THE OSTRICH

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EGG-COVERING IN THE CHARADRII

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SUMMARY

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Deliberate egg-covering in the Charadrii (waders) occurs in at least 13 species in four families (Jacanidae, Glareolidae, Charadriidae and Thinocoridae). The habit is most widely developed in the genus *Charadrius*, of which at least four species cover their eggs. Egg-covering is done by kicking material over the eggs with the feet in most species, but in the Glareolidae and probably some other groups, only the bill is used.

The primary function of egg-covering appears to be concealment, but the secondary function of thermoregulation appears to have become almost as important in a few species, especially as a device to insulate the eggs against exposure to the sun. It is not surprising that egg-covering is most highly evolved in tropical and subtropical regions where predator-pressure may be higher, and the danger of overheating by direct sun is greater, than elsewhere.

INTRODUCTION

The purpose of the present paper is to review the occurrence of egg-covering in the Charadrii in a attempt to analyse its functions against the background of wader ecology and of the occurrence and possible functions of egg-covering in other avian taxa. "Egg-covering" here refers only to covering of the eggs with nest material or sand; it is not synonymous with incubation, which here means covering of the eggs by the parent's own body, unless otherwise stated. The two main functions of egg-covering in any group of birds are (a) to protect the eggs from extremes of heat or cold and (b) to conceal the eggs from predators, especially those that hunt by sight. Both these functions may be served by egg-covering in the Charadrii, but its primary function seems to be concealment.

The habit of covering the eggs with nest material or with loose nest substrate is not confined to the Charadrii. Among waterbirds it is well known in the grebes (Podicipedidae) and many waterfowl (Anatidae). Less well known perhaps are the screamers (Anhimidae) of South America, which also cover their eggs, at least in the genus *Chauna* (Kear 1970). These families lay pale coloured eggs without markings, so that egg-covering might be assumed to hide the conspicuous eggs from predators. The same could be assumed in the case of the ground-nesting tinamous (Tinamidae) of South America, whose eggs are remarkable for their unusual colours and very high gloss; some tinamous cover their eggs with leaves or feathers when they leave the nest (Sick 1964). But the Charadrii lay cryptically coloured eggs. This would appear to cast doubt on the function of egg-covering as solely for concealment.

Egg-burial occurs as a matter of course in the Australasian megapodes (Megapodiidae) for the purpose of incubation; these birds use a variety of materials that generate the necessary warmth for initiating and maintaining embryonic development, the parent birds being freed from direct incubation (Clark 1964; Frith 1962).

OCCURRENCE OF EGG-COVERING

The species of Charadrii in which egg-covering has been reported in the literature are listed in Table 1, together with a summary of their methods of covering, geographical ranges (at least over which egg-covering in the species is known) and references. I shall now present the information on each family in detail before discussing it.

Jacanidae

Phelan (1970) observed an African Jacana *Actophilornis africana* covering its eggs with nest material before leaving the nest at 14:30. There were only two eggs in this nest; since the normal clutch of this species is four eggs, it is possible that the bird was covering an incomplete clutch.

TABLE 1

SUMMARY OF INFORMATION ON CHARADRII IN WHICH EGG-COVERING OCCURS; CLUTCH SIZES FROM MACLEAN (1972)

