

CLUTCH SIZE AND EVOLUTION IN THE CHARADRII

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ONE of the most recent statements on the significance of clutch size variations in birds is Ricklefs' (1970) comment: "variation in clutch size among birds remains inadequately explained." This is even more surely the case among precocial than among altricial birds, and it is nowhere less adequately explained than in the Charadrii (waders or shorebirds). As Boyd (1962) has shown, a study of clutch size as a measure of fertility or reproductive rate "is unrewarding in the case of waders, in which most Palaearctic species have a modal clutch of four." Boyd's study shows, for example, that in four species of *Charadrius* the annual egg production per female varies from 3.0 to 6.3, yet the annual recruitment of individuals into the population remains much the same for each species.

The present paper sets out the data concerning variations in clutch size among the Charadrii from a phylogenetic viewpoint rather than one of adaptive significance. I do not wish to imply that clutch size has no adaptive significance, but I hope to show that clutch size in the Charadrii has some real phylogenetic significance when used in conjunction with other characters of known phylogenetic use. The theory of clutch size that I shall try to substantiate depends upon the assumption that the ancestral clutch in the waders is 4 eggs. From the following review I shall draw certain conclusions about the evolution and taxonomy of the Charadrii, using clutch size as the main criterion.

CLUTCH SIZE AND DISTRIBUTION

Table 1 shows clutch sizes in the 205 extant or recently extinct species of Charadrii. The geographical distributions of the families within the suborder appear in Figures 1 to 11.

JACANIDAE. Except for the small size of *Microparra capensis*, the jaçanas are a homogeneous family, pantropical in distribution (Figure 1) and share a similar habitat of floating vegetation around the margins of fresh waters. Most lay clutches of 4 eggs, but *M. capensis* often lays only 2 or 3.

ROSTRATULIDAE. The Old World Painted Snipe *Rostratula benghalensis* has a wide range from Africa to Australia, lays a clutch of 4 eggs and is probably closer to the ancestral rostratulid than the New World Painted Snipe *Nycticryphes semicollaris* with a restricted range in South America (Figure 2) and an invariable clutch size of 2 eggs. The two species share similar marshy habitats.

HAEMATOPODIDAE. The Haematopodidae comprise a single cosmopolitan

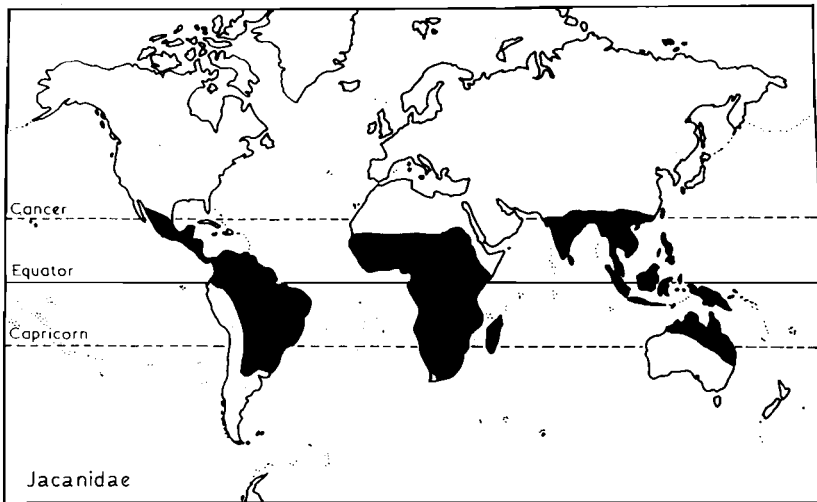


Figure 1. Distribution of the Jacanidae.

TABLE 1
CLUTCH SIZES IN THE CHARADRII

| Family and species | Region | Clutch size | References |
|----------------------------------|-----------------|-------------|----------------------------------|
| JACANIDAE | | | |
| <i>Microparra capensis</i> | East Africa | 2-4 | Mackworth-Praed and Grant (1952) |
| | South Africa | 3-4 | McLachlan and Liversidge (1957) |
| <i>Actophilornis africana</i> | Nigeria | 4 | Serle (1939) |
| | South Africa | 4 | Maclean (pers. obs.) |
| <i>A. albinucha</i> | Malagasy | 4 | Rand (1936) |
| <i>Irediparra gallinacea</i> | Australia | 4 | Cayley (1963) |
| <i>Hydrophasianus chirurgus</i> | India | 4 | Ali and Ripley (1969a) |
| | China | 4 | Hoffmann (1949) |
| | Burma | 4 | Smythies (1953) |
| <i>Metopidius indicus</i> | India | 4 | Mathew (1964) |
| | Burma | 4 | Smythies (1953) |
| <i>Jaçana spinosa</i> | Central America | 4 | Bent (1929) |
| ROSTRATULIDAE | | | |
| <i>Rostratula benghalensis</i> | South Africa | 3-5 | McLachlan and Liversidge (1957) |
| | Congo | 4 | Chapin (1939) |
| | India | 4 | Ali and Ripley (1969a) |
| | Burma | 4-6 | Smythies (1953) |
| | China | 3-4 | Caldwell and Caldwell (1931) |
| | Japan | 3-4 | Kobayashi (1956) |
| <i>Nycticryphes semicollaris</i> | Australia | 4 | Lowe (1963) |
| | South America | 2 | Maclean (pers. obs.) |

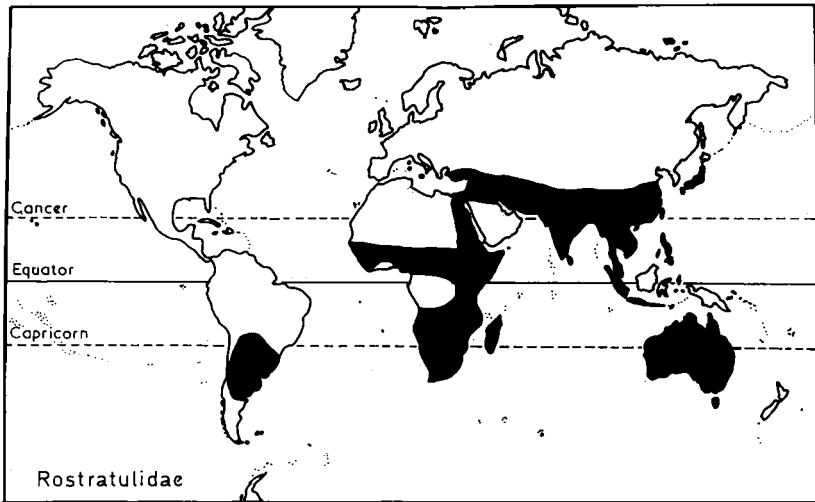


Figure 2. Distribution of the Rostratulidae.

TABLE 1 Continued

| Family and species | Region | Clutch size | References | |
|---------------------------------|----------------------|---------------|------------------------------|----------------------|
| HAEMATOPODIDAE | | | | |
| <i>Haematopus ostralegus</i> | Europe | 2-4 | Bent (1929) ; Koch (1957) | |
| | U.S.S.R. | 3 | Kozlova (1961) | |
| | Pakistan | 2 | Ali and Ripley (1969a) | |
| | China | 3 | Caldwell and Caldwell (1931) | |
| | North America | 2-3 | Bent (1929) | |
| | Central America | 1-3 | Bent (1929) | |
| | South America | 2-3 | Maclean (pers. obs.) | |
| | Galápagos Islands | 1-2 | Lévêque (1964) | |
| | New Zealand, S. Is. | 2 | Oliver (1955) | |
| | New Zealand, N. Is. | 3 | Oliver (1955) | |
| | <i>H. bachmani</i> | North America | 1-4 | Bent (1929) |
| | <i>H. leucopodus</i> | South America | 2 | Maclean (pers. obs.) |
| <i>H. fuliginosus</i> | Australia | 1-3 | Burton (in litt.) | |
| <i>H. ater</i> | South America | 1-2 | Johnson (1965) | |
| <i>H. unicolor</i> | New Zealand | 2-3 | Oliver (1955) | |
| <i>H. moquini</i> | South Africa | 2 | Maclean (pers. obs.) | |
| IBIDORHYNCHIDAE | | | | |
| <i>Ibidorhyncha struthersii</i> | Kirghiz | 4 | Yanushevich (1959) | |
| | Himalayas | 4 | Ali and Ripley (1969a) | |
| | Kashmir | 3-5 | Phillips (1945) | |
| | U.S.S.R. | 4 | Kozlova (1961) | |
| | China | 4 | Meise et al. (1938) | |

