Research news and comment

Contributions are invited for this new series featuring news and comments on wader research. The plan is to provide an informal means of disseminating news about the activities of wader researchers and their results. We also hope that this will become a forum for comment and debate as well as for airing views, floating theories and stimulating research in new directions. Tamás Székely (Dept. of Biology and Biochemistry, University of Bath, Claverton Down, Bath BA2 7AY UK, phone: +44 1225 383676, fax: +44 1225 386779; e-mail T.Szekely@bath.ac.uk) will act as co-ordinator of this series. Contributions can be sent either to him or to the Editor.

Putting all eggs into one basket: Review of Klaassen, Lindström, Meltofte & Piersma (2001) "Arctic waders are not capital breeders." (*Nature* 413: 794)

Arctic-breeding waders have only a short time-window for producing eggs and raising chicks before the brief summer ends. To gain precious time, these birds may store nutrients before or during migration in order to produce the clutch shortly after arrival on their breeding grounds. This strategy is well-known in Arctic breeding migratory geese (Drent & Daan 1980). Now, research teams from The Netherlands, Sweden and Denmark, led by Marcel Klaassen, have studied ten species of waders but have found no evidence that this strategy is adopted by any of them.

Klaassen and his colleagues used a sophisticated technique, carbon-isotope analysis, to identify the origin of eggs and feathers. This method is based upon the premise that each habitat has its specific carbon-isotope ratio ($^{13}C/^{12}C$), a sort of signature. For instance, prey items in estuaries have high isotope ratios whereas terrestrial and fresh-water habitats have low ratios. Therefore those tissues and organs that are produced from nutrients in marine habitats should have higher isotope ratios than the ones that are extracted from inland habitats.

Klaassen *et al.* found that the eggs of Ruddy Turnstone *Arenaria interpres*, Red Knot *Calidris canutus* and Dunlin *C. alpina* had low isotope signatures consistent with a terrestrial/freshwater origin for the nutrients from which they were derived (Fig. 1). Moreover, in a range of species, both the natal down of chicks and the flight feathers of juveniles had low isotope signatures like the eggs, indicating a similar nutritional source. In contrast, adult flight feathers that would have been replaced on wintering grounds and adult shoulder feathers that would have been replaced during spring migration, all showed the high isotope ratio that is characteristic of estuary habitats. Interestingly, body size does not seem to affect the time when egg-making nutrients are ingested, because the isotope-signatures for the eggs and chicks of small waders, such as the sandpipers *Calidris* spp., were similar to those of the larger ones, such as Grey Plover *Pluvialis squatarola*.

The eggs used for the isotope analyses were collected from abandoned nests. It might be argued that these egg-samples do not represent the whole breeding population. Let us suppose, for example, that females in good body condition do use stored nutrients (or perhaps a mixture of stored and local nutrients), whereas females in poor condition use only local resources. If females in poor body condition are more likely to abandon their clutch than females in good condition, the egg-samples may be biased toward local nutrients. Klaassen *et al.*'s results would suggest that this scenario is at least a possibility because two of the three species for which they have egg-samples appear to have lower carbon-isotope ratios than any of their samples from down or the feathers of juveniles (Fig. 1). However, although further investigation of this particular issue may be warranted, it does not affect what Klaassen *et al.* have shown so clearly: that the young of Arctic waders derive wholly or mainly from local nutrients.

This excellent study indicates that in 1999 and 2000 in NE Greenland and Arctic Canada, waders did not use stored materials to produce their eggs. Given the geographical range and the two year's data, this would seem to be a such a firm result that future investigation is unlikely to show anything different. One may wonder, however, whether it is invariably true for all wader species throughout the Arctic in every year.

It is likely that most waders (of both sexes) arrive on the breeding grounds with at least some stored nutrients. For example, many Red Knots leave Delaware Bay, USA, at >200 g and therefore carry considerably more resources than they need for the 3,000 km flight to the breeding grounds. In females, such resources may potentially be available for egg-production. However, this may not be the case if resources have to be used for maintenance when feeding conditions are poor on arrival. Alternatively, the birds may arrive without spare resources either because the last leg of migration was particularly energy-consuming or because food resources were insufficient at the last stop-over. Thus females might not have any stored reserves left by the time they lay their clutch. Alternatively perhaps female waders are physiologically incapable of utilising stored resources for this purpose. Hopefully, future studies will unravel these intriguing questions.