Family and species	Covering by bill or feet	Clutch size	Geographical distribution	References
Jacanidae				
Actophilornis africana	bill?	4	Africa S of Sahara	Phelan (1970)
Glareolidae				
Pluvianus aegyptius	bill	2-3	Tropical Africa	Butler (1931), Jourdain & Shuel (1935), Ogilvie-Grant & Hawker (1902), Serle (1939)
Rhinoptilus cinctus	bill	2	Tropical Africa	Archer & Godman (1937), Kemp & Maclean (1973)
Charadriidae				
Vanellus spinosus	?	3-4	Tropical Africa, Mediterranean	Hall (1965), Koenig (1928), Makatsch (1962)
V. armatus	?	4	Africa S of Sahara	Brown (1972), pers. obs.
V. superciliosus	?	2-4	Tropical Africa	Serle (1956)
V. senegallus	?	4	Africa S of Sahara	Hall (1965)
Charadrias pecuarius	feet	2	Africa and its islands	Belcher(1930), Betham (1929), Eeven & Chiazzari (1943), Blaker (1966), Conway & Bell (1968), Hall (1958, 1959, 1965), James (1921, 1922), Pitman (1965), Taylor (1959)
C. marginatus	feet	2-3	Africa	Alexander (1900), Betham (1929), Hall (1960), Jourdain & Shuel (1935), Liversidge (1965), Serle (1939), Shewell (1951)
C. venustus	?	2	Africa	Cunningham-van Someren (1971)
C. alexandrinus	feet	2-3	Arabia	Meinertzhagen (1954)
C. dubius	?	4	"hot climates"	Meinertzhagen (1954)
Peltohyas australis	feet	3	Arid Australia	Maclean (1973)
Thinocoridae				
Thinocorus rumicivorus	feet	4	W and S South America	Maclean (1969)
T. orbignyianus	feet	4	Andes and austral South America	Maclean (1969)
Attagis malouinus	?	4	Austral South America	Johnson (1965).

Glareolidae

Complete egg-covering with the sand of its nesting substrate is well known in the Egyptian Plover *Pluvianus aegyptius*. Serle (1939) noted that the parent bird covered its eggs by digging in the sand with its bill several times around the nest, leaving only some superficial scratches in the sand at the site. On its return the bird uncovered its eggs by scattering the sand with its bill. The bird appears to incubate the eggs in a partly buried state.

Ogilvie-Grant & Hawker (1902) saw a *P. aegyptius* scratching the sand away and sitting down on a clutch of three eggs that it had covered on leaving; the authors do not indicate whether the scratching was done with the bill or with the feet. Jourdain & Shuel (1935) stress that *P. aegyptius* always covers its eggs before leaving them; they mention that the eggs may be buried to a depth of 5-7,5 cm in sand.

Butler (1931) and Jourdain & Shuel (1935) state that *P. aegyptius* will also cover small chicks with sand, whether at the nest or elsewhere after they have left the nest. The chicks make for a natural depression and are covered with sand thrown by the parent's bill. Chicks may be completely covered, and the sand moistened by the parent regurgitating water over the spot. Chicks have been found buried to a depth of 2,5 cm.

The Threebanded Courser *Rhinoptilus cinctus* incubates its eggs in a partly buried condition (Archer & Godman 1937; Kemp & Maclean 1973). The nest scrape is filled with soil by side-throwing with the bill until the eggs are about two-thirds covered. The eggs are never completely covered when the parent leaves the nest, nor are they uncovered any more than this during incubation.

Charadriidae

(a) Subfamily Vanellinae

Deliberate egg-covering in the vanelline plovers, to the point of complete burial of the eggs, occurs only in a few species before the clutch is complete, and then not invariably. This has been recorded for the Spurwinged Plover *Vanellus spinosus* (Makatsch 1962) and the Blacksmith Plover *V. armatus* (Brown 1972; pers. obs.). After the clutch is complete the eggs lie on top of the nest-lining material, or only partly embedded in it. Partial covering of eggs with loose nest material after completion of the clutch seems to be incidental and has been noted in *V. spinosus* (Hall 1965; Koenig 1928), the Brownchested Plover *V. superciliosus* (Serle 1956) and the African Wattled Plover *V. senegallus* (Hall 1965). In these cases the eggs are not more than half to one-third buried, and then not invariably so.

(b) Subfamily Charadriinae

Deliberate, complete or partial covering of the eggs has been recorded in four species of the genus *Charadrius*. The best known and by far the most widely documented example is that of Kittlitz's Plover *Charadrius pecuarius* (see Table 1 for references).

James (1922) describes how a pair of *C. pecuarius* formed a deep nest scrape and filled it with small pieces of dung, stones and earth. On the eighth day after starting the scrape, after it was fully lined, the complete clutch of two eggs was laid and incubation had begun. From my own experience *C. pecuarius* may line its nest scrape with almost any loose material available – dry vegetable matter, soil, sand, pieces of clay, small stones, and so on.