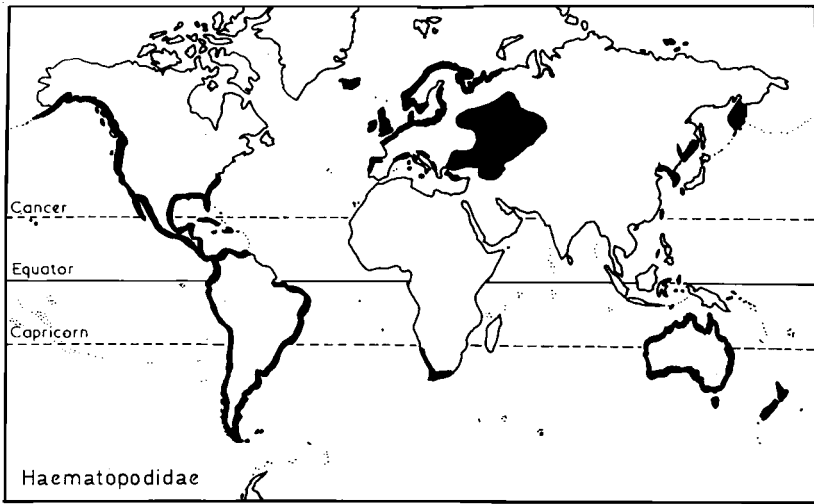


Figure 3. Distribution of the Haematopodidae.

TABLE 1 *Continued*

| Family and species | Region | Clutch size | References |
|------------------------------------|-------------------|-------------|----------------------------------|
| RECURVIROSTRIDAE | | | |
| <i>Himantopus himantopus</i> | Palaearctic | 4 | Kozlova (1961) |
| | India | 4 | Dharmakumarsinhji (1964) |
| | North America | 4 | Bent (1927) |
| | Galápagos Islands | 4 | Lévêque (1964) |
| | Hawaii | 4 | Berger (1967) |
| | South America | 4 | Johnson (1965) |
| | East Africa | 3-4 | Mackworth-Praed and Grant (1952) |
| | South Africa | 4 | McLachlan and Liversidge (1957) |
| | Australia | 4 | Cayley (1963) |
| | New Zealand | 4 | Oliver (1955) |
| <i>Cladorhynchus leucocephalus</i> | Australia | 2-4 | Cayley (1963) |
| <i>Recurvirostra avosetta</i> | Palaearctic | 4 | Koch (1957) |
| | India | 4 | Ali and Ripley (1969a) |
| | South Africa | 3-5 | McLachlan and Liversidge (1957) |
| <i>R. americana</i> | North America | 4 | Bent (1927) |
| <i>R. novaehollandiae</i> | Australia | 4 | Bryant (1947, 1948) |
| <i>R. andina</i> | South America | 4 | Johnson (1965) |
| BURHINIDAE | | | |
| <i>Burhinus oedicnemus</i> | Europe | 2 | Koch (1957) |
| | North Africa | 2 | Etchécopar and Hüe (1967) |
| | India | 2 | Ali and Ripley (1969b) |
| | Burma | 2 | Smythies (1953) |

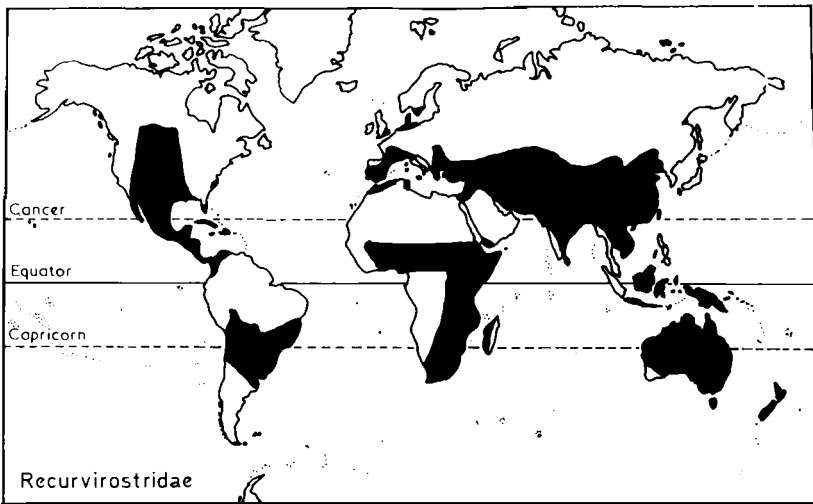


Figure 4. Distribution of the Recurvirostridae.

TABLE 1 Continued

| Family and species | Region | Clutch size | References |
|------------------------------|-----------------|-------------|----------------------------------|
| <i>B. senegalensis</i> | North Africa | 2 | Etchécopar and Hüe (1967) |
| | East Africa | 2 | Mackworth-Praed and Grant (1952) |
| <i>B. vermiculatus</i> | East Africa | 2 | Mackworth-Praed and Grant (1952) |
| | South Africa | 2 | McLachlan and Liversidge (1957) |
| <i>B. capensis</i> | East Africa | 2 | Mackworth-Praed and Grant (1952) |
| | South Africa | 2 | Maclean (pers. obs.) |
| <i>B. bistriatus</i> | Central America | 2 | Dickey and Van Rossem (1938) |
| <i>B. superciliaris</i> | South America | 2 | Bruhn (in litt.) |
| <i>B. magnirostris</i> | Australia | 2 | Cayley (1963) |
| <i>Esacus recurvirostris</i> | India | 2 | Ali and Ripley (1969b) |
| | Ceylon | 1-2 | Henry (1955) |
| <i>E. magnirostris</i> | Australia | 1-2 | Cayley (1963) |
| | Burma | 2 | Smythies (1953) |
| GLAREOLIDAE | | | |
| <i>Stiltia isabella</i> | Australia | 2 | Cayley (1963) |
| <i>Glareola pratincola</i> | Palaearctic | 2 | Cayley (1963) |
| | East Africa | 2-3 | Mackworth-Praed and Grant (1952) |
| | Congo | 2-3 | Chapin (1939) |
| | South Africa | 2-3 | McLachlan and Liversidge (1957) |

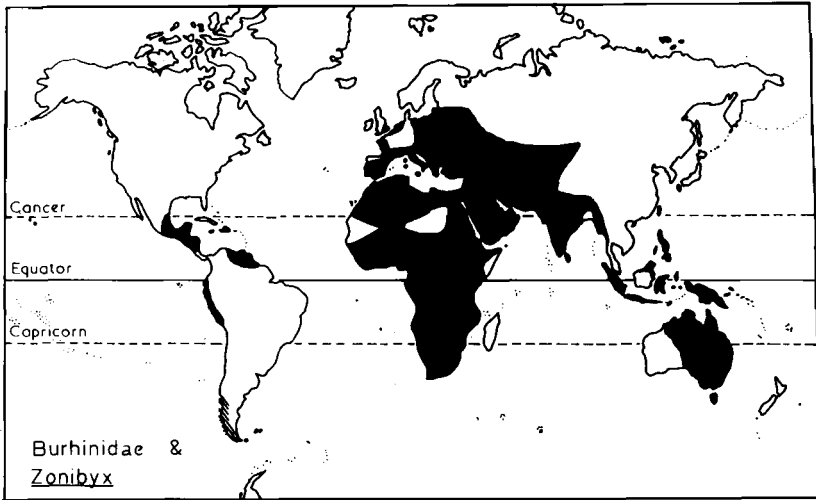


Figure 5. Distribution of the Burhinidae (black) and the charadriine genus *Zonibyx* (diagonal hatching).

