbreeding	35	(0.9-0.7)	13	108	6-23-70
	124(124)	nonbreeding	79	(1.5-1.4)	16	damaged	7- 6-70
Ruddy	36	partial	39	(1.5 - 1.2)	19	damaged	6-12-70
Turnstone	67	partial	23	(1.4-1.1)	damaged	19	6-16-70
	68	partial	64	(1.6 - 1.3)	damaged		6-16-70
	117(110)	partial	24	(1.1-0.9)	damaged	128	6-26-70
	122(99)	partial	26	(1.1–0.7)	19	54	7- 5-70

TABLE 2. Records of the breeding condition of female shorebirds.

<sup>a</sup> Where available, body weights (g) are shown in parentheses.
 <sup>b</sup> Measurements give the range of diameters of the five largest ovarian follicles.
 <sup>c</sup> If no weight is shown, the bursa was absent.
 <sup>d</sup> Numbers prefixed by M are American Golden Plovers (P. d. dominica) collected in Minnesota.

" No plumage description has been given since basic and alternate plumages are not readily separable.

In general, all females collected at Eniwetok displayed small and apparently inactive reproductive organs (table 2). There was no recrudescence comparable to that seen in American Golden Plovers migrating through Minnesota. In a few cases, slight recrudescence may have produced minor variations. For example, compare organ parameters (table 2) for Wandering Tattler 45 relative to 114; or Ruddy Turnstone 68 with 117. In contrast to male Whimbrel 48 (table 1), the single female obtained showed no evidence of gonadal activity. The ovaries of Knots, Dunlins, and Ruddy Turnstones examined by van Oordt (1928, 1931) were uniformly inactive, with follicular diameters not exceeding 1.5 mm. Similar findings were reported in Semipalmated Plovers, Knots, Short-billed Dowitchers (Limnodromus griseus), and Sanderlings (Cal*idris alba*) by Loftin (1962).

Based on relative reproductive development when American Golden Plovers arrive in northwestern Minnesota, it is likely that upon reaching the nesting grounds males would be fully recrudesced and females would not. Data from female Dunlins and Wilson's Phalaropes (Steganopus tricolor) in full breeding condition (Holmes 1966; Höhn 1967) infer that female American Golden Plovers collected in Minnesota are much further from reproductive maturity than are the males. Extrapolating from the Dunlin and phalarope data with specimen M11 (table 2) as a base of reference, it appears that ovarian and oviducal weights must increase at least 10 times, and follicular diameters by 5 to 7 times before full recrudescence would be attained. Similar developmental asynchrony between the sexes was noted in the species mentioned above (Holmes 1966; Höhn 1967), and is a generality which emerges in review treatments (Marshall 1961; Lofts and Murton 1968).

Summer populations of nonbreeding Knots and Ruddy Turnstones in Holland appeared to contain a marked preponderance of males (van Oordt 1928). A similar disparity was found at Eniwetok, but only in the American Golden Plover sex ratio. Some specimens were used for other purposes (see Acknowledgments), and hence do not appear in tables 1 and 2. Excluding the Bristle-thighed Curlew where only one bird was obtained, the complete tally was: American Golden Plover: 12 males, 2 females; Ruddy Turnstone: 9 males, 7 females; Wandering Tattler: 3 males, 5 females; Whimbrel: 2 males, 2 females. There is little doubt that the foregoing reflects random sampling since individuals were collected opportunistically.

Species	Dates and numbers of birds seen													
	6/9ª AM	6/12 PM	6/13 PM	6/15 <sup>b</sup> PM	6/18 AM	6/21 PM	6/23° AM	6/26 PM	6/28 PM	6/30 PM	7/1 AM	7/4 PM	7/5 PM	7/6 PM
American Golden Plover	15– 20 <sup>մ</sup>	15– 20	8	3	6	7	0	30– 35	25– 30	10 - 15	20– 25	20– 25	20– 25	31
Whimbrel	2	3	6	1	0	0	0	1	1	1	3	1	4	1
Bristle-thighed Curlew	0	0	0	1	0	0	0	1	0	0	0	0	0	0
Wandering Tattler	12	7	3	1	2	1	1	1	0	1	1	4	0	2
Ruddy Turnstone	20– 25	25– 30	6	12	6	1	0	6	4	0	15	25– 30	15	12

TABLE 3. Chronological summary of shorebird observations at Eniwetok.

