

## African-Eurasian Flyways

### Why do Crab Plovers *Dromas ardeola* breed in colonies?

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The Crab Plover *Dromas ardeola* is unusual among birds and unique among waders in breeding colonially underground. It exhibits extreme clutch reduction, breeds at the hottest time of year on tropical desert island coasts and may be energetically stressed during the breeding season. At present there are only nine known colonies worldwide. This note proposes an hypothesis for the origins of the bird's coloniality. We suggest that this behaviour hinges around three factors; regionally and seasonally patchy food availability substratum specificity for burrowing and the need to breed on predator-free islands. The combination of these factors may account for the bird's natural rarity. Underground nesting is a consequence of the timing of breeding rather than being an anti-predator strategy.

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#### INTRODUCTION

Approximately 13% of the world's bird species, belonging to 60 families or sub-families, breed colonially: this behaviour is most pronounced in marine and freshwater nidicolous species (Lack 1968). Many colonial bird species have been well studied, but there is little in the way of unifying theory that explains the evolution of this behaviour.

Recently, there has been a trend towards viewing coloniality as a trade-off between costs and benefits in which the latter should outweigh the former for the behaviour to evolve and persist (reviewed by Wittenberger & Hunt 1985). Coloniality may be forced on birds through nest site limitation, as is almost certainly the case in several seabird species which breed on oceanic islands or cliffs (Nelson 1980). Costs that could be incurred as a result include competition for food (due to localised depletion around the colony), for nest sites and nesting material, or for mates (e.g. Ashmole 1963; Furness & Birkhead 1984). The dense packing of individuals within colonies can lead to an increased risk of disease or parasite transfer (Jennings & Soulsby 1958), an increased incidence of both aggression and intraspecific egg- and chick-killing (Davis & Dunn 1976), as well as a heightened risk of misdirected parental care (Holley 1981). By contrast, coloniality can reduce vigilance costs and provide protection from predators through co-operative

mobbing and the 'swamping' of predators with potential food (Birkhead 1977). There is evidence that dense packing of individuals and highly synchronous breeding both serve to increase individual reproductive output (Birkhead 1977), although absolute colony size may be negatively linked to individual reproductive success (Furness & Birkhead 1984). There is a tendency for colonial breeders to forage in flocks (Lack 1968) and it has been suggested that colonies function as 'information centres' leading to increased food-finding efficiency (Brown 1986). Support for this hypothesis comes from the disproportionately large number of colonial bird species which eat either seeds or aerial insects (Lack 1968). Apart from Crab Plovers *Dromas ardeola*, the only waders which are colonial or semi-colonial are either granivores (seedsnipes), insectivores (pratincoles) or highly erratic breeders (Banded Stilt *Cladorhynchus leucocephalus*). Several species, such as Black-winged Stilt *Himantopus himantopus* could be described as 'loosely colonial'.

Understanding the ways in which coloniality might have evolved is complicated by the problem that adaptations to coloniality are simultaneously both dependent and independent variables which interact in a complex network of selective pressures and adaptive responses (Wittenberger & Hunt 1985). In this note we attempt to unravel the interacting factors which may have resulted in Crab Plovers breeding colonially. Our inferences are

based largely on observations of breeding Crab Plovers on the island of Abu al Abyadh in Abu Dhabi Emirate, United Arab Emirates (24° 15'N, 53° 45'E).

## CRAB PLOVER BIOLOGY IN PERSPECTIVE

The Crab Plover is a biological and taxonomic enigma. DNA-DNA hybridisation suggests that its closest relatives are the pratincoles and coursers, with divergence occurring about 35 million years ago, during the Oligocene (Sibley & Ahlquist 1985). Ecomorphologically, however, its closest analogue is probably the Beach Thick-knee *Esacus magnirostris* of south-east Asia, Indonesia and Australasia (Hockey *et al.* 1996). The world population of Crab Plovers has been estimated at 43 000 to 50 000 birds whose breeding range is confined to the north-western Indian Ocean. During the non-breeding season their range extends as far south as Mozambique and as far east as Thailand (Rose & Scott 1994; Hockey & Aspinall 1996).