TABLE 1 *Continued*

| Family and species | Region | Clutch size | References |
|------------------------------|--------------|-------------|----------------------------------|
| <i>G. maldivarum</i> | Pakistan | 2 | Burton (in litt.) |
| | Burma | 2-3 | Smythies (1953) |
| | India | 2-3 | Ali and Ripley (1969b) |
| | China | 3 | Caldwell and Caldwell (1931) |
| <i>G. nordmanni</i> | U.S.S.R. | 3 | Burton (in litt.) |
| | Turkey | 2 | Burton (in litt.) |
| <i>G. ocularis</i> | Malagasy | 3 | Bruhn (in litt.) |
| | | 2 | Burton (in litt.) |
| <i>G. lactea</i> | India | 2-4 | Dharmakumarsinhji (1964) |
| | Burma | 2 | Smythies (1953) |
| <i>Galachrysis nuchalis</i> | East Africa | 2 | Mackworth-Praed and Grant (1952) |
| | Congo | 2 | Chapin (1939) |
| | South Africa | 2-3 | McLachlan and Liversidge (1957) |
| <i>G. cinerea</i> | Nigeria | 1-2 | Serle (1939) |
| | Congo | 1-2 | Chapin (1939) |
| <i>Rhinoptilus africanus</i> | East Africa | 1 | Moreau and Moreau (1937) |
| | South Africa | 1 | Maclean (1967) |
| <i>R. cinctus</i> | East Africa | 2 | Mackworth-Praed and Grant (1952) |
| | South Africa | 2 | McLachlan and Liversidge (1957) |

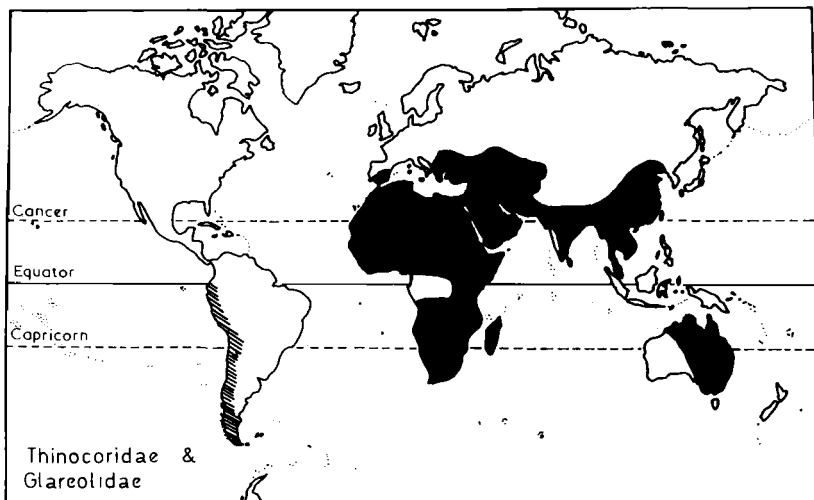


Figure 6. Distribution of the Thinocoridae (diagonal hatching) and the Glareolidae (black).

TABLE 1 *Continued*

| Family and species | Region | Clutch size | References |
|--------------------------|--------------|-------------|----------------------------------|
| <i>R. chalconotus</i> | East Africa | 2-3 | Mackworth-Praed and Grant (1952) |
| | Congo | 3 | Chapin (1939) |
| | Zambia | 2-3 | Chapin (1939) |
| | South Africa | 2-3 | McLachlan and Liversidge (1957) |
| <i>R. bitorquatus</i> | India | 2 | Baker (1929) |
| <i>Cursorius cursor</i> | North Africa | 2 | Etchécopar and Hüe (1967) |
| | East Africa | 2 | Mackworth-Praed and Grant (1952) |
| <i>C. rufus</i> | South Africa | 2 | Maclean (pers. obs.) |
| <i>C. coromandelicus</i> | India | 2-3 | Ali and Ripley (1969b) |
| <i>C. temminckii</i> | Congo | 2 | Chapin (1939) |
| | South Africa | 2 | McLachlan and Liversidge (1957) |
| CHARADRIIDAE | | | |
| <i>Vanellus vanellus</i> | Palaearctic | 4 | Bent (1929) |
| <i>V. crassirostris</i> | East Africa | 2-3 | Mackworth-Praed and Grant (1952) |
| | Congo | 2-4 | Chapin (1939) |
| | South Africa | 2 | McLachlan and Liversidge (1957) |
| <i>V. armatus</i> | East Africa | 2-4 | Mackworth-Praed and Grant (1952) |
| | Congo | 2-4 | Chapin (1939) |
| | South Africa | 4 | Maclean (pers. obs.) |

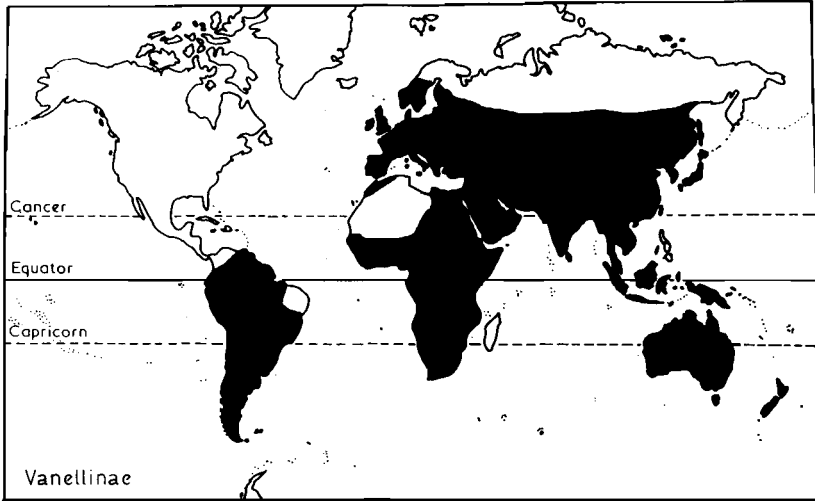
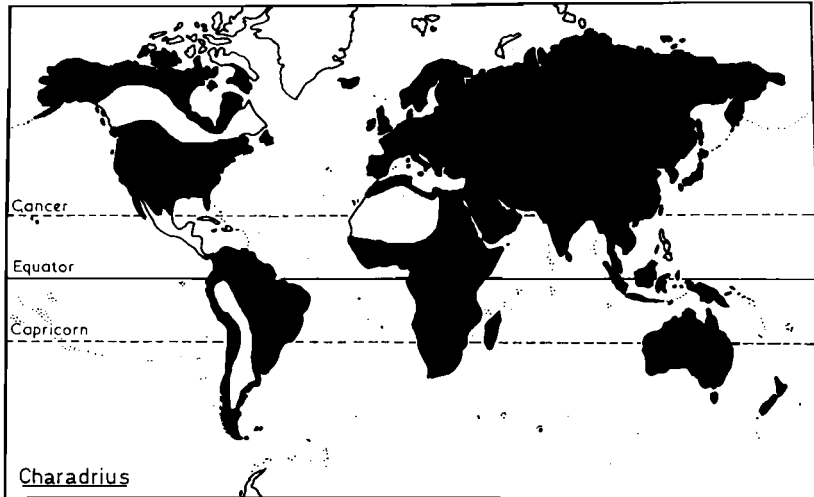


Figure 7. Distribution of the Vanellinae.