Klaassen *et al.*'s study has two important implications. The first relates to our understanding of certain wader breeding systems of which there is an immense diversity. Indeed much of this variation is encompassed by the very species Klaassen *et al.* studied. For instance, female Sanderlings *Calidris alba* are polyandrous, and often desert their mate (and clutch), and then re-mate and re-nest with a new male. It has been argued that such deserting females have exhausted their body reserves by laying their clutch, and are thus forced to terminate incubation and brood care prematurely (Graul *et al.* 1977). In the light of Klaassen *et al.*'s

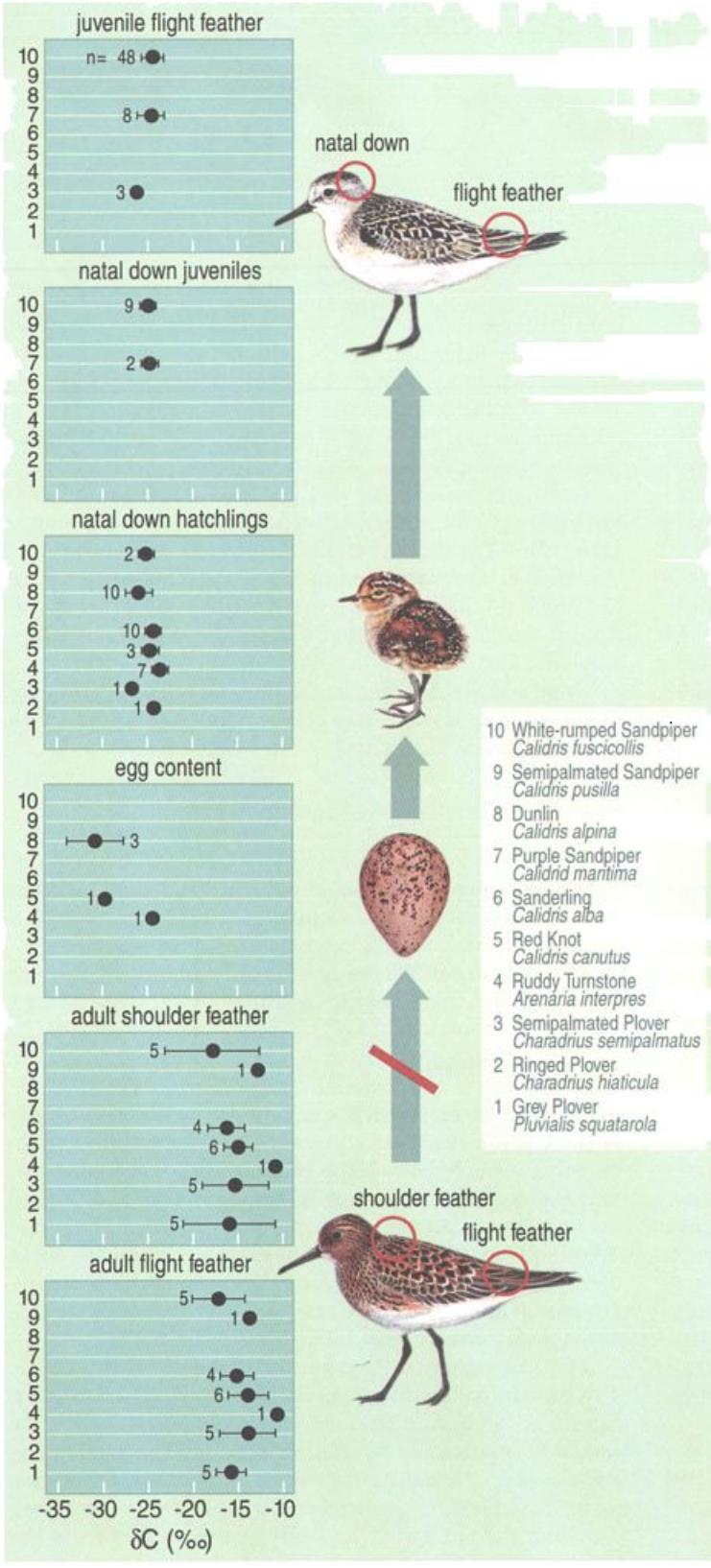

Fig. 1. Carbon stable-isotope ratios of eggs, natal down and feathers of different species of Arctic-breeding waders at different times during the year (mean ± SD). Feathers collected from nest-attending adults were grown either in winter (adult flight feathers) or during spring migration (adult shoulder feathers). Eggs were collected from deserted nests (egg content); natal down was collected from hatchlings. Data are also presented for natal down still attached to the tips of neck and head feathers of independent young, and for secondary flight feathers from independent young.

results, this explanation does not seem likely, because female waders do not appear to use stored nutrients to produce the clutch.

Second, breeding conditions in the Arctic may have a more significant impact on reproductive behaviour than we had thought. For instance, if the distribution and abundance of nutrients in the breeding grounds change, perhaps through the effects of global warming or airborne pollution, this could initiate a cascade effect on egg size, offspring survival, and many other life-history traits. The long-term consequences of these effects are very difficult to foresee.

I am grateful to Dick Visser and Theunis Piersma for providing Fig. 1, which is based on the data presented by Klaassen *et al.*

REFERENCES

Drent, R.H. & S. Daan. 1980. The prudent parent: Energetic adjustments in avian breeding. *Ardea* 68: 225–252.

Graul, W.D., S.R. Derrickson & D.W. Mock. 1977. The evolution of avian polyandry. *American Naturalist* 111: 812–816.

Klaassen, M., Å. Lindström, H. Meltofte & T. Piersma. 2001. Arctic waders are not capital breeders. *Nature* 413: 794.

Tamás Székely, Dept. of Biology and Biochemistry, University of Bath, Claverton Down, Bath BA2 7AY, UK, e-mail: T.Szekely@bath.ac.uk