

SYMP15 The energetics of breeding in precocial waders

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Our main emphasis here is on the energetics of the growth of wader chicks from hatching to fledging in relation to a variety of factors that impinge on growth: temperature, latitude and foraging behaviour. The research presented in this symposium builds on the recent finding that doubly labelled water methods can be applied to rapidly growing animals. The presentations cover a range of aspects related to the energetics of precocial waders. The study areas range from Siberia and Canada through Spain to South Africa, and the species represent several families of waders, including plovers, sandpipers, oystercatchers and avocets. In most wader species, chicks feed themselves from hatching, and consequently spend more energy on activity and thermoregulation than do parent-fed chicks; the oystercatchers are exceptional, in that they are examples of parent-fed chicks that are precocial in their development at hatching, and we present here the first results on the energetics of chick growth for a species in this unusual category. We also describe energy expenditure in relation to breeding systems and describe the development of feeding in wader chicks.

SYMP15-1 Avocet *Recurvirostra avosetta* chicks at different latitudes: comparisons of thermoregulatory behaviour, energetics and growth of chicks from northern Germany and southern Spain

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Most studies on ecophysiological adaptations of young birds to climate are based on interspecific comparisons of closely related species or on comparisons of measured values with expected values taken from allometric relationships. Compared to other wader species, the breeding distribution of avocets covers a wide latitudinal range. Their breeding area extends from the Wadden Sea coast in north western Europe to continental central Asia, the Mediterranean southward to eastern and southern Africa. Within this area they are exposed to a wide range of climatic conditions. This offers the opportunity for intraspecific comparisons of thermoregulatory behaviour and energetics of chicks growing up under contrasting climatic conditions. We studied thermoregulatory behaviour, energy budgets and growth of avocets chicks in the north west European Wadden Sea, at the northern border of the species range, and in the Bay of Cadiz, in southern Spain. The results indicate that Avocets chicks did not develop any special adaptations to unfavourable climatic conditions in northern breeding areas. A high degree of behavioural and physiological flexibility allows them to adjust their energy budget and growth rate to local climatic conditions.



SYMP15-2 Chick energetics of african black oystercatchers Haematopus moquini

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Many studies have focused on the energetic requirements of birds during incubation and chick rearing in a range of positions on the altricial-precocial spectrum. In altricial species the chick-rearing period is often the most energetically expensive period for adult birds because food needs to be collected and transported to the nestlings. In most species of the sub-order Charadrii, the chicks are precocial and the burden of collecting food is shifted to the chicks resulting in greater energy requirements for activity and for thermoregulation and, thus, greater energetic demands. The oystercatchers Haematopodidae are exceptions, in that the chicks hatch as developed as other charadriid chicks, but are parent-fed, because the prey capture and handling process is too complex for the chicks. The burden of collecting food is shifted back to the adults. These "semi-precocial" chicks may, therefore, be able to grow at a faster rate than self-feeding precocial chicks. This study explores the ecological consequences of this developmental mode for african black oystercatchers *Haematopus moquini*. Fieldwork, on Robben Island, South Africa, included the determination of chick energetics using doubly labelled water methods, time budgets and growth rates.

SYMP15-3 Foraging behaviour and body temperatures of precocial plover and quail chicks in relation to weather conditions

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We studied how time budgets and body temperatures of precocial chicks are influenced by environmental conditions. In golden plover chicks on the tundra at Churchill, Canada, foraging time decreased with ambient temperatures and levels of solar radiation, and increased with age. The decrease in foraging time was due to a decrease in the length of foraging bouts. The length of brooding bouts averaged 12 min, independent of ambient conditions or age. Body temperatures were lower under colder environmental conditions and increased with age. At the end of a foraging bout, body temperature never fell below 35.5° C, high for a precocial chick. By minimizing foraging bout length in favour of parental brooding, chicks may increase their digestive efficiency and save energy otherwise expended on thermoregulation and locomotion.