C. pecuarius covers its eggs by kicking rapidly with the feet, often turning around as it does so, usually in a clockwise direction (Conway & Bell 1968). Hall (1965) noted that one bird continued egg-covering movements for 1,5 min, but usually the covering takes just a few seconds (Conway & Bell 1968). Evidence indicates that *C. pecuarius* covers its eggs only in the face of human intrusion and not when disturbed by falcons, cattle, donkeys, or other animals, nor when leaving the nest at nest-relief (Conway & Bell 1968; Hall 1958; James 1922). Sometimes a parent may run from the nest, with or without attempting to cover the eggs, and then return, cover the eggs some more, and run away again (Conway & Bell 1968; Hall 1959).

C. pecuarius may also cover newly hatched young as long as they are still in the nest scrape, although it seems as if the chicks' heads are usually left exposed (Betham 1929; Conway & Bell 1968; James 1921, 1922; Taylor 1959).

Hall (1959) describes an incident in which a sitting *C. pecuarius* did not cover the eggs as it left the nest when disturbed by a man, but its mate nearby came and covered the eggs before it ran away; Hall interpreted this to suggest that egg-covering occurs only in birds with a strong incubatory drive. Another factor contributing to an absence of egg-covering is soaking of the nest lining by rain. Pitman (1965) mentions also that birds nesting on hard substrates may lack sufficient material for adequate egg-covering.

When *C. pecuarius* returns to its nest, it pecks rapidly at the nest material with the bill, tossing aside larger bits, or even probing into the covering material, finally uncovering the eggs to the required degree by making nest-scraping movements with the feet as it pivots on its breast (Conway & Bell 1968; Hall 1965; pers. obs.). One account tells of a bird that had covered its eggs on leaving them, but found them uncovered when it returned; the bird made "an abortive attempt" to cover the eggs before settling down to incubate them (Beven & Chiazzari 1943). This suggests that egg-covering is released at least partly by the sight of exposed eggs.

Contrary to the situation in *Vanellus armatus* which covers only incomplete clutches, *Charadrius pecuarius* may leave the first egg of the clutch uncovered: egg-covering seems to begin with the completion of the two-egg clutch and the start of incubation (Conway & Bell 1968), thus supporting

Hall's (1959) suggestion that the behaviour is manifested only by birds with a strong incubation drive.

The literature on egg-covering in the Whitefronted Plover *C. marginatus* is also extensive, but somewhat conflicting (for references see Table 1). Although Alexander (1900) wrote of "*Charadrius pallidus*" on the Zambesi River, he was most likely watching *C. marginatus;* Belcher (1930) suggested that Alexander's bird was in fact *C. pecuarius*, but this is unlikely, because Alexander called his bird "Kentish Plover" and would hardly have confused it with *C. pecuarius*. Furthermore the habitat (a sandbank on the Zambesi) was more that of *C. marginatus* than *C. pecuarius*. Alexander noted that on seven occasions his plover covered its eggs completely during the hot hours of the day from about 08:00 onwards; the parent bird incubated the eggs at 05:30 and at 08:00, but it is not clear from the account if incubation by the bird occurred after 08:00 when egg-covering was observed, or if the eggs were left covered throughout the heat of the day until evening.

Betham (1929) claimed that egg-covering in *C. marginatus* on the Cape Peninsula was occasioned by high winds. That egg-covering is deliberate in this species, however, is evident from my own observations and those of Alexander (1900), Jourdain & Shuel (1939), Shewell (1951), Hall (1960) and Liversidge (1965). The last two workers state that the eggs are covered by kicking sand with the feet as does *C. pecuarius*, and I have confirmed this by my own observations.

Shewell (1951) noted a correlation between the degree of egg-covering in *C. marginatus* and the weather. Thus on hot sunny days the eggs were usually half to three-quarters buried by about 09:00, while on cold rainy days, and also at night, they were not buried at all. He claimed never to have seen parents bury their eggs as a reaction to disturbance at the nest, adding that egg-covering "just seems to be done as a regular practice to keep them from getting overheated on hot days". However, Liversidge (1965) says that *C. marginatus* covers its eggs as a matter of course on disturbance by man, but not by a mongoose. Hall (1960) did a fairly extensive quantitative analysis of this phenomenon in *C. marginatus* and showed that eggs were better covered on second inspections than on first, indicating that egg-covering is a reaction to human intrusion. I have confirmed this observation.