Their breeding biology incorporates features that are unusual among birds and unique among waders. Crab Plovers breed in colonies comprising self-excavated burrows on flat or gently sloping sandbanks. They lay a single, large white egg which, relative to adult body mass, is among the largest laid by any bird (Lack 1968). The chick is semi-nidifugous (Cramp & Simmons 1993), remaining tied to its nest burrow until fledging. As soon as a chick fledges, it leaves the colony in the company of its parents, which may continue to feed the chick for as much as six months (Hockey & Aspinall 1996; Hockey *et al.* 1996). Crab Plovers are thought to be primarily monogamous, but co-operative breeding may occur (Cramp & Simmons 1983). Aggression is frequent within colonies, especially early in the breeding season (Brown *et al.* 1991). All evidence points to its being almost exclusively a crab-eater on the breeding grounds (e.g. Morris 1992). Outside the breeding season, other invertebrates and fish feature in the diet, but crabs still predominate (Hockey *et al.* 1996).

Although the behaviour is widespread among rodents, very few bird species nest colonially in burrows on flat or gently-sloping ground. Exceptions include *Spheniscus* penguins, some island-breeding Procellariiforms (Nelson 1980), Rosy Bee-eater *Merops malimbicus* (Fry *et al.* 1992), African River Martin *Pseudochelidon eurystomina*, Grey-rumped Swallow *Pseudhirundo griseopyga* and White-backed Swallow *Cheramoeca leucosternus* (Turner & Rose 1989). The Crab Plover is the only species of burrow-nesting colonial wader and the only wader to lay a white egg (Hockey & Aspinall 1996). It is also the only wader with semi-nidifugous young.

There are several aspects of the breeding cycle and behaviour of Crab Plovers that beg an explanation. Only two other species of wader in the world lay a modal clutch of one egg, and the only one which breeds on the coast is the Beach Thick-knee, the other being the Double-banded Courser *Rhinoptilus africanus* which occurs in the deserts and semi-deserts of eastern and southern Africa. Crab

Plovers breed at the hottest and driest time of year, when shade temperatures in Abu Dhabi reach 48°C, regularly exceed 40°C and rarely fall below 28°C (Pearce & Smith 1984). At this time of year, coastal humidity levels frequently rise above 90%; it is likely, therefore, that overheating is a greater stress than is dehydration. The peaks of Crab Plover foraging activity occur in early morning and late afternoon regardless of the state of the tide (Hockey & Aspinall 1996). This behaviour may be dictated either by the effects of thermal stress on the birds or the activity rhythms of crabs (see Hughes 1988). Towards the end of the breeding season there is evidence that Crab Plovers are energy-stressed: adults may fly up to 6 km away from the colony on a single foraging trip to deliver one crab to their chick (Hockey & Aspinall 1996). Most resident birds of the region, including the other waders, breed earlier in the year when ambient temperatures are lower (Pearce & Smith 1984; Aspinall 1996). There are a few exceptions to this: Crested and Lesser Crested Terns *Sterna bergii/bengalensis* and Chestnut-bellied Sandgrouse *Pterocles exustus* breed on unshaded ground during the summer (Aspinall 1996).

These observations raise a puzzling, multi-faceted question: why should Crab Plovers breed colonially at the hottest time of year when they are probably energetically and thermally stressed? Below, we advance an hypothesis answering this question, and identify lines of evidence that will need to be sought to test this hypothesis.

