How many eggs in one basket?

EGG AND CLUTCH SIZES IN BIRDS

Text by Phil Hockey

The life of a bird – or indeed of any animal – is driven by the outcomes of the 'decisions' that it makes. These decisions are made on time scales of seconds to seasons; seconds in the case of the best tactic to employ in evading a predator, to seasons in the case of decisions about reproduction or migration. The lifetime achievements of a bird boil down to its performance as a parent – how many offspring does it produce during its life which themselves survive to breed?

Decisions about reproduction are not simple – choices must be made concerning mate, breeding site, the timing of breeding, how many eggs to lay, how big those eggs should be, and how best to care for the young. Not all of these decisions are open-ended; they may be constrained by the availability of mates, food or nest sites, or by the physical condition of the bird itself.

One factor that limits the number of young that can be reared in a single breeding attempt is the number of eggs that are laid. Occupying the extreme position of laying only one egg are, among others, the petrels, shearwaters and albatrosses. Extreme even among these is the Wandering Albatross *Diomedea exulans*. This giant seabird of the southern oceans lays only a single egg at each breeding attempt. Incubation takes about two months and the nestling period may last for another year. Thus, not only does the bird lay the smallest clutch possible, but it can only lay its single egg every second year! To compound the effects of small clutch size, a Wandering Albatross may only breed for the first time when it is 10 years old.

The other extreme is typical of small songbirds, especially those that live ▷

The Wandering Albatross Diomedea exulans *lays only a single egg. Even so, the time from egg-laying to fledging is about 14 months and these birds can only breed every other year.*

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The Helmeted Guineafowl **Numida meleagris**, *like many other gamebirds, lays a large clutch of eggs. The female Red-legged Partridge* **Alectoris rufa** *of Europe sometimes lays two clutches, one immediately after the other. She incubates one of the clutches and her mate incubates the other. This breeding system is known as 'rapid multiclutching'.*

at high latitudes. Some of these birds lay more than 10 eggs in a single clutch, the combined weight of which can exceed the weight of the incubating adult. They may also rear more than one brood in a single breeding season: a Wandering Albatross takes 40 years or more to lay the same number of eggs. How has such variation in clutch size evolved and, more importantly, why?

COULD BIRDS LAY MORE EGGS THAN THEY DO?

A bird's egg is made up of water, protein, fat and calcium, so the female must garner each of these above and beyond the amount she needs for herself. Getting the right balance may not always be easy: water may be in short supply for desert birds and calcium may be a problem for others. Relative to the amount of calcium that a bird normally carries in its body, its needs for egg-laying can be considerable. For the European Blue Tit *Parus caeruleus* to lay a clutch of eggs, it needs nearly one and a half times as much calcium as is contained in its own skeleton.

It has been demonstrated many times for many species that if eggs are removed from a nest before the clutch is completed, the female will continue to lay additional eggs to replace the losses, suggesting that she has little problem acquiring enough calcium. In one extreme example, a Northern Flicker *Colaptes auratus*, a North American woodpecker which normally lays a clutch of six to eight eggs, laid no fewer than 71 eggs in 73 days.

However, there are instances when calcium deficiency does cause problems. Acid rain in parts of Europe has resulted in a decrease in the amount of calcium available in the environment (because calcium becomes more soluble as acidity increases). Concomitantly, during the 1980s and 1990s, there has been an increase in the proportion of birds which lay thin-shelled eggs, or lay no eggs at all. If calcium-rich food is provided to these birds, the trend is reversed. Thus, although birds have to spend time collecting extra calcium ▷

for eggshell formation, there is little evidence, under natural conditions, that calcium deficiency limits clutch size.

TRUTHS AND EXCEPTIONS

Clutch sizes in birds make for an attractive field of study – it is fairly easy to increase or decrease clutch size artificially and record the consequences in terms of an increase or decrease in breeding success. However, it is not practical (or ethical) to attempt such manipulations on a large geographical scale or to attempt them on rare and endangered species (although at least one bird species, the Chatham Islands Robin *Petroica traversi*, was brought back from the edge of extinction in exactly this way). Although many advances in our understanding of clutch sizes have come from experiments, the design of these experiments has been set by observations made in nature.

The following are some observations which have been instrumental in focusing the minds of scientists on the problems of egg and clutch size variation.