TABLE 1 *Continued*

| Family and species | Region | Clutch size | References |
|------------------------|-------------------------|-------------|------------------------------------|
| <i>V. spinosus</i> | Greece | 4 | Makatsch (1962) |
| | East Africa | 3-4 | Mackworth-Praed and Grant (1952) |
| | Uganda | 1-3 | Hall (1965) |
| <i>V. duvaucellii</i> | Congo | 3-4 | Chapin (1939) |
| | India | 4 | Ali and Ripley (1969a) |
| <i>V. tectus</i> | Burma | 3-4 | Smythies (1953) |
| | East Africa | 2-3 | Mackworth-Praed and Grant (1952) |
| <i>V. malabaricus</i> | India | 4 | Jayakar and Spurway (1965a, 1965b) |
| <i>V. albiceps</i> | West and Central Africa | 2-4 | Mackworth-Praed and Grant (1952) |
| | Nigeria | 2-3 | Serle (1939) |
| | Congo | 3 | Chapin (1939) |
| | South Africa | 3-4 | McLachlan and Liversidge (1957) |
| <i>V. lugubris</i> | East Africa | 3-4 | Mackworth-Praed and Grant (1952) |
| | Congo | 4 | Chapin (1939) |
| | South Africa | 2-4 | McLachlan and Liversidge (1957) |
| <i>V. melanopterus</i> | East Africa | 3 | Mackworth-Praed and Grant (1952) |
| | South Africa | 3-4 | McLachlan and Liversidge (1957) |
| | | 2-3 | Maclean (pers. obs.) |

Figure 8. Distribution of the charadriine genus *Charadrius*.TABLE 1 *Continued*

| Family and species | Region | Clutch size | References |
|--------------------------|---------------|-------------|--------------------------------------|
| <i>V. coronatus</i> | East Africa | 2-4 | Mackworth-Praed and Grant (1952) |
| <i>V. senegallus</i> | South Africa | 2-4 | Maclean (pers. obs.) |
| | Uganda | 1-4 | Hall (1965) |
| | East Africa | 3-4 | Mackworth-Praed and Grant (1952) |
| <i>V. melanocephalus</i> | South Africa | 4 | Little (1967) |
| | Ethiopia | 4 | Mackworth-Praed and Grant (1952) |
| <i>V. superciliosus</i> | West Africa | 2-4 | Serle (1956) |
| <i>V. gregarius</i> | Palaearctic | 4 | Koch (1957) |
| | Kazakhstan | 2-4 | Chekmenev (1961) |
| | U.S.S.R. | 4-5 | Kozlova (1961) |
| <i>V. leucurus</i> | Transcaucasia | 4 | Vinogradov (1963) |
| | U.S.S.R. | 3-4 | Kozlova (1961) |
| <i>V. cayanus</i> | Brazil | 2 | Sick (in litt.); Wied-Neuwied (1833) |
| <i>V. chilensis</i> | Chile | 2-4 | Maclean (pers. obs.) |
| <i>V. resplendens</i> | Chile | 4 | Johnson (1965) |
| <i>V. cinereus</i> | China | 2-4 | Caldwell and Caldwell (1931) |
| | Japan | 4 | Kobayashi (1956) |
| | India | 4 | Dharmakumarsinhji (1964) |
| <i>V. indicus</i> | Burma | 4 | Smythies (1953) |
| | Malaya | 2-4 | Madoc (1956) |

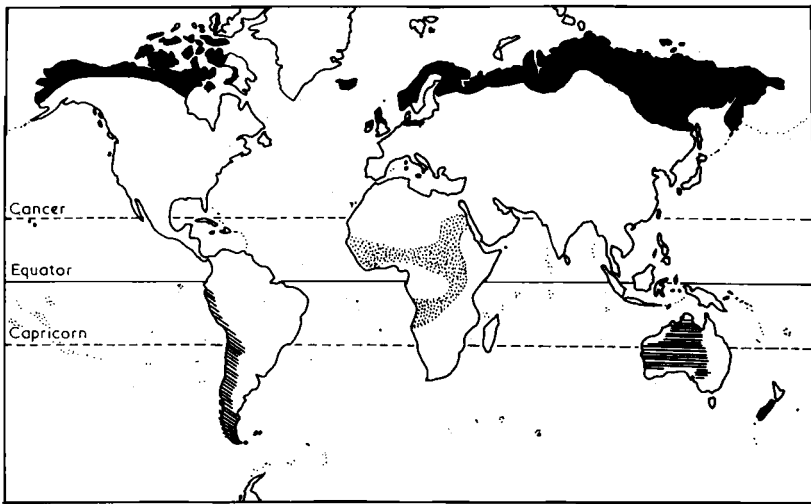


Figure 9. Distribution of the genera *Pluvialis* (black), *Pluvianus* (stippled), *Oreopholus* (diagonal hatching) and *Peltodyas* (horizontal hatching), all of the sub-family Charadriinae.

TABLE 1 *Continued*

| Family and species | Region | Clutch size | References |
|-----------------------------|---------------|-------------|----------------------------------|
| <i>V. macropterus</i> | Indonesia | 4 | Bruhn (in litt.) |
| <i>V. tricolor</i> | Australia | 4 | Cayley (1963) |
| <i>V. miles</i> | Australia | 4 | Cayley (1963) |
| <i>V. novaehollandiae</i> | Australia | 4 | Cayley (1963) |
| | Tasmania | 4 | Thomas (1969) |
| | New Zealand | 2-3 | Oliver (1955); Sansom (1951) |
| <i>Charadrius hiaticula</i> | Palaearctic | 4 | Laven (1940) |
| <i>C. semipalmatus</i> | Nearctic | 4 | Bent (1929) |
| <i>C. placidus</i> | India | 4 | Baker (1929) |
| | Japan | 3-4 | Kobayashi (1956) |
| <i>C. dubius</i> | Palaearctic | 4 | Bent (1929) |
| | Burma | 4 | Smythies (1953) |
| <i>C. wilsonia</i> | North America | 2-4 | Bent (1929) |
| <i>C. vociferus</i> | North America | 4 | Maclean (pers. obs.) |
| <i>C. melodus</i> | North America | 4 | Bent (1929) |
| <i>C. thoracicus</i> | Malagasy | ? | |
| <i>C. pecuarius</i> | East Africa | 2 | Mackworth-Praed and Grant (1952) |
| | Uganda | 1-2 | Hall (1965) |
| | Congo | 2 | Chapin (1939) |
| | South Africa | 2 | Maclean (pers. obs.) |
| | Captivity | 2 | Conway and Bell (1968) |

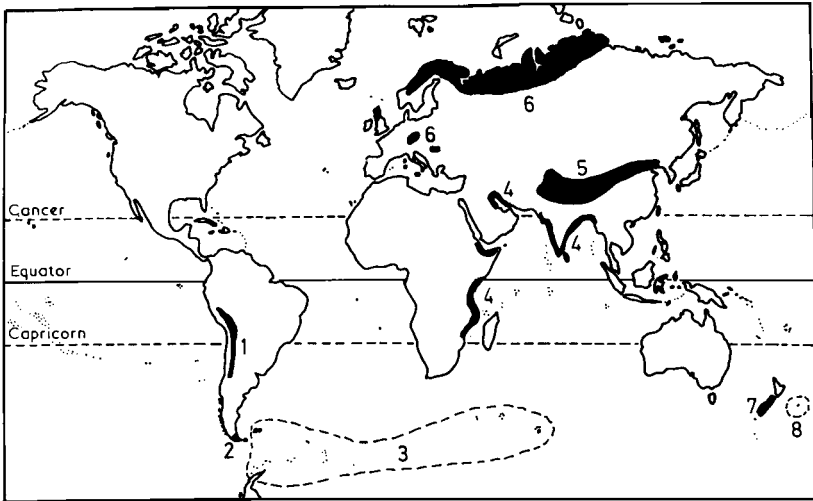


Figure 10. Distribution of (1) genus *Phegornis*, (2) genus *Pluvianellus*, (3) family Chionididae, (4) family Dromadidae, (5) family Ibidorhynchidae, (6) genus *Eudromias*, (7) genus *Anarhynchus*, and (8) genus *Thinornis*. The five genera are all in the subfamily Charadriinae.

