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From an egg to a fledgling

Tjørve, Kathleen Marjorie Calf

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Shorebirds form a diverse group of bird species exhibiting a variety growth rates, reproduction strategies and behaviours which enable them to survive in the different environments in which they live and breed. This variation makes this group of species an ideal subject to study latitudinal adaptations. During each life stage shorebirds are subject to selective pressures from these different environments. Adaptations to survive in these environments are not limited to specialised egg structure or large fat reserves to survive harsh conditions. There are other adaptations, also physiological, that enable shorebirds to survive in harsh climates; for example, metabolic adaptations in chicks. I discuss the adaptations of shorebird (Charadrii) chicks that enable them to grow and fledge successfully in their environment.

Breeding phenology, breeding success and population trends of African Black Oystercatchers, Haematopus moquini, were monitored over three austral summers on Robben Island, South Africa, from the 2001-2002 to the 2003-2004 breeding seasons. The start of the breeding season of oystercatchers seems to be influenced mostly by environmental conditions and predation risk; birds choosing to lay eggs once the frequency of storms in the Western Cape reduced and laying more synchronously when exposed to greater predation risk. Despite differences in the start of the breeding season oystercatchers seem to attempt to start incubation before a certain time. In a comparison within the species, the potential success of a breeding attempt decreased if the clutch was initiated later in the breeding season. Between seasons, the number of fledglings produced per pair decreased from 0.74 to 0.41 and 0.35 in the first, second and third breeding season, respectively. This decline is a result of increased depredation of eggs and chicks and extreme high tide events. Predation of oystercatcher eggs and chicks was most likely by Kelp Gulls, Larus dominicanus, mole snakes, Pseudaspis cana, and feral cats, Felis catus. Predation can be aggravated by human disturbance and it was found that the area with greatest resident and tourist activity had the greatest egg and chick losses in all three breeding seasons.

A large part of this thesis was on the prefledging growth and energetics of shorebird chicks; in particular, the Little Stint, *Calidris minuta* (Scolopacidae), Kittlitz's Plover, *Charadrius pecuarius* (Charadriidae), Blacksmith Lapwing, *Vanellus armatus* (Charadriidae), Crowned Lapwing, *V. coronatus* (Charadriidae), African Black Oystercatcher (Haematopodidae) and Spotted Thick-knee, *Burbinus capensis* (Burhinidae). See Table 1.1 for a description of the species. These species were selected on the basis of different adult body masses, different modes of development and different timing of breeding. Together with data from the literature we could also investigate the influence of (adult) geographical breeding distribution on the growth and energy expenditure of shorebird (Charadrii and Lari) chicks.

Little Stint chicks at Medusa Bay, Siberia (73°N), grew relatively quickly; their growth rate coefficient was 14% greater than the prediction (from Beintema and Visser 1989) for a bird their size. Their total metabolisable energy, TME, over the 15-day prefledging period was 107% greater than the allometric prediction (from Weathers 1992) for a bird the size of a Little Stint. Therefore their small size and large surface area-to-volume ratio may have resulted in greater relative heat loss and thus

impacted their energy expenditure and growth. To obtain the observed growth rates, chicks had to rely on a high rate of food intake.

Kittlitz's Plover, Blacksmith Lapwing and Crowned Lapwing chicks were studied in a warm, sub-tropical environment, South Africa (34°S). Body size, timing of breeding, mode of development, and habitat all impacted the growth and energetics of the three species. Their small growth rate coefficients, low resting metabolic rates (RMR) and low daily energy expenditure (DEE) may be adaptations to low food availability and mild ambient temperatures. The three precocial species exhibited slower growth, longer fledging periods and lower daily energy expenditure than arctic and temperate zone relatives of similar size.

African Black Oystercatcher chicks are semi-precocial; they are mobile soon after hatching but are parentally fed. Growth rate influenced fledging success, the length of the prefledging period and mass at fledging. Chicks exhibited a large variation in growth rate coefficients and chicks with comparatively slow growth rates were able to fledge. Chicks with small growth rate coefficients for body mass exhibited retarded growth of all body measures except wing length. Therefore slow growing chicks were able to fledge in a shorter period of time than their slow growth would otherwise have allowed. Sibling rivalry occurs in African Black Oystercatchers and once a dominance relationship is established the larger chick remains so throughout the prefledging period. The larger sibling fledges earlier and at a heavier mass and may thus, have improved its chances of survival. The observed average growth rate coefficient of African Black Ovstercatcher chicks on Robben Island (33°S) was only 2% less than predicted from the Beintema and Visser (1989) allometric equation. Its relative (observed versus predicted) growth rate coefficient was closer to the predicted value for shorebirds than those of three precocial, selffeeding shorebird species in the Western Cape. The growth rate coefficient of African Black Oystercatcher chicks was smaller than that of other oystercatcher species which may be a consequence of differences in body size and differences in climate and food availability. RMR, peak daily metabolisable energy (DME) and total metabolisable energy (TME) of African Black Oystercatchers were similar to those expected for the species (from Weathers 1992 and based on comparisons with the Eurasian Oystercatcher). They spent less time foraging and more time inactive than precocial species. Therefore the mode of development of African Black Oystercatcher chicks enabled them to reduce energy costs from thermoregulation and activity and they were able to grow relatively faster than precocial shorebird species in similar climatic conditions.

Spotted Thick-knees are also semi-precocial shorebirds found in the Western Cape (34°S). Their growth rate coefficient, RMR, peak DME and TME were similar to predictions. The potential negative impact of nocturnal feeding on chick growth may be countered by parental feeding reducing chick energy expenditure on thermoregulation and activity and adults potentially extending their foraging time into the day as their chicks become larger. Their relative energy requirements were greater than those of precocial shorebird chicks in the same environment and lower than those of similar-sized shorebirds breeding in temperate or arctic zones. Therefore the

semi-precocial mode of development of Spotted Thick-knees enabled faster relative growth than that of precocial species at the same latitude and is thus important in the survival of this species.

Through a study of shorebirds (Charadrii) as a group and through comparing them with other Charadriiformes (Lari) we were able to investigate the importance of adult body mass, mode of development and latitude in shorebird growth and energy expenditure. Shorebird growth rate coefficients decreased whereas energy expenditure increased with increasing adult body mass. Semi-precocial shorebirds exhibited faster relative growth rates than precocial species at similar latitudes. This was particularly obvious when comparing the growth of African Black Oystercatcher and Spotted Thick-knee chicks to that of precocial shorebirds in southern Africa. Habitat type and food availability are a consequence of latitude. The growth rate coefficients and metabolisable energy expenditure of shorebirds increased with increasing latitude, thus food availability and habitat type are influencing factors in shorebird growth and energetics. Chicks at higher latitudes may be able to compensate for their greater energy expenditure due to greater thermoregulatory energy costs through greater food intake than chicks at lower latitudes. RMR appeared to be unaffected by latitude therefore one can conclude that energy expenditure at higher latitudes is driven more by thermoregulation and activity costs than by RMR. Shorebird chicks at higher latitudes spend their time brooding or foraging and spent little or no time in other activities whereas shorebird chicks in the Western Cape did not seem to be limited by time available for foraging but rather by food availability.