## AN EXPLANATION FOR COLONIALITY

Along the coasts of the north-western Indian Ocean, the spatial distribution of crabs is uneven. The large crabs favoured by Crab Plovers, such as *Metopograpsus messor* (Morris 1992; Hockey & Aspinall 1996), tend to be associated with mangrove woodlands (mangals), which themselves are patchily distributed. The functional response of predators leads to the prediction that if the availability of food at a regional level is patchy, birds dependent on this food should aggregate where prey are common. Such a situation could explain why Crab Plovers aggregate when breeding, but does not provide an explanation for coloniality. A potential consequence of predator aggregations is to depress the abundance of prey. This can lead to local food shortages, as have been inferred in the vicinity of seabird colonies (Ashmole 1963; Nelson 1980). During the breeding season, adult Crab Plovers clearly have to satisfy not only their own energetic demands, but also those of their chick. We suggest that the single egg is an adaptation to minimising brood energy demand. The fact that the egg is also very large may be an adaptation to reducing fledging period, but extensive analysis is required to test this. Breeding within the colonies is synchronous and the immediate post-fledging dispersal of both young and adults can be interpreted as an additional adaptation for minimising energy stress associated with being tied to the colony. Again, however, this does not explain coloniality *per se*.

If Crab Plovers are energetically stressed while breeding (whether colonially or not), the laying of a single egg is one evolutionarily adaptive solution to this problem. Additional solutions include breeding when food availability is maximal or exerting behavioural control over colony size, either absolutely, or functionally through partially staggered breeding. Crab Plovers catch their prey exclusively at the substratum surface, *i.e.* when the prey themselves are active. As yet, we cannot prove whether crab availability is maximal in July/August, when the Crab Plovers are feeding young: in southern Africa, mangrove crab abundance is greatest in the summer

months (Branch & Branch 1980). Circumstantial evidence that there is only a narrow, food-linked window of breeding opportunity is that the birds only arrive at the colony site shortly before breeding and leave the area again as soon as breeding is over: the latter observation is also consistent with progressive food depletion around the colony. There is some evidence that breeding within colonies is partly asynchronous. In 1993 and 1994, fledging at the Abu al Abyadh colony took place over a period of more than four weeks: in 1996 it lasted at least three weeks (unpubl. data).