Curiously, however, both Hall (1960) and Liversidge (1965) said that weather (cloud, wind, temperature) had no significant effect on the extent of egg-covering. This is in conflict with Shewell's (1951) claims. Nonetheless Hall (1960) found that the eggs of *C. marginatus* were better covered between 07:00 and 15:00 than at other times. Therefore egg-covering might seem to be associated only indirectly with temperature in that air temperatures are highest between 07:00 and 15:00 regardless of other weather conditions. Egg-covering in *C. marginatus* may serve the dual function of concealment and protection from the sun, with concealment the more important of the two.

It is clear, however, from the data of all the authors cited that the degree of egg-covering by *C. marginatus* is seldom as great as by *C. pecuarius* and is far more individually variable.

Another species of *Charadrius* that has been reported as covering its eggs is *C. venustus*. Cunningham-van Someren (1971) writes of this species at Lake Nakuru, Kenya, that he "took photographs of the exposed eggs and later again when the eggs had been covered and concealed by the bird". He watched the bird as it "returned to its nest site, scraped away some pebbles and sat down". In reply to my further enquiries into these observations, Cunningham-van Someren (*in litt.*) writes that *C. pecuarius* also occurs at Lake Nakuru (so confusion between the two species can be ruled out) and that *C. venustus* is very common on Lake Magadi where he had found "dozens of nests but never seen them covered", possibly because the hard soda surface of the shoreline did not allow of the collection of loosed material in the nest scrape. He added that the substrate at Lake Nakuru is more or less sand, which may be why egg-covering occurs only in the Nakuru population of *C. venustus*, because in other habitats throughout its range it usually nests on hard saline and clay flats. Egg-covering by *C. venustus* has not been reported anywhere else in the literature, even by those who have watched the species closely in the field (e.g. Jeffery & Liversidge 1951; Robinson & Robinson 1951).

Meinertzhagen (1954) wrote that the Kentish Plover *C. alexandrinus* often covers its nest in Arabia, using its feet to move the nest material over the eggs. He adds that *C. alexandrinus* does not seem to do this in Europe, and that "in hot climates the eggs of both the little ringed plover (*C. dubius*) and the Kentish plover are arranged with the points downwards, so that the broad ends alone are visible in the form of small domes."

Egg-covering in the desert-dwelling Australian Dotterel *Peltohyas australis* has already been reviewed in detail (Maclean 1973). This species appears to cover its eggs as a matter of course whenever it leaves them, but whether the reasons are mainly for concealment or for thermoregulation is not yet established.

Thinocoridae

At least three of the four species of seedsnipe are known to cover their eggs when they leave the nest. In *Thinocorus rumicivorus* and *T. orbignyianus* only the female incubates; she covers her eggs with foot movements (in exactly the same way as *Charadrius pecuarius*) whenever she leaves the nest and for whatever reason she may leave it. She also covers young that are still in the nest scrape; I have evidence that she covers small chicks away from the nest too, provided she has loose dry plant material nearby. The only eggs ever found of the Whitebellied Seedsnipe *Attagis malouinus* were buried in the nest lining (Johnson 1965), presumably having been deliberately covered by the sitting female.

DISCUSSION

The taxonomic distribution of egg-covering in the Charadrii seems to indicate that it has arisen independently in those taxa in which it occurs. This is also borne out by the different methods employed; the Glareolidae use the bill, while the plovers and seedsnipe use the feet. The geographical distribution of egg-covering in the Charadrii is interesting (Fig. 1) in that it occurs only on the three southern continents of South America, Africa and Australia. Egg-covering in the Podicipedidae and Anatidae is a worldwide phenomenon. In the Anhimidae and Tinamidae it is restricted to tropical South America.

The functions of egg-covering are at least twofold: (a) for concealment and (b) for thermoregulation. In *Charadrius marginatus* at least, it appears that concealment is a more important function than thermoregulation, but this conclusion is derived from studies done on the beaches of relatively temperate parts of southern Africa. The protective function of egg-covering against the direct rays of the sun may be far more important in tropical inland habitats such as the Zambesi and other large African rivers. However, in none of these habitats has any measurement been made of the effects of insolation, radiation or ambient temperature on the eggs of ground-nesting birds.