TABLE 1 Continued

| Family and species | Region | Clutch size | References |
|--------------------------|---------------|-------------|----------------------------------|
| <i>C. sanctaehelenae</i> | St. Helena | 1-2 | Haydock (1954) |
| <i>C. tricoloris</i> | Congo | 2 | Chapin (1939) |
| | South Africa | 2 | Maclean (pers. obs.) |
| | Malagasy | 1 | Rand (1936) |
| <i>C. forbesi</i> | East Africa | 2-3 | Mackworth-Praed and Grant (1952) |
| <i>C. alexandrinus</i> | North America | 2-3 | Bent (1929) |
| | Europe | 3 | Rittinghaus (1961) |
| | India | 1-3 | Dharmakumarsinhji (1964) |
| | Japan | 3 | Kobayashi (1956) |
| | Chile | 2-3 | Maclean (pers. obs.) |
| | Australia | 2 | Cayley (1963) |
| | New Zealand | 2 | Oliver (1955) |
| <i>C. marginatus</i> | Nigeria | 2 | Serle (1939) |
| | East Africa | 2-3 | Mackworth-Praed and Grant (1952) |
| | Congo | 3 | Chapin (1939) |
| | South Africa | 2-3 | Maclean and Moran (1965) |
| <i>C. peronii</i> | Malaya | 3-4 | Madoc (1956) |
| <i>C. venustus</i> | East Africa | 2 | Mackworth-Praed and Grant (1952) |
| | South Africa | 2 | Jeffery and Liversidge (1951) |

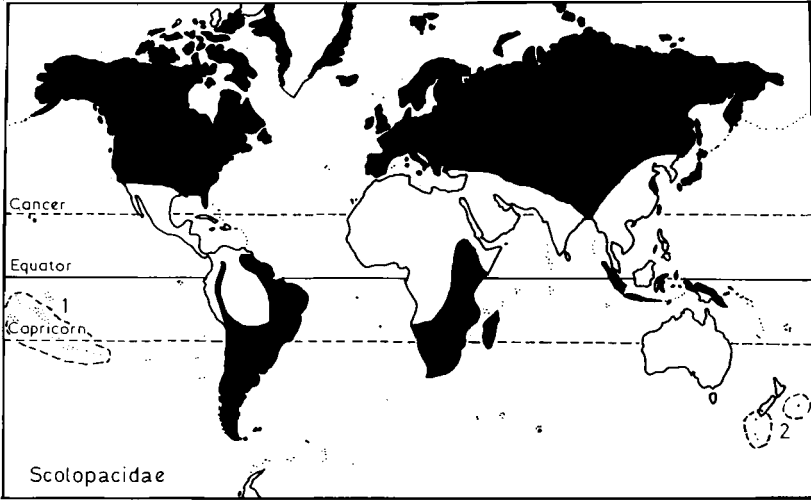


Figure 11. Distribution of the Scolopacidae, including the genera *Prosobonia* (1) and *Coenocorypha* (2).

TABLE 1 Continued

| Family and species | Region | Clutch size | References |
|----------------------------------|---------------|-------------|-------------------------------|
| <i>C. collaris</i> | South America | 2 | Johnson (1965) |
| <i>C. bicinctus</i> | New Zealand | 2-4 | Stidolph (1944) |
| <i>C. falklandicus</i> | Chile | 3 | Maclean (pers. obs.) |
| <i>C. alticola</i> | Argentina | 2 | Hoy (1967) |
| <i>C. mongolus</i> | U.S.S.R. | 3 | Kozlova (1961) |
| | Tibet | 3 | Ali and Ripley (1969a) |
| | China | 2 | Meise et al. (1938) |
| <i>C. leschenaultii</i> | Somalia | 3 | Harrison (1963) |
| | U.S.S.R. | 3 | Kozlova (1961) |
| | Kirghiz | 2 | Meise et al. (1938) |
| | China | 3 | Caldwell and Caldwell (1931) |
| <i>C. asiaticus</i> | Central Asia | 3-4 | Baker (1929) |
| <i>C. montanus</i> | North America | 3 | Bent (1929) |
| <i>C. melanops</i> | Australia | 3 | Serventy and Whittell (1967) |
| <i>C. cinctus</i> | Australia | 4 | Cayley (1963) |
| <i>C. rubricollis</i> | Australia | 2-3 | Cayley (1963) |
| <i>Thinornis novaeseelandiae</i> | New Zealand | 2-3 | Oliver (1955) |
| <i>Phegornis mitchellii</i> | Chile | 2 | Johnson (1964) |
| <i>Anarhynchus frontalis</i> | New Zealand | 2-3 | Oliver (1955) |
| <i>Zonibyx modestus</i> | Patagonia | 2 | Johnson (1965) |
| <i>Pluvialis apricaria</i> | Palaearctic | 4 | Bent (1929) |
| <i>P. squatarola</i> | Holarctic | 4 | Bent (1929) |
| <i>P. dominica</i> | Holarctic | 3-4 | Bent (1929); Steiniger (1959) |

TABLE 1 *Continued*

| Family and species | Region | Clutch size | References |
|------------------------------------|---------------------|-------------|----------------------------------|
| <i>P. obscura</i> | New Zealand | 3 | McKenzie (1951, 1952, 1953) |
| <i>Eudromias morinellus</i> | Palaearctic | 3 | Rittinghaus (1962) |
| <i>Oreopholus ruficollis</i> | South America | 4 | Maclean (pers. obs.) |
| <i>Pluvianellus socialis</i> | Patagonia | 2 | Maclean (pers. obs.) |
| <i>Pluvianus aegyptius</i> | Nigeria | 2-3 | Serle (1939) |
| | Nile Valley | 2-4 | Chapin (1939) |
| | East Africa | 2-3 | Mackworth-Praed and Grant (1952) |
| <i>Peltohyas australis</i> | Australia | 3 | Cayley (1963) |
| SCOLOPACIDAE | | | |
| <i>Limosa limosa</i> | Palaearctic | 4 | Bent (1927) |
| <i>L. haemastica</i> | Nearctic | 4 | Bent (1927) |
| <i>L. lapponica</i> | Holarctic | 4 | Bent (1927) |
| <i>L. fedoa</i> | Nearctic | 4 | Bent (1927) |
| <i>Numenius minutus</i> | Siberia | 4 | Kozlova (1962) |
| <i>N. borealis</i> | Nearctic | 4 | Bent (1929) |
| <i>N. phaeopus</i> | Holarctic | 4 | Bent (1929) |
| <i>N. tahitiensis</i> | Nearctic | 4 | Allen (1951) |
| <i>N. tenuirostris</i> | U.S.S.R. | 4 | Dementiev and Gladkov (1951) |
| <i>N. arquata</i> | Palaearctic | 4 | Bent (1929) |
| <i>N. madagascariensis</i> | U.S.S.R. | 4 | Kozlova (1962) |
| <i>N. americanus</i> | Nearctic | 4 | Bent (1929) |
| <i>Bartramia longicauda</i> | Nearctic | 4 | Bent (1929) |
| <i>Tringa erythropus</i> | Palaearctic | 4 | Koch (1957) |
| <i>T. totanus</i> | Palaearctic | 4 | Bent (1927) |
| <i>T. stagnatilis</i> | Palaearctic | 4 | Kozlova (1961) |
| <i>T. nebularia</i> | Palaearctic | 4 | Bent (1927) |
| <i>T. guttifer</i> | Palaearctic | 4 | Baker (1935); Kozlova (1961) |
| <i>T. melanoleuca</i> | Nearctic | 4 | Bent (1927) |
| <i>T. flavipes</i> | Nearctic | 4 | Bent (1927) |
| <i>T. solitaria</i> | Nearctic | 4 | Bent (1929) |
| <i>T. ochropus</i> | Palaearctic | 4 | Bent (1929) |
| <i>T. glareola</i> | Palaearctic | 4 | Bent (1929) |
| <i>Catoptrophorus semipalmatus</i> | Nearctic | 4 | Bent (1929) |
| <i>Xenus cinereus</i> | Palaearctic | 4 | Kozlova (1961) |
| <i>Actitis hypoleucos</i> | Palaearctic | 4 | Kobayashi (1956); Koch (1957) |
| <i>A. macularia</i> | Nearctic | 4 | Maclean (pers. obs.) |
| <i>Heteroscelus brevipes</i> | Siberia | 4 | Neufeldt et al. (1961) |
| <i>H. incanus</i> | Nearctic | 4 | Bent (1929) |
| <i>Prosobonia cancellatus</i> | Tuamotu Archipelago | 2 | Greenway (1958) |
| <i>P. leucoptera</i> (extinct) | Society Islands | ? | |
| <i>Arenaria interpres</i> | Holarctic | 4 | Bent (1929) |
| <i>A. melanocephala</i> | Nearctic | 4 | Bent (1929) |