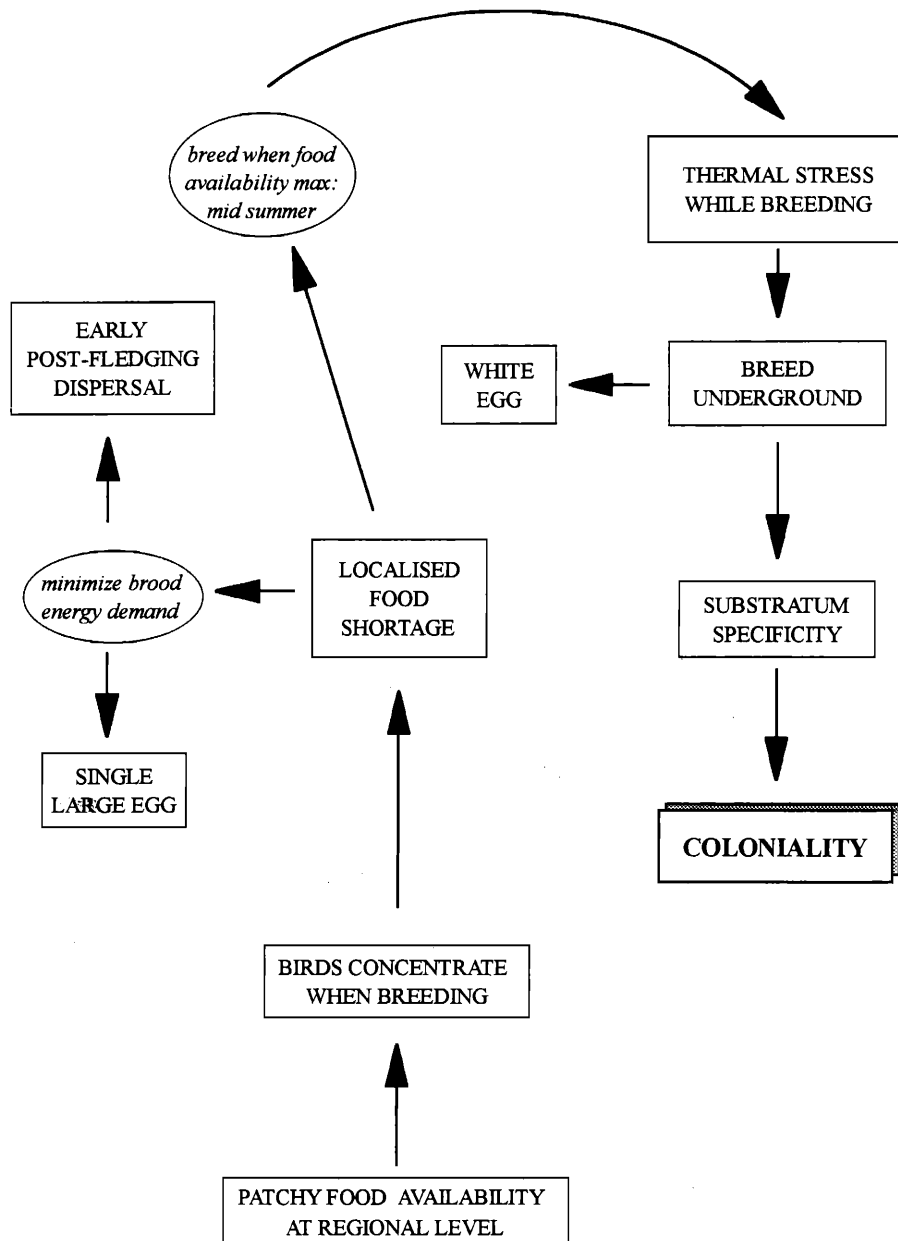


Figure 1. A schematic representation of the interacting factors which we hypothesize force Crab Plovers to breed colonially and when thermal stresses are high.

If there is only a small window of the year when food availability is adequate to sustain aggregated breeding,

and this period coincides with the hottest time of year, it is not difficult to explain the adoption of a subterranean

breeding habit or the fact that the egg, hidden from predators, is white. The latter is presumably a derived condition in as much as the eggs of all other waders are cryptically patterned. Egyptian Plovers *Pluvianus aegyptius* also use sandy substrata for breeding and regularly experience temperatures as high as 45°C. Although the nest scrape is made at the sand surface, the eggs are covered with sand for much of the time. This covering sand is regularly wetted by the adults when ambient temperatures exceed about 40°C. After the chicks hatch they too are frequently buried and wetted until they are about three weeks old (Howell 1979). Howell (*op. cit.*) proposed, although we would not necessarily agree, that the original adaptive advantage of this behaviour was concealment and that thermoregulatory benefits were secondary.

Underground burrowing places two opposing constraints on the choice of nest site. Firstly the sand must be sufficiently friable that the bird is physically able to excavate a burrow. Counteracting this condition is the requirement that the sand must also be sufficiently firm that the burrow does not collapse following excavation. Optimal conditions for burrowing will thus be determined by a combination of sediment particle size composition and moisture content. We suggest that there will be very few sites where these conditions occur and, whilst the ultimate factor promoting coloniality in Crab Plovers is the regionally patchy distribution (and seasonal availability) of food, the proximate factor driving coloniality is highly specific substratum requirements. The other Crab Plover colony in Abu Dhabi, on the island of Umm Amin, supports only 35-38 pairs (Evans 1994), although there is apparently no shortage of suitable burrowing substratum. However, it appears that colony size at Umm Amin is limited by the food supply - there are no mangroves nearby and the breeding birds forage on open mud- and sandflats. The highly fragmented breeding distribution of Egyptian Plover (Hayman *et al.* 1986) may also reflect highly specific substratum requirements, in this instance riverine sandbanks which remain exposed throughout the breeding season.

The sequence of selective pressures promoting coloniality in Crab Plovers and their adaptive consequences are depicted diagrammatically in Figure 1. In terms of the most frequently invoked explanations for coloniality (predator avoidance, food-finding efficiency and nest site limitation), our hypothesis for the cause of coloniality in Crab Plovers falls in the last category, but differs slightly in that an additional limitation is imposed by patchily distributed food. Patchiness is a relative concept which, as yet, we are unable to define. Given the spacing of known breeding colonies (Hockey & Aspinall 1996), the scale of relevance to Crab Plovers may be hundreds of kilometres.

