election favours individuals that raise the most offspring. However, from the parents' perspective the optimum investment in any one offspring typically is less than the investment desired by their offspring. As human parents know all too well, this can result in conflict over the intensity and duration of parental care. So how do parents decide when to cut the apron strings?

Petrels provide a useful model to answer this question: they have only one chick (thus removing conflict between siblings) and it obtains all its parental care in the nest. Petrel chicks accumulate large fat reserves, peaking at weights 30 to 50 per cent more than an adult, then lose weight prior to fledging as parental feeds become increasingly less frequent. By manipulating the number and ages of chicks we can tease apart who drives this process – the parents or the chick.

Twinning experiments show that adult petrels usually have some spare capacity to provision their chick. When given an extra chick, adults increase their food delivery rate, but each chick obtains less food than a single one would, resulting in reduced growth and fledging mass. Because juvenile survival is strongly linked to fledging mass, it doesn't pay petrels to lay more than one egg.

Cross-fostering chicks of different ages between pairs offers a more subtle test of these relationships. Much of this work has been done on the Manx Shearwater, a species that is readily accessible to UK-based researchers. Like most birds, shearwater chicks use begging to signal their need for food. Begging allows parents to allocate resources efficiently, but it can be manipulated by chicks to garner more resources than they really need.

Young Manx Shearwater chicks increase begging effort in relation to body condition, thus providing an honest signal of need. However, chicks differ in their begging rate, so that immediately after crossfostering there is a period of adjustment,



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as parents learn to judge how 'serious' their chick's pleas for food really are. The female is most responsive to the chick's begging. Male shearwaters work harder than their partners, making frequent food deliveries, whereas females vary their delivery rate in relation to the chick's condition.

However, as chicks get older, they become less honest. When an older chick is swapped for a young chick, the older chick continues to beg and the adults continue to provision it for longer than is typically the case. Adults seem to have a built-in timer that tells them how long a chick should be fed, and older chicks that are cross-fostered can take advantage of this. When a younger chick is swapped for an older chick it fledges at a lower mass, because even though it begs more its parents reduce feeding sooner than they should in terms of the chick's age and development. However, most parents do continue to feed their chick for longer than expected, showing some reaction to an under-developed chick.

Interestingly, the timing of fledging seems to be determined solely by the chick's age. Fledging is related to a rapid

A Grey Petrel chick with its parent. Recent studies have disentangled the factors that determine how much effort petrels invest in their chicks.

increase in corticosterone stress hormones, irrespective of the chick's condition or fostering history. However, the magnitude of this hormonal spike is related to body condition, with small chicks having lower hormone concentrations.

Much of this probably strikes a chord with human parent-offspring relationships. The message from the shearwaters is that parents should place a finite limit on their support, and become less sensitive to their children's pleas as they approach independence. However, unlike the shearwaters, not all children have an internal mechanism to stimulate fledging, and increasingly seem to need to be encouraged to leave the nest. PETER RYAN

Reference: Riou et al. 2012. 'Parent-offspring conflict during the transition to independence in a pelagic seabird.' Behavioural Ecology 23: 1102-1107.

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