TABLE 1 *Continued*

| Family and species | Region | Clutch size | References |
|--------------------------------|------------------|-------------|------------------------------------|
| <i>Phalaropus tricolor</i> | Nearctic | 4 | Bent (1927) |
| <i>P. lobatus</i> | Nearctic | 4 | Bent (1927) |
| <i>P. fulicarius</i> | Holarctic | 4 | Bent (1927) |
| <i>Scolopax rusticola</i> | Paleartic | 4 | Bent (1927) |
| <i>S. mira</i> | Taiwan | ? | |
| <i>S. saturata</i> | Java | 2 | Hellebrekers and Hoogerwerf (1967) |
| <i>S. celebensis</i> | Sulawesi | ? | |
| <i>S. rochussenii</i> | Ceram | ? | |
| <i>S. minor</i> | Nearctic | 4 | Bent (1927) |
| <i>Coenocorypha auklandica</i> | New Zealand | 2 | Oliver (1955) |
| <i>C. pusilla</i> | New Zealand | 3 | Oliver (1955) |
| <i>Gallinago solitaria</i> | Paleartic | ? | Kozlova (1962) |
| <i>G. hardwickii</i> | Japan | 4 | Kobayashi (1956) |
| <i>G. nemoricola</i> | India | 4 | Baker (1929) |
| <i>G. stenura</i> | U.S.S.R. | 4 | Kozlova (1962); Krechmar (1966) |
| <i>G. megala</i> | U.S.S.R. | 4 | Kozlova (1962) |
| <i>G. media</i> | Paleartic | 4 | Bent (1927) |
| <i>G. gallinago</i> | Europe | 4 | Bent (1927) |
| | China | 4 | Caldwell and Caldwell (1931) |
| | North America | 4 | Maclean (pers. obs.) |
| | South America | 2 | Maclean (pers. obs.) |
| <i>G. nobilis</i> | Colombia | 2 | Burton (in litt.) |
| <i>G. undulata</i> | Brazil | 2-3 | Sick (in litt.) |
| <i>G. imperialis</i> | South America | ? | |
| <i>G. jamesoni</i> | Ecuador | 2 | Burton (in litt.) |
| <i>G. stricklandii</i> | Tierra del Fuego | 2 | Johnson (1965) |
| <i>G. nigripennis</i> | East Africa | 2-3 | Mackworth-Praed and Grant (1952) |
| | South Africa | 2 | Maclean (pers. obs.) |
| <i>G. macrodactyla</i> | Malagasy | 1 | Rand (1936) |
| <i>Lymnocyptes minima</i> | Paleartic | 4 | Bent (1927); Krechmar (1966) |
| <i>Limnodromus griseus</i> | Nearctic | 4 | Bent (1927) |
| <i>L. scolopaceus</i> | Nearctic | 4 | Bent (1927) |
| | Siberia | 4 | Kozlova (1962) |
| <i>L. semipalmatus</i> | U.S.S.R. | 2-3 | Hachlow (1932); Kozlova (1962) |
| <i>Aphriza virgata</i> | Nearctic | 4 | Bent (1929) |
| <i>Calidris tenuirostris</i> | Siberia | 4 | Kozlova (1962) |
| <i>C. canutus</i> | Nearctic | 4 | Bent (1927) |
| <i>C. alba</i> | Holarctic | 4 | Bent (1927) |
| <i>C. pusilla</i> | Nearctic | 4 | Bent (1927) |
| <i>C. mauri</i> | Nearctic | 4 | Bent (1927) |
| <i>C. ruficollis</i> | Siberia | 4 | Kozlova (1962) |

TABLE 1 *Continued*

| Family and species | Region | Clutch size | References |
|--------------------------------|----------------------|-------------|--|
| <i>C. minuta</i> | U.S.S.R. | 4 | Burton (in litt.); Kiff (in litt.) |
| <i>C. subminuta</i> | Siberia | 4 | Kozlova (1962) |
| <i>C. minutilla</i> | Nearctic | 4 | Bent (1927) |
| <i>C. fuscicollis</i> | Nearctic | 4 | Bent (1927) |
| <i>C. bairdii</i> | Nearctic | 4 | Bent (1927) |
| <i>C. melanotos</i> | Nearctic | 4 | Bent (1927) |
| | Palaearctic | 4 | Portenko (1968) |
| <i>C. acuminata</i> | U.S.S.R. | 4 | Houmann (1966); Kozlova (1962); Vorob'ev (1963). |
| <i>C. maritima</i> | Holarctic | 4 | Bent (1927) |
| <i>C. ptilocnemis</i> | Nearctic | 4 | Bent (1927) |
| <i>C. alpina</i> | Holarctic | 4 | Soikkeli (1967) |
| <i>C. ferruginea</i> | Palaearctic | 4 | Portenko (1959) |
| <i>Eurynorhynchus pygmaeus</i> | Siberia | 4 | Bent (1927) |
| | | 3 | Portenko (1957) |
| <i>Limicola falcinellus</i> | Palaearctic | 4 | Kozlova (1962) |
| <i>Micropalama himantopus</i> | Nearctic | 4 | Bent (1927) |
| <i>Tryngites subruficollis</i> | Nearctic | 4 | Bent (1929) |
| <i>Philomachus pugnax</i> | Palaearctic | 4 | Kozlova (1962) |
| DROMADIDAE | | | |
| <i>Dromas ardeola</i> | East Africa | 1-2 | Mackworth-Praed and Grant (1952) |
| | Persian Gulf | 1 | Ali and Ripley (1969a) |
| THINOCORIDAE | | | |
| <i>Attagis gayi</i> | Chile | 4 | Maclean (pers. obs.) |
| <i>A. malouinus</i> | Isla Navarino, Chile | 4 | Johnson (1965) |
| <i>Thinocorus orbignyianus</i> | Chile | 4 | Maclean (1969) |
| <i>T. rumicivorus</i> | South America | 4 | Maclean (1969) |
| CHIONIDIDAE | | | |
| <i>Chionis alba</i> | South Orkney Islands | 1-4 | Jones (1963) |
| <i>C. minor</i> | Kerguelen Island | 2-3 | Burton (in litt.); Kidder (1876) |

genus, *Haematopus* (Figure 3). All but one species (*H. leucopodus*) are essentially shoreline dwellers and are comparatively large-bodied. Most lay clutches of 2 or 3 eggs, occasionally only 1, and sometimes as many as 4, although 4-egg clutches are very rare in southern hemisphere forms. The grasslands *H. leucopodus* of Patagonia never lays more than 2 eggs per clutch.

IBIDORHYNCHIDAE. *Ibidorhyncha struthersii*, the sole representative of

the family, is endemic to montane streams and rivers of Central Asia (Figure 10) and usually lays a 4-egg clutch.

RECURVIROSTRIDAE. Widespread in the temperate and tropical regions of the world (Figure 4), the avocets and stilts form a family of six well-defined species in three genera. All inhabit inland waters, at least when breeding, and all but one species lay an almost invariable clutch of 4 eggs. *Cladorhynchus leucocephalus* is exceptional in its habitat of saline waters and often lays only 2 or 3 eggs.

