CONSTRAINT AND RESTRAINT IN BREEDING BIRDS

by David Atkinson and D.B.A. Thompson

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Why do older or more experienced birds breed earliest and most successfully? This note discusses the relevant concepts of constraint and restraint, and shows how the two may be distinguished to answer the question.

REPRODUCTIVE CHANGES WITH AGE

In at least seven species of wader (Charadrii) it has been shown that older/more experienced birds breed earlier in the season: Semi-palmated Sandpiper *Calidris pusilla* (Gratto *et al.* 1983), Least Sandpiper *C. minutilla* (Miller 1983), Stilt Sandpiper *Micropalama himantopus* (Jehl 1973), Spotted Sandpiper *Actitis macularia* (Oring and Lank 1982), Redshank *Tringa totanus* (Thompson 1986), Greenshank *T. nebularia* (Thompson *et al.* 1987) and Red-necked Phalarope *Phalaropus lobatus* (Hilden and Vuolanto 1972). In Spotted Sandpipers, Redshank and Greenshank it also appears that older birds breed more successfully than those breeding for the first time. Most of these studies have demonstrated the effect of age or experience by following the fate of individuals. Those which simply compare old and young birds, however, do not eliminate the possibility that birds breeding late in the season suffer disproportionately higher mortality. If this is the case, only early breeders will reach old age, accounting for older birds breeding earliest.

There are two kinds of explanation for these changes with age or experience. The first is the "constraint" hypothesis (Curio 1983) which assumes that young birds are unavoidably constrained by lack of experience or other handicaps of youth. For instance, young birds may not have had enough time to perfect their feeding skills (*e.g.* Groves 1978), and thus fail to: (i) achieve breeding condition quickly; and (ii) breed successfully. Also, in birds which normally return with the same mate to familiar nesting grounds (*e.g.* Gratto *et al.* 1983; Oring and Lank 1982; Thompson *et al.* 1987) youngsters may be forced to spend more effort in territory acquisition, courtship and finding food, and so have less time and energy for nesting. In a free-for-all situation, experienced pairs may settle on good areas first or be better competitors, and so breed earliest. Younger males are therefore left with poorer territories; may attract lower-quality females; and may breed later, with less success (see *e.g.* Nol and Smith's 1987 study of song sparrows, *Melospiza melodia*). Here, an effect of age may only be evident when there is a shortage of good breeding sites *e.g.* in years when population size is high (Nol and Smith 1987).

The second kind of explanation for changes with age or experience is the "restraint" hypothesis (Curio 1983), which assumes that young individuals refrain from some activities associated with breeding which carry a high risk of death. If birds have less to lose as they get older (*i.e.* have an increased risk of dying) it would be adaptive to channel increasingly more resources to reproduction. Thus older birds would become more reckless, and successful.

Both types of explanation may apply at the same time, each accounting for part of the difference in success between young and experienced breeders, and thus making interpretation of the differences difficult. Their relative