<sup>a</sup> Unless otherwise indicated, counts represent Eniwetok islet. Work was conducted in either the morning or afternoon, a typical period of observation was 2-3 hr. <sup>b</sup> Observations made at Libiron islet—area surveyed on foot. <sup>c</sup> Observations made at Chinimi islet—area surveyed on foot. <sup>d</sup> Ranges indicate a degree of disturbance among small flocks caused by our census procedure. Under these conditions only close estimates and not actual numbers could be determined.

#### SHOREBIRD ABUNDANCE

American Golden Plovers and Ruddy Turnstones were the most abundant and commonly observed species during the study (table 3). This agrees with the findings of Woodbury (1962) and Carpenter et al. (1968). The latter publication documents portions of four boreal summers at Eniwetok, during which plovers and turnstones were found on every islet often in flocks of 30 or more. Woodbury's (1962) census of shorebirds on Fred islet from late February to early May 1962, coincided with the migrational season. Hence, his figures for plovers, turnstones, and tattlers are roughly two to three times greater than those in table 3. It is of interest that our counts of Whimbrels exceed the numbers recorded by Woodbury; with Bristle-thighed Curlews uniformly scarce.

Intraspecific daily fluctuations in abundance (table 3) evidently reflected movements of flocks between adjacent islets and had no migrational significance. The disturbance associated with collecting specimens often caused flocks to disperse widely, and on several occasions groups of birds disappeared from view presumably to alight on nearby islets. Baker (1951) found American Golden Plovers undergoing postnuptial molt in July at Guam and considered them to be early migrants from the north. However, it seems more plausible that they were nonmigratory birds based upon records of the fall migration schedule (Henshaw 1910; Johnston and Mc-Farlane 1967), plus the frequency of nonmigratory plovers in breeding plumage (this paper).

## PLUMAGE

Detailed plumage analyses were not done; however, field observations together with notes on each specimen furnish some perspective in this area. A particular effort was made to assess plumage development among American Golden Plovers since they frequented the runway more than the other species and thus were readily observable. Although most of the plovers seen were in nonbreeding plumage, at least some in partial or complete breeding plumage (fig. 2) could be found at any time. On 6 July, the last day of observations (table 3), we were able to categorize every plover on the area with essentially no disturbance of the birds. The results were: 20 in nonbreeding plumage; 6 in partial breeding plumage; and 5 in full breeding plumage. The presence of plovers in breeding plumage disagrees with Henshaw's (1910) observations in the Hawaiian Islands, but confirms Carpenter et al. (1968) who found "some plovers . . . in alternate plumage" at Eniwetok. Among American Golden Plovers summering on Kauai, nonbreeding plumage prevailed except for a few birds in partial breeding plumage (Richardson and Bowles 1964). Present findings are similar to those of Liversidge et al. (1958), who observed Black-bellied Plovers during the boreal summer along the southwestern coast of South Africa. They noted that while most birds retained nonbreeding plumage, a few displayed either breeding or partial breeding coloration.

Most of the turnstones observed and collected at Eniwetok were in partial breeding



FIGURE 2. Two contrasts in the plumage of American Golden Plovers collected at Eniwetok. The bird on the left (no. 74, table 2) was in a partial breeding plumage indicated by a suffusion of black feathers on the cheeks, throat, and breast; plus a fairly distinct white stripe over the eye and down the side of the neck. The other specimen (no. 75, table 1) displayed complete breeding plumage.

plumage. A typical specimen possessed a few chestnut-colored feathers dorsally, and a lightly colored head on which there was a faint but definite harlequin pattern (fig. 3). Carpenter et al. (1968) did not describe the plumages of Ruddy Turnstones which they encountered, except to note the presence of some in alternate plumage. Liversidge et al. (1958) stated that "many (Ruddy Turnstones) attain full breeding plumage while remaining at Langebaan in our mid-winter." I saw only a few Ruddy Turnstones in which the plumage approached breeding coloration. One of these was collected (no. 125, table 1). Its back was richly suffused with chestnut and the black-and-white harlequin face pattern, though not intense, was relatively well developed. Although not quite so colorful as typical breeding birds, it closely resembled the latter.