Japanese quail chicks, raised under either high (24° C) or low (7° C) ambient temperatures, similarly reduced foraging time when exposed to low temperatures. Body temperature during foraging was lower in cold-exposed chicks, but did not drop below 37.8° C, suggesting that the end a foraging bout was not caused by body temperature. Metabolic rate of cold-exposed chicks was reduced when switching from foraging to brooding, and may be a factor determining foraging behaviour of precocial chicks. Mass-specific food intake of cold-exposed chicks exceeded that of warm chicks by 15%. Cold-exposed chicks increased their foraging efficiency to reach this intake during their reduced foraging time. Metabolic rates initially were similar in both groups, but increased rapidly and were elevated in cold-exposed chicks from 15 days. Growth rate was initially reduced in cold-ex-



posed chicks, exceeding growth of warm chicks after 21 days of age. These results suggest that pirds have considerable latitude to modify the relationship between growth rate and thermoregulatory function, and that in reponse to cold a shift in balance occurs to thermoregulatory function.

SYMP15-4 Energy expenditure in incubating and chick-rearing arctic breeding shorebirds in relation to breeding systems

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Energetically, incubation is regarded as a low cost activity, but recent studies show that arctic-breeding shorebirds face high costs of incubation. For altricial species, the chick-rearing period is energetically stressful for the parents; however, in precocial species, including most waders, chicks feed themselves from the first day. The chick-rearing period may therefore be less stressful, as no time needs to be allocated for food provisioning, although chicks need to be brooded, because they cannot initially maintain body temperatures. Apart from time allocated to brooding and guarding chicks, parents can feed themselves. This time and energy allocation might differ between breeding strategies which coexist in arctic regions. Species in which one parent incubates the clutch and care for the young (uniparental species) have little time to feed during the nest period (because eggs cannot be left unattended for long periods), while after hatching this time allocation problem might be less urgent. In biparental species both parents take turns in incubation; in some species one parent leaves after the chicks have hatched, while in others both parents stay until the chicks fledge. To investigate in trade-offs resulting from different breeding systems, we measured energy expenditure in relation to time budgets in incubating and chick-rearing parents of two species at a same study area in northwestern Taimyr (Siberia): uniparental little stints Calidris minuta and biparental dunlins C. alpina. In little stints daily energy expenditure was related to weather conditions but was similar for incubating and chick-rearing birds. However as a result of an increase in potential foraging time in the chickrearing period the required intake rate was lower than during incubation. For dunlins, feeding time for the parent is 50% during incubation but is reduced in the chick-rearing period, because the male takes care of the chicks. Therefore required intake rate is higher in the chick-rearing period. In conclusion, the time-energy budget for the two species (as representatives of two different breeding systems) differs in the two phases of breeding, resulting in an energetically more stressful incubation period for uniparental and an energetically more stressful chick-rearing period for biparental species.

SYMP15-5 Development of foraging behaviour in self-feeding precocial chicks

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Self-feeding precocial birds hatch with well-developed functional capabilities, yet still undergo a significant ontogenic change between hatching and fledging. I studied the development of feeding

behaviour in chicks of the black-tailed godwit *Limosa limosa* in the field, using a combination of behavioral observations and doubly-labeled water measurements of energy expenditure. Chicks feed for themselves from the hatching day onwards, taking small arthropods from the vegetation while walking through their grassland habitat. Feeding time, distance covered, and peck rates increased during the first week of the 25–day prefledging period, and fluctuated around a stable level thereafter. Comparison of intake rates with measurements of energy expenditure suggested that mean size of prey taken increased as chicks grew older, and this co-occurred with a decrease in pacing speed, suggesting that they became more selective towards larger insects.

Feeding time, energy expenditure and feeding success were all affected by weather conditions. Feeding success was influenced most by wind speed, either through a reduction in the availability of prey or by problems for the visually foraging chicks to detect them in the moving vegetation. I explore how these simultaneous effects of weather affect energy budgets of chicks and their chances for survival.

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