- First-time breeders tend to lay smaller clutches than older, more experienced birds: young birds tend to be less adept than older ones at finding food.
- Within a species, there is a tendency for clutches laid early in the breeding season to be larger than clutches laid later in the season. Early breeders also tend to be more successful.
- Within a species, clutch size tends to be smaller in years when food is scarce than in years when food is abundant.
- Among closely related species, and even within the same species, clutch size tends to decrease towards the equator. By way of example, clutch sizes of the Great Tit *Parus major* in some parts of England are more than three times as large as in parts of India.
- When the densities of adult birds are high (that is, when the population is large), both egg sizes and clutch sizes tend to be smaller than when adult densities are low.

FROM PATTERN TO PARADIGM?

The trends above all point to one conclusion – clutch size is controlled by food availability; either the availability of food for adults to produce eggs or to feed their young.

Some 50 years ago, the eminent ornithologist and population biologist David Lack also thought clutch size was linked to food supply. He argued that clutch sizes should be adjusted to maximize the number of young produced, but appreciated that this would not necessarily be an inevitable consequence of laying as many eggs as possible. A clutch that was too large could mean that several young die in the nest or fledge in poor condition and thus have little chance of reaching maturity. A clutch that was too small would represent missed opportunity because the number of eggs laid was less than the number of chicks that could have been reared successfully. Lack proposed that the optimal clutch size would lie somewhere between these extremes and was able to show that intermediate-sized clutches produced more offspring than did the extremes.

Lack used several ingenious lines of evidence to support his contention that food was the key to explaining clutch size. These included the observation that when large cuckoo species lay eggs in the nests of small host species, the young cuckoo ejects all the eggs or chicks of the host (so that the host parents would be able to provide ▷

The specialized diet of the Bearded Vulture* Gypaetus barbatus *makes it highly unlikely that this species would ever suffer from a shortage of calcium from which to form eggshells. For some species, however, the search for calcium can make considerable inroads into their daily foraging time.

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Several species, such as the Caspian Tern Hydroprogne caspia *(**below**) have reduced clutch sizes in the tropics and subtropics. The Pied Avocet* Recurvirostra avosetta *(**above**) is an exception, possibly because it breeds in temporary wetlands and has to compress its annual breeding effort into a short period of time.*

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enough food for their 'super-chick'). The Great Spotted Cuckoo *Clamator glandarius*, by contrast, parasitizes large hosts which would, under normal conditions, have to provide large amounts of food to their young. At the time of laying, the female cuckoo removes only one egg from the host's clutch and the young cuckoo is reared together with the host's remaining offspring.

Other supporting evidence comes from western Australia, where three species of raptors increased their clutch sizes in response to invasion of their habitats by alien rabbits – an excellent additional food supply.

ARE EGG AND CLUTCH SIZES SMALLER THAN THEY SHOULD BE?

In an address to the International Ornithological Congress in Vienna in 1994, Chris Perrins of the Edward Grey Institute of Field Ornithology at ▷

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Large numbers of noisy chicks in a nest makes the nest relatively easy for predators to find and can place both the young, such as these Fiscal Shrike **Lanius collaris** *chicks, and their visiting parents at risk.*

Oxford University concluded '... some birds seem to vary their egg size in a predictable way, which strongly suggests that they ... *are* (my emphasis) constrained by food supply'.

Perrins was concerned about the sizes of eggs rather than the numbers of eggs in a clutch, but there are important linkages between the two. Within a species (in Perrins' case, the Great Tit), large eggs have a higher hatching success than small eggs and chicks from large eggs have a higher fledging success. Large hatchlings also fledge more quickly, which may be important if adults are at risk from predators while making frequent visits to feed their young. But, if having a large egg confers all of these advantages, why not always lay large eggs?

In reaching his conclusion about food determining egg size, Perrins draws on two contrasting trends: clutches laid early in the season produce more young, but clutches laid later in the season contain larger eggs. This apparent paradox can be resolved. The combined energy demands of adults and nestlings are greatest when the nestlings are large. Consequently, eggs should be laid at the time that ensures large chicks are in the nest when the most food is available. Thus, egg-laying should occur earlier in the season than does the peak abundance of food. Early in the season food may be in short supply, forcing the female to lay small eggs. Birds which start breeding later in the season are laying eggs when food is more abundant and therefore females can produce larger eggs. But, by the time the late breeders' chicks are close to fledging, food may again be in short supply, leading to a low breeding success because of chick starvation.