Wandering Tattlers were somewhat difficult to observe because they often fed amid the surge channels of the seaward reef margin. Most birds seen were in nonbreeding plumage,



FIGURE 3. Typical plumage among Ruddy Turnstones collected at Eniwetok. Note the partially developed harlequin face pattern. The specimen shown is no. 35 in table 1.

but some in breeding plumage were present. Two of the latter were collected. Unfortunately, one was badly damaged and no data were obtained, the other is specimen no. 45 in table 2. Henshaw (1902) reported that Wandering Tattlers summering in the Hawaiian Islands were invariably in nonbreeding plumage.

## BURSA OF FABRICIUS AND BODY FAT

In an effort to gain some insight as to relative age, each specimen was examined for a bursa of Fabricius. Bursae were found frequently (tables 1 and 2), with Ruddy Turnstones particularly noteworthy since 10 of 12 birds collected contained bursae. This, coupled with partial breeding plumage in 11 of the 12 specimens, infers strongly that turnstones lingering in the Pacific are mostly first-year birds. Max C. Thompson (pers. comm.) has reached the same conclusion based upon his studies of turnstone plumage development and banding records. The situation is less clear in American Golden Plovers. None of the birds in breeding plumage collected at Eniwetok contained bursae. On the other hand, several of the migrating plovers (in

breeding plumage) collected in Minnesota did exhibit this organ. Furthermore, some plovers in nonbreeding plumage possessed bursae, others did not (table 1). Lacking details on the rate of bursal atrophy, it is possible only to suggest that American Golden Plovers sampled at Eniwetok represented a mixture of age groups. Data for the other species do not allow much conjecture, except to note that the Wandering Tattler obtained in breeding plumage (no. 45, table 2) lacked a bursa. McNeil and Burton (1972), in a study involving numerous shorebird species, stated categorically that the bursa of Fabricius "is eliminated within the first year of growth," and that it "was absent in yearling specimens taken in May and June." Obviously, my data do not substantiate these findings.

Some morphological features of the bursa are worthy of comment. Extremes of bursal weights recorded in tables 1 and 2 range from 19 to 855 mg. The relationship of size (expressed as length  $\times$  diameter in mm) over this weight range was approximately  $6 \times 2$ to  $21 \times 9$ . The shape of the organ differed interspecifically. In American Golden Plovers and Whimbrels, the bursa resembles a blind cylindrical tube tapering at each end, which is a relatively common configuration in many species of birds. Wandering Tattlers and Ruddy Turnstones exhibited bursae which were Y-shaped, the blind end forking near the apex of the organ. Forbes (1877) and Jolly (1915) described bursal morphology in over 100 species [including only two shorebirds, the Stone Curlew (Burhinus oedic*nemus*) and a seedsnipe (Attagis sp.)] from a variety of avian groups. The only bifid condition found was in a jay (Garrulus glandu*larius*) examined by Jolly.

Detailed notes were not made as to fat deposits in each specimen collected at Eniwetok. However, many of the individuals examined were very fat; some were relatively lean. Both situations prevailed without obvious relationship to plumage status. These findings disagree with Henshaw's (1910) statement as to the lack of fat in summering shorebirds from the Hawaiian Islands. The plovers collected in Minnesota all contained substantial amounts of fat.

# SUMMARY

Five species of shorebirds (American Golden Plover, Whimbrel, Bristle-thighed Curlew, Wandering Tattler, and Ruddy Turnstone) which had not migrated to their northern breeding grounds were studied during the boreal summer at Eniwetok Atoll, Marshall Islands. Plovers and turnstones were particularly abundant throughout the period of observations (9 June to 6 July 1970).