The cooling effect of moistening the sand with water must add greatly to the protective function of egg-covering in *Pluvianus aegyptius* in its tropical environment. Evaporative cooling of eggs or young covered with nest material cannot play an important role in the biology of other Charadrii, however, because wetting of the material inhibits egg-covering and may prevent it altogether.

Concealment seems to be the primary function of egg-covering in *Charadrius pecuarius* because it covers its eggs only when disturbed by man and not by other animals.

However, because the Least Seedsnipe *Thinocorus rumicivorus* always covers its eggs when it leaves the nest for whatever purpose, it is not possible to say what the main function of the habit is in this family. It may be protective against excessive cooling in *Attagis malouinus* which breeds on islands south of the Beagle Channel at about 55 S, where it may be extremely cold even in summer. This would be advantageous in a species in which only the female incubates and is obliged to leave the nest sometimes to feed.

A different kind of thermoregulatory role of egg-covering is indicated by the suggestive information on *Peltohyas australis* which appears to cover its eggs and leave them for long periods in warm weather, but to incubate them in the normal way in cool weather (Maclean 1973).

Figure 1 shows that egg-covering is a tropical to subtropical phenomenon in the Charadrii for the most part. This may reinforce the idea of a primarily protective function against overheating by direct sunlight. There is also the possibility of greater predator-pressure in the tropics as an important selective force for egg-covering as a concealing mechanism. The covering of incomplete clutches by tropical jacanas and vanelline plovers might seem to lend support to the idea that the eggs should be protected against the hot sun when the parents are away from the nest, but these birds do not invariably cover incomplete clutches, even in very hot weather, and they may cover them in winter. So concealment may after all be the primary selective force here too.

Whatever the selective advantages of egg-covering, it is not easy to understand why it should