BURHINIDAE. The burhinids are relatively large-bodied birds, mostly nocturnal and mostly nonaquatic. They are mainly tropical in distribution (Figure 5). The normal clutch size for all species is 2 eggs, although *Esacus* species often lay only 1.

GLAREOLIDAE. The glareolids are all tropical to subtropical birds of the Old World (Figure 6). The aerial-feeding pratincoles (Glareolinae) normally lay clutches of 1 to 3 eggs; instances of 4-egg clutches are rare and may be the result of more than one female laying in the same scrape, an occurrence facilitated by the birds' colonial nesting habits. Few of the desert to semidesert coursers (Cursoriinae) lay clutches of more than 2 eggs, and none lays more than 3.

CHARADRIIDAE. The plovers are worldwide in their distribution. They are divisible into the lapwings (Vanellinae) and the "sandplovers" and other smaller species (Charadriinae). The Vanellinae are primarily tropical (Figure 7); most lay clutches of 4 eggs at least occasionally and most live away from water in open country. Clutches of 2 and 3 eggs are common, especially among southern African species. The only two species that normally lay 2-egg clutches are the somewhat aberrant *Vanellus crassirostris* (a long-toed species of rather jaçana-like habits) and *V. cayanus* (a small lapwing of forest rivers in tropical South America). *V. novaehollandiae* is an Australian species that has invaded New Zealand only since about 1940 (Sansom, 1951); in its native Australia and Tasmania it normally lays a 4-egg clutch, but in New Zealand it lays only 2 or 3 eggs.

The Charadriinae comprise the remaining plover genera. *Charadrius* is by far the largest genus and has a worldwide distribution (Figure 8); 4-egg clutches are usual only in six Holarctic species and in *C. cinctus* of Australia. All the remaining species of the tropics and southern hemisphere, as well as the open grassland species of the Holarctic, lay clutches of 3 eggs or less. The only other charadriine genus that is not monotypic is *Pluvialis*, with three Holarctic species laying 4-egg clutches and one New Zealand species that lays only 3 eggs (Figure 9).

The remaining nine genera of charadriine plovers are monotypic. All but *Eudromias* (Figure 10) are tropical or southern hemisphere birds,

and all but *Oreopholus* (Figure 9) lay clutches of less than 4 eggs; *Oreopholus ruficollis* lays a 4-egg clutch. The remaining genera are *Thinornis*, *Phegornis*, *Anarhynchus* (Figure 10); *Zonibyx* (Figure 5); *Pluvianellus* (Figure 10); *Pluvianus* and *Peltohyas* (Figure 9).

SCOLOPACIDAE. The Scolopacidae are a large and diverse family of overwhelmingly Holarctic breeding distribution, with a few South American, Pacific, African, and Indonesian species (Figure 11). All but one of the Holarctic scolopacids lay 4-egg clutches. The sole exception is *Limnodromus semipalmatus* of Central Asia, which lays only 2 or 3 eggs. The two southern hemisphere island genera, *Prosobonia* (*sensu* Zusi and Jehl, 1970), and *Coenocorypha*, usually lay 2-egg clutches, as do the southern hemisphere forms of *Gallinago*. The same seems to apply to the Indonesian forms of *Scolopax*, on which little information exists.

DROMADIDAE. *Dromas ardeola* is a burrow-nester and usually lays a single white egg; the chick is partly nidicolous. The family has a coastal distribution around the northern and western Indian Ocean (Figure 10).

THINOCORIDAE. Peculiarly South American in distribution (Figure 6), all four seedsnipec species lay 4-egg clutches.

CHIONIDIDAE. The sheathbills are subantarctic in their distribution (Figure 10). Both species lay 2 or 3 eggs per clutch, although *Chionis alba* sometimes lays 4.

DISCUSSION

No species among the Charadrii normally lays a clutch of more than 4 eggs, regardless of its degree of specialization. It seems as if the ancestor of the suborder early fixed this maximum, which is still the determinate clutch of many living forms in a great variety of habitats and almost every type of zoogeographical distribution. The adaptive significance of a maximal clutch of 4 eggs is not immediately apparent, although there must be a good reason for setting this limit. It is unproved, but if we assume that living forms laying 4 eggs are adhering to the ancestral clutch size of the Charadrii, it follows that the laying of fewer than 4 eggs is a deviation from the ancestral condition occasioned by some more recent specialization. I believe that the ancestral clutch size of the Charadrii was 4 eggs and that species or other taxa within this suborder that still lay 4 eggs have arisen within that taxon's present distribution and, furthermore, that any taxon laying fewer than 4 eggs has deviated in some way from its ancestor.

The evidence in support of the idea that clutch size is adaptive is too good to be refuted, whether one subscribes to the views of Lack (1968) or of Wynne-Edwards (1962). Since the maximal clutch size of any species of wader is 4 eggs, one might expect to find clutches smaller than

this among species that feed their young, assuming that the energetics involved require fewer young in all species concerned. This is broadly true of the families Burhinidae, Haematopodidae, Dromadidae, Chionidae, and Glareolidae (e.g. Kendeigh, 1952; von Frisch, 1959, 1961; Jones, 1963; Maclean, 1967). Some northern hemisphere Haematopodidae and a few individuals of *Chionis alba* occasionally lay clutches of 4 eggs, even though they may not rear all the chicks; this may constitute an intermittent reversion to the ancestral clutch size. Some Charadrii that normally lay 4-egg clutches also feed their young, but only up to the age of about a week, e.g. *Gallinago gallinago* (von Frisch, 1959).

It may be that feeding the young in these species that do so increases the chicks' chances of survival, so that the clutch size may be reduced, and not that the habit of feeding the young imposes any restriction on the parents' ability to raise more than one, two, or three chicks. If the latter were true, it seems unlikely that the habit of feeding the young would have evolved at all, since it might seem to lead to the ultimate survival of fewer and not more birds. Whatever the case may be, why should *Gallinago gallinago* be able to raise broods of four in the northern hemisphere and only two in the southern? Similarly, why should a number of *Charadrius* species in the northern hemisphere be able to raise larger broods than in the southern hemisphere, even though they do not feed their young anywhere in the range of the genus? The answer may lie in such a theory as that of Ricklefs (1970) concerning predator-prey relationships, rather than in the more direct relationship between parent and young, but as yet we do not know. In the same way it is difficult to account for so rapid a change in clutch size of *Vanellus novaehollandiae* in New Zealand from its clutch of 4 eggs in Australia.

Gallinago gallinago is not the only southern hemisphere scolopacid to lay fewer than 4 eggs; all southern scolopacids do so, including *Prosobonia*, *Coenocorypha*, and *Scolopax*. Greenway (1958) says that *Prosobonia* "unlike all other birds of the Pacific islands (except Hawaii) is probably a very old colonist from North America." The genera *Coenocorypha*, *Gallinago*, and *Scolopax* are all good Scolopacinae (Jehl, 1968), a subfamily of undoubted northern hemisphere origin. All southern scolopacids are therefore immigrants whose change of geographical distribution has been accompanied by a reduction in clutch size, as in all other Charadrii.

It is generally true to say that tropical birds lay smaller clutches than those of temperate or boreal regions, but this does not hold for certain Charadrii endemic to tropical regions, such as the Jacanidae, Rostratulidae, Recurvirostridae, and Vanellinae, all of which lay 4-egg clutches.

One argument in support of 4-egg clutches in northern hemisphere

waders whose southern representatives lay only 2 or 3 eggs is that the northern species are migratory, the southern ones not. The evidence for this view rests upon the probability of a higher mortality rate among the adults of migrants than among residents. The work of Boyd (1962) on Palearctic Charadrii, as well as the fact that 4-egg layers do not seem to increase in numbers any more than 2-egg layers, may support such an argument. It is nevertheless curious that a northern species like *Limnodromus semipalmatus* should be able to maintain its numbers adequately on clutches of 2 or 3 eggs, while its congeners, like the rest of the migratory tundra-nesting scolopacids, lay 4 eggs. Moreover, both the migratory and nonmigratory populations of *Thinocorus rumicivorus* in South America invariably lay clutches of 4 eggs, regardless also of habitat.