Spermatogenic activity was relatively slight in American Golden Plovers, Wandering Tattlers, and Ruddy Turnstones; recrudescence had not progressed beyond limited numbers of primary spermatocytes in synapsis. Contrarily, Whimbrel and Bristle-thighed Curlew testes exhibited moderate numbers of spermatozoa. All females collected at Eniwetok contained inactive reproductive organs, with ovarian follicles seldom exceeding 1.5 mm in diameter. Comparative data are presented from American Golden Plovers nearing reproductive maturity when collected in Minnesota during northward migration. The sex ratio of plovers at Eniwetok was strongly biased toward males, and apparently balanced in the other species.

Nonbreeding, partial breeding, and full breeding plumages were found among American Golden Plovers, Wandering Tattlers, and Ruddy Turnstones. Partial breeding plumage was particularly common in turnstones. Plumage development and testicular histology were not correlated; this was especially striking in plovers where males with breeding plumage contained immature testes.

Almost all turnstones displayed bursae Fabricii which, coupled with their plumage development, infer that nonmigratory individuals are mostly first-year birds. Similar data for plovers suggested a mixture of age groups at Eniwetok. Information was inadequate to speculate on the relationship between migration and age in the other shorebirds examined.

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#### LITERATURE CITED

- AMERSON, A. B. 1969. Ornithology of the Marshall and Gilbert Islands. Atoll Res. Bull. No. 127.
   AMERSON, A. B. 1971. The natural history of
- AMERSON, A. B. 1971. The natural history of French Frigate Shoals, northwestern Hawaiian Islands. Atoll Res. Bull. No. 150.
- BAKER, R. H. 1951. The avifauna of Micronesia, its origin, evolution and distribution. Univ. Kansas Pub., Mus. Nat. Hist. 3:1–359.
- BANNERMAN, D. A., AND W. M. BANNERMAN. 1963– 68. Birds of the Atlantic Islands. Vols. 1–4. Oliver and Boyd, Edinburgh.
- BENT, A. C. 1929. Life histories of North American shorebirds. Part 2. U.S. Natl. Mus., Bull. 146.
- BOURNE, W. R. P. 1971. The birds of the Chagos Group, Indian Ocean. In D. R. Stoddart and J. D. Taylor [eds.] Geography and ecology of Diego Garcia Atoll, Chagos Archipelago. Atoll Res. Bull. No. 149.
- BURLAND, J. C. 1964. Some notes on the bird life of Palmerston Atoll. Notornis 11:145–154.
- CARPENTER, M. L., W. B. JACKSON, AND M. W. FALL. 1968. Bird populations at Eniwetok Atoll. Micronesica 4:295–307.
- EDGAR, A. T., H. R. MCKENZIE, AND R. B. SIBSON. 1969. Arctic waders in northern New Zealand summer 1968–69. Notornis 16:285–287.
- FORBES, W. A. 1877. On the bursa Fabricii in birds. Proc. Zool. Soc. London, p. 304–318.
- HENSHAW, H. W. 1902. Birds of the Hawaiian Islands. Thrum, Honolulu.
- HENSHAW, H. W. 1910. Migration of the Pacific plover to and from the Hawaiian Islands. Auk 27:245-262.
- HÖHN, E. O. 1967. Observations on the breeding biology of Wilson's Phalarope (Steganopus tricolor) in central Alberta. Auk 84:220-244.
- HOLMES, R. T. 1966. Breeding ecology and annual cycle adaptations of the Red-backed Sandpiper (*Calidris alpina*) in northern Alaska. Condor 68:3-46.
- JOHNSON, O. W. 1961. Reproductive cycle of the Mallard duck. Condor 63:351–364.
- JOHNSTON, D. W., AND R. W. MCFARLANE. 1967. Migration and bioenergetics of flight in the Pacific Golden Plover. Condor 69:156–168.
- JOLLY, J. 1915. La bourse de Fabricius et les organes lympho-épithéliaux. Arch. Anat. Micros. 16:363-547.
- LIVERSIDGE, R., G. J. BROEKHUYSEN, AND A. R. THESEN. 1958. The birds of Langebaan Lagoon. Ostrich 29:95-106.
- LOFTIN, H. 1962. A study of boreal shorebirds summering on Apalachee Bay, Florida. Bird-Banding 33:21-42.
- LOFTS, B. 1962. Cyclical changes in the interstitial and spermatogenic tissue of migratory waders "wintering" in Africa. Proc. Zool. Soc. London 138:405-413.
- LOFTS, B., AND R. K. MURTON. 1968. Photoperiodic and physiological adaptations regulating avian