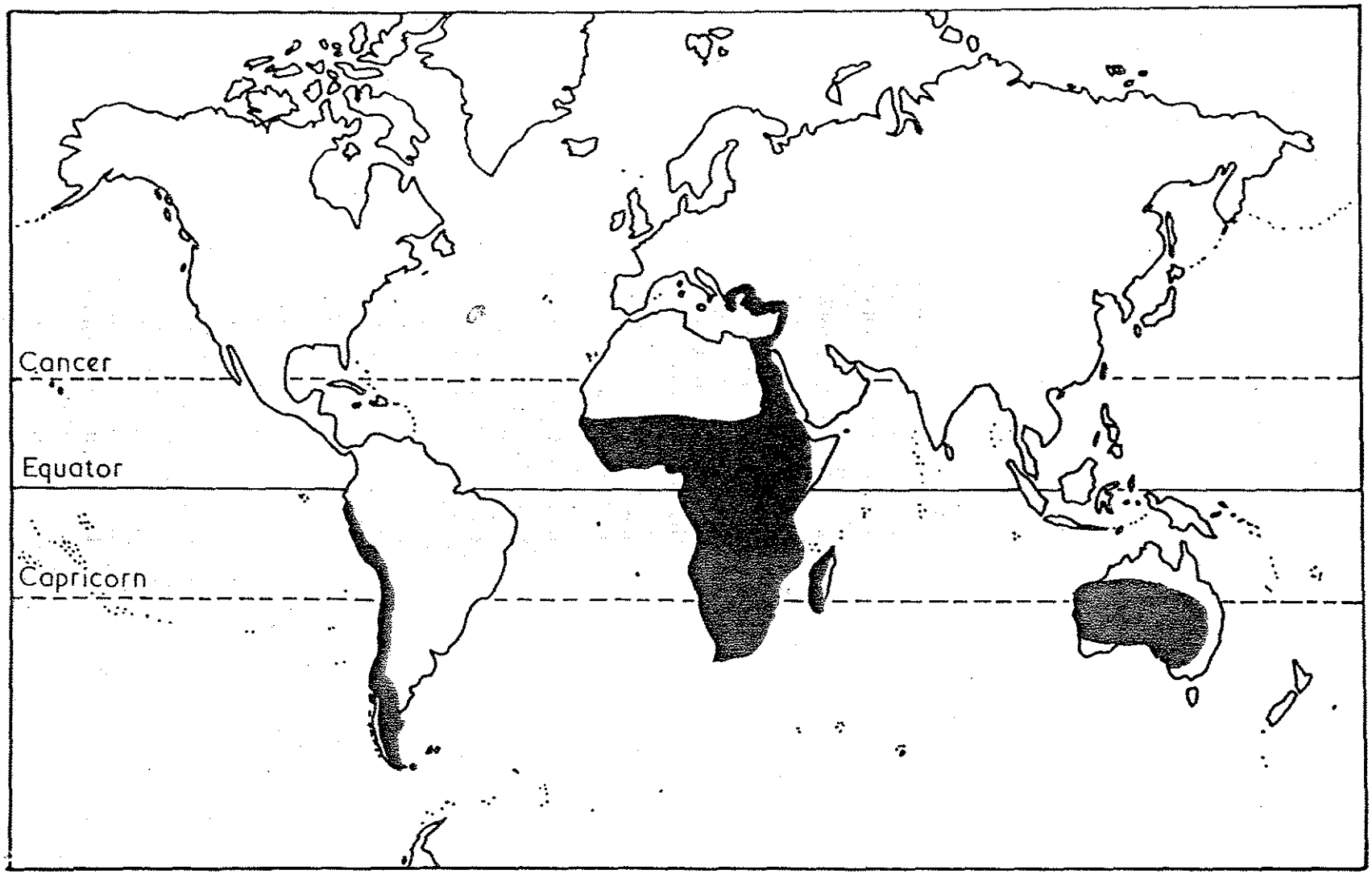

FIGURE 1

The geographical distribution of egg-covering in the Charadrii

have evolved at all, because most Charadrii (and other ground-nesters too) in the tropics and elsewhere can survive perfectly well without covering their eggs. And many of them have eggs that are less cryptically coloured than the egg-covering species. Egg-covering is not related to clutch size either. Southern hemisphere Charadrii tend to lay smaller clutches than northern (Maclean 1972), but the egg-covering seedsnipe lay the maximal clutch of four eggs found in the suborder, while the other habitual egg-covering species lay only two or three eggs. Thus, although egg-covering seems at first to be unrelated to reproductive potential, it may be related to survival rate. No quantitative data are available to show this relationship in the relevant southern hemisphere forms.

In my opinion the evidence points to concealment as the primary function of egg-covering in the waders, but the advantages of insulation may in many cases be equally great and may secondarily have assumed the major role. That it is a concealing mechanism in the forest nesting tinamous, however, is shown by the fact that incompletely covered eggs are invariably discovered by monkeys (Koepcke 1972). Egg-covering in the Anatidae has apparently not received close attention to date. Kear (1970) writes that "the value of down is that it conceals eggs from predators and perhaps insulates the clutch while the female is feeding". But even hole nesting waterfowl may cover their eggs, as well as some, like *Dendrocygna*, that normally have no down in the nest. The genus *Chauna* of the South American anseriform family Anhimidae also covers its eggs which, like those of the ducks, are large, pale and laid in an open nest in a marsh. It seems implicit in Kear's statement quoted above that she considers concealment to be the primary function of egg-covering and thermoregulation a possible secondary one.

But why should egg-covering in the Charadrii occur almost exclusively in the southern hemisphere? The ability to detect buried eggs at the nest site is fully developed even in northern hemisphere forms that do not normally bury their eggs. For example Nickell (1943) reports that a female Killdeer *Charadrius vociferus* (a North American species) whose incomplete clutch of two eggs had become buried under about 18 cm of snow dug down with her bill and laid a third egg after clearing the scrape of snow. In a series of experiments on *C. alexandrinus* and *C. dubius* in the field, Walters (1956) showed that both species could find artificially buried eggs with difficulty by probing in the sand and then unearthing the eggs with the bill – never with the feet. Unlike the Little Grebe *Podiceps ruficollis* whose egg-covering behaviour may be derived from nest-building movements (Broekhuysen 1973), egg-covering in the Charadrii must be a *de novo* activity, especially in those species that use their feet for the purpose.

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