What determined the maximal number of 4 eggs in the ancestral wader? It did not depend on the number of eggs the incubating parent could cover; Sharland (1943a, 1943b) mentions several examples of *Vanellus tricolor* and *V. novaehollandiae* successfully incubating 5 or 6 eggs at a time. *Recurvirostra avosetta* occasionally lays 5 eggs and covers them without difficulty. Raising four young or less clearly balances mortality in all living Charadrii, most of which are capable of laying and incubating more than the normal number of eggs per clutch. What then is the adaptive significance of a reduction in clutch size within a group of waders that undergoes a change or extension of its original distribution? I do not have the answer, but the rule seems general in the Charadrii, not only in terms of changes in distribution, but apparently also of changes in body size (e.g. Haematopodidae), habitat (e.g. Cursoriinae), diurnal rhythm (e.g. Burhinidae), and other factors.

The evidence in support of the theory that a clutch of 4 eggs in the Charadrii is a more primitive condition than a smaller clutch is considerable. It is widely accepted that the Charadriinae and Scolopacidae have Holarctic origins; only in the arctic regions do representatives of these two taxa normally lay clutches of 4 eggs. Species that occur elsewhere must necessarily be of more recent origin and, except for *Charadrius cinctus* and *Oreopholus ruficollis*, normally lay less than 4 eggs. *Dromas ardeola*, one of the most highly specialized of the Charadrii, lays only 1 egg, but the bird retains the ancestral condition of two lateral brood patches (Ali and Ripley, 1969a), indicating that its ancestor once laid a larger clutch. The Haematopodidae, structurally homogeneous and adapted to a diet of bivalve molluscs, almost all lay up to 3 and even 4 eggs per clutch, but the aberrant *Haematopus leucopodus* never lays more than 2. Its adoption of a grassland habitat and the consequent change in diet is a comparatively recent development and constitutes a divergence from the ancestral oystercatcher condition.

I know of no evidence to suggest that any living Charadrii that today lay 4-egg clutches might have arisen from an ancestor laying less than 4 eggs. Thus, for example, it is unlikely that the Charadriidae could have arisen from the Glareolidae, to which they are closely related (Bock, 1964), but rather the other way round, especially since general evolutionary trends are for the generalized to give rise to the specialized and not *vice versa*. As species laying clutches of fewer than 4 eggs, occurring in groups where most species lay 4-egg clutches in their ancestral distributions and habitats, are of more recent origin than the 4-egg layers, it may follow that families in which 2-egg clutches are the rule are of more recent origin than families in which 4-egg clutches are the rule. Larson (1957) uses a different systematic plan for the Charadrii, as well as different criteria for determining phyletic relationships within the suborder, from those that I have used, so it is hard to draw comparisons; but it is interesting that his "three early Tertiary stocks" of the Charadriodea include 4-egg layers, while his two superfamilies Burhinoidea and Glareoloidea, both 1- to 3-egg layers, "have no living descendant elements from the highlands." This may mean that the Charadriodea are older than either the Burhinoidea or the Glareoloidea, as these groups are used by Larson, an interpretation that I believe to be correct.

It is significant that, of the five families of Charadrii whose clutch size is normally less than 4 eggs, three are tropical in origin (Glareolidae, Burhinidae, and Dromadidae), while the other two have their centers of radiation in the southern hemisphere (Haematopodidae and Chionididae). My tentative interpretation of this situation is that the suborder Charadrii has a basically northern hemisphere origin. From the ancestor arose very early such tropical families as the Jacanidae, Rostratulidae, Recurvirostridae, and Thinocoridae, while the Charadriidae, Scolopacidae, and Ibidorhynchidae remained essentially northern; only much later did some scolopacids and charadriine plovers spread southwards. The Vanellinae must also have arisen quite early in the tropics. All these ancient families and subfamilies retained the 4-egg clutch in their ancestral ranges. The more recently evolved families of the tropics and southern hemisphere either reduced their clutch size or arose from species with already reduced clutches, in line with the members of ancient families that left their ancestral geographical regions.

The systematic position of *Ibidorhyncha* has been in dispute ever since its discovery. Jehl (1968) writes: "whether *Ibidorhyncha* represents an early offshoot from this line [i.e. Haematopodidae-Burhinidae-Recurvirostridae] or rapid recent divergence is not known." On the basis of clutch size, *Ibidorhyncha* constitutes a group at least as old as the Recurviro-

stridae, but older than either the Haematopodidae or the Burhinidae. For this reason I agree with Jehl's (1968) decision to retain the Ibidorhynchidae as a separate family.

There are a few apparently anomalous cases that, on closer examination, can be adequately explained on the basis of the criteria I have outlined for the Charadrii as a whole. Firstly, *Microparra capensis* is a jaçana that often lays fewer than 4 eggs per clutch. This small species appears to be an offshoot of the *Actophilornis* stock, probably by a process of paedomorphism, because the adult plumage of *Microparra* resembles the immature plumage of *Actophilornis*. As a relatively recent divergence in terms of body size (and perhaps also of diet) it might be expected to reduce its clutch size even though it has remained in its ancestral range.

Secondly, *Limnodromus semipalmatus* is an otherwise rather typical boreal scolopacid that lays a clutch of only 2 or 3 eggs. Two species of *Limnodromus* (*griseus* and *scolopaceus*) breed in North America and only one (*semipalmatus*) is exclusive to Asia. The eastern Siberian population of *L. scolopaceus* has probably spread from Alaska, for it still retains the ancestral migratory route to the southern United States and northern South America (Kozlova, 1962). It seems as if *L. semipalmatus* has diverged from its American congeners by moving permanently from the apparent ancestral distribution of the genus.

Thirdly, if *Oreopholus ruficollis* of South America conformed to the trend among other Charadriinae of the southern hemisphere, it should not lay 4-egg clutches as it does. Two explanations are possible. Either *O. ruficollis* is a good charadriine plover that has retained the ancestral condition of 4 eggs (as may be the case with *Charadrius cinctus* of Australia), or it is the sole representative of an exclusively South American subfamily of the Charadriidae. It differs from both Vanellinae and Charadriinae in a number of ways, especially with regard to plumage patterns of both adult and chick. This is not the place for a detailed discussion of the systematic position of *Oreopholus*, but the evidence of clutch size suggests that it is a member of an endemic South American subfamily of about the same evolutionary age as the Vanellinae and Charadriinae. In the absence of more detailed information I cannot explain the incidence of 4-egg clutches in *Charadrius cinctus*.

Finally, the Haematopodidae are also somewhat anomalous in that 4-egg clutches are most often found in northern hemisphere forms, while the main radiation of the family is southern. The fact that the systematics of the group is highly controversial, especially regarding southern forms, suggests that the southern radiation is a recent phenomenon in which speciation in many forms is incomplete. The oystercatchers probably

arose therefore in the north temperate regions and later underwent a major radiation in the south temperate regions.

I believe that the evidence of clutch size in the Charadrii as I have presented it is a useful and valid aid to the study of wader phylogeny. At least my discussion may provide food for thought towards research into the adaptive significance of clutch size in this suborder of birds.

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SUMMARY

From a study of clutch size in the Charadrii (waders or shorebirds), the following conclusions are drawn: The ancestral clutch size of the Charadrii is 4 eggs. No group of Charadrii laying fewer than 4 eggs per clutch gave rise to any group laying a 4-egg clutch. Any group of Charadrii laying 4 eggs per clutch does so only in its ancestral geographical distribution. In a group in which at least some representatives still lay 4-egg clutches, members that now lay fewer than 4 eggs no longer live in that group's ancestral range; or they may have diverged from the ancestor in one or more of several other ways (body size, diet, diurnal rhythm, habitat, parental care, etc.). Taxa within the Charadrii that today lay fewer than 4 eggs per clutch are younger in evolutionary terms than taxa whose members lay 4-egg clutches, even if these members do so only in that taxon's ancestral range.

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