Clutch sizes observed in the field tend on average to be *smaller* than those which produce the most offspring. If, as Lack argued, birds try to produce as many chicks as they can at each breeding attempt, there seems to be an inconsistency here in that the birds are not performing to their maximum potential. What Lack failed to incorporate explicitly into his reasoning, and has subsequently been demonstrated in several studies, is that a very large breeding effort in one season can reduce fertility and breeding success in subsequent seasons to the point where future losses exceed present gains. In other words, he failed to factor the *lifetime* component of breeding success into his equation.

WHY SMALLER CLUTCHES IN THE TROPICS?

Reduced clutch size in the tropics is widespread, even within a species. For example, both the Caspian Tern *Hydroprogne caspia* and the Red-winged Pratincole *Glareola pratincola* lay smaller clutches in Africa than they do in Europe.

Lack thought that larger clutches at high latitudes were possible because ▷

of the long summer days allowing plenty of time for adults to find food for large broods of chicks. There are two problems with this explanation. Firstly, as one moves from the equator towards the poles, clutch sizes do not increase in proportion to the increase in summer day length. Secondly, and perhaps more telling, is that nocturnal birds, especially owls, follow the same pattern. During the summer months, nocturnal birds experience *shorter* nights the further away from the equator they breed.

The true explanation for the tropical-temperate difference is almost certainly linked to an increasingly seasonal environment as one moves north or south from the equator. High northern latitudes are very seasonal, swinging annually from perpetual daylight in summer to permanent darkness in winter. Even at moderate latitudes, few birds are able to survive through the winter. Those that do stick it out are rewarded with a food bonanza in the spring months as the weather starts to warm. Because there are relatively few birds, spring numbers are well below those which the environment can support and a sufficient food surplus exists to rear large broods. These seasonally good breeding conditions are also enjoyed by many migrant species, but there is little evidence that they are food-stressed by the time they start their southward journey to more benign non-breeding grounds.

In more tropical environments, the situation is rather different. Because food production is much less seasonal in the tropics, there is a much greater tendency for tropical birds to be resident. The risks of dying during a tropical winter are almost certainly less than those of dying in a temperate winter. As a result, many tropical species have large, and relatively stable, adult populations which are closely tied to the food supply. There is thus far less 'surplus' food available during the breeding season for provisioning young – hence the smaller clutch sizes.

WARWICK TARBOTON

Populations of hole-nesters, such as the Red-billed Woodhoopoe **Phoeniculus purpureus**, *are probably more often regulated by the availability of nest sites than by food. They tend to lay large clutches and local populations can be increased by the provision of artificial nest sites.*

The clutch of the White-fronted Plover **Charadrius marginatus (below)** *is usually only half the size of that of its northern counterpart, the Kentish Plover* **C. alexandrinus**.

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Tropical species may be at a disadvantage relative to temperate breeders in terms of food availability, but they do have a potential advantage in that they can extend their breeding season over a much greater part of the year because they do not experience the equivalent of a temperate winter.

CONCLUSIONS

It is clear that understanding why a clutch of eggs is the size that it is, is not quite as simple as one might imagine! There are variations between closely related species in the same area, among the same species in different places and between individuals of a species in the same place: even the same individual can lay eggs and clutches of different sizes in the same or different seasons.

Ultimately, all individuals are trying to choose the best personal strategy – the one that should ensure that their own lifetime reproductive success will be the greatest. This boils down to balancing the number of young that can be produced now with the potential number that could be produced in the future. This is a complex equation for any animal to solve and, as environmental conditions change, so will the solution to the equation.

Complexities apart, the fine tuning of egg and clutch size to the environment does mean that they could be useful tools in monitoring the effects of man's activities on the environment. A trend of decreasing egg or clutch size could be a very good early warning that all is not well. Just as changes have highlighted ecological problems associated with acidification in Europe, the same patterns might be evident on the South African highveld where acid rain prevails. Other areas and problems that may warrant investigation include insecticide spraying around the Okavango Swamps in Botswana, replacement of natural high-altitude grasslands with *Themeda* monocultures, reclamation of floodplains and possible overfishing of both marine and freshwater stocks. □