breeding cycles and their ecologic significance. J. Zool., London 155:327-394.

- MACKWORTH-PRAED, C. W., AND C. H. B. GRANT. 1952. Birds of Eastern and North Eastern Africa. Vol. 1. Longmans, Green, London.
- MACKWORTH-PRAED, C. W., AND C. H. B. GRANT. 1962. Birds of the southern third of Africa. Vol. 1. Longmans, Green, London.
- MACKWORTH-PRAED, C. W., AND C. H. B. GRANT. 1970. Birds of West Central and Western Africa. Vol. 1. Longmans, Green, London.
- MARSHALL, A. J. 1961. Reproduction. In A. J. Marshall [ed.] Biology and comparative physiology of birds. Academic Press, New York.
- MAYR, E. 1945. Birds of the Southwest Pacific. Macmillan, New York.
- MCNEIL, R. 1970. Hivernage et estivage d'oiseaux aquatiques nord-américains dans le Nord-Est du Venezuela (mue, accumulation de graisse, capacité de vol et routes de migration). L'Oiseau Rev. Francaise Ornithol. 40:185–302.
- MCNEIL, R., AND J. BURTON. 1972. Cranial pneumatization patterns and bursa of Fabricius in North American shorebirds. Wilson Bull. 84: 329–339.
- MORGAN, B., AND J. MORGAN. 1965. Some notes on birds of the Fiji Islands. Notornis 12:158– 168.
- PALMER, R. S. 1967. Species accounts. In G. D. Stout [ed.] Shorebirds of North America. Viking Press, New York.
  PAYNE, R. B. 1972. Mechanisms and control of
- PAYNE, R. B. 1972. Mechanisms and control of molt. In D. S. Farner and J. R. King [eds.] Avian biology. Vol. 2. Academic Press, New York.
  RICHARDSON, F., AND J. BOWLES. 1964. A survey
- RICHARDSON, F., AND J. BOWLES. 1964. A survey of the birds of Kauai, Hawaii. Bernice P. Bishop Mus., Bull. 227.
- STICKNEY, E. H. 1943. Northern shorebirds in the Pacific. Amer. Mus. Novitates 1248:1-9.
- THOMAS, D. G. 1968. Waders of Hobart. Emu 68:95-125.
- THOMAS, D. G. 1970. Fluctuation of numbers of waders in south-eastern Tasmania. Emu 70: 79–85.
- VAN OORDT, G. J. 1928. Studies on the gonads of summering birds. I and II. The Knot and the Turnstone. Tijdschr. Ned. Dierk. Ver. 1:25-30.
- VAN OORDT, G. J. 1931. Studien über die Gonaden übersommernder Vögel. III. Das Verhältnis zwischen dem mikroskopischen Bau der Gonaden übersommernder Schnepfenvögel (*Calidris canutus, Calidris alpina*, und *Arenaria interpres*) und dem Federkleid. Z. Mikrosk. Anat. Forsch. 25: 539–560.
- VOITKEVICH, A. A. 1966. The feathers and plumage of birds. October House, New York.
- VOLSOE, H. 1950. Spring observations on migrant birds in the Canary Islands. Vidensk. Medd. Dansk Naturhist. Foren. 112:75–117.
- WOODBURY, A. M. 1962. A review of the ecology of Eniwetok Atoll, Pacific Ocean. Inst. Environ. Biol. Res., Univ. Utah.

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