The anti-predator advantages of colonial breeding by surface-nesters are largely, but not entirely, irrelevant in the case of birds that breed underground because chicks at the surface are potentially at risk from predators. Further evidence that underground breeding did not evolve as a result of predator pressure is that all of the known breeding colonies (except perhaps the two pairs at Khor

Govater, Iran) are on islands (Ash & Miskell 1983; Evans 1994). We suspect, but cannot as yet prove, that helpers (of unknown relatedness to breeders) are present at Crab Plover colonies. The primary rôle of these birds appears to be vigilance, despite the fact that the vigilance demands on breeding adults may already be reduced because of underground breeding. When danger threatens, the 'helpers' call loudly and 'usher' chicks which are on the surface back down their burrows. The presence of such helpers could serve to increase foraging time of actively breeding adults by further reducing the commitment the latter have to chick-guarding.

The likelihood that breeding colonies function as information centres for birds to access prime foraging areas is also low because Crab Plovers are well dispersed when foraging at this time of year. During the non-breeding season they do form loose foraging flocks and roost communally: there is a possibility, therefore, that roosts could function as information centres away from the breeding grounds (Hockey *et al.* 1996).

If our hypothesis is correct (or largely so), we would predict that there are few localities where the two requirements of high food availability and suitable substrata for burrowing can be found together. If, as seems to be the case, the choice of predator-free islands for breeding is also important (terrestrial mammals such as foxes could easily excavate nest chambers), this further narrows the options for breeding sites. At present, there are, in total, only nine known colonies and four suspected colonies of Crab Plovers worldwide. However, the disparity between the known world population of this species and the number accounted for at the known colonies is so great that other colonies must exist (Hockey & Aspinall 1996). If the paucity of colonies does reflect low availability of suitable conditions, we also predict that natal philopatry will be strong.

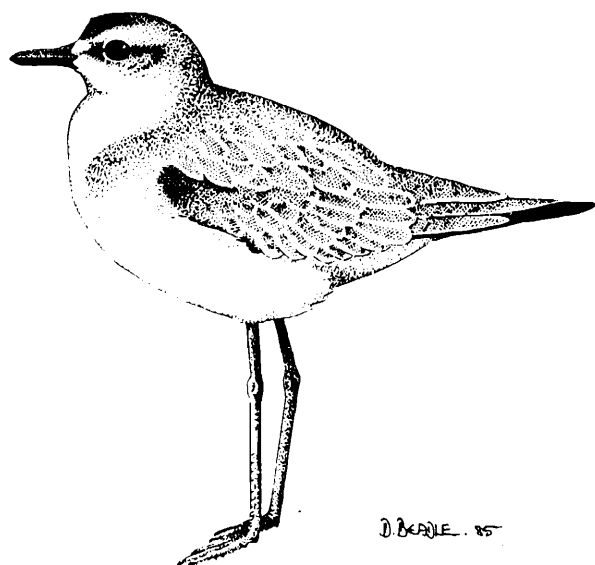
Over the next two years, we plan to test the following, as yet unquantified, elements of our hypothesis.

- 1) Crab surface activity (and/or energy content) is maximal in the Arabian Gulf during the height of summer;
- 2) crab abundance is regionally patchy;
- 3) prey depletion during the breeding season results in a progressive increase in adult energy expenditure which may in turn lead to reproductive failure of some pairs;
- 4) staggered breeding is effective in reducing energy stress because it allows for more efficient usage of the prey size spectrum available (*i.e.* prey size is linked to chick size); and
- 5) the substratum required for burrowing by Crab Plovers represents a 'rare' habitat type or occurs only rarely in conjunction with adequate food resources on predator-free islands.

Coupling this information with our existing data, we intend using the Crab Plover as a model for the evolution of natural rarity.

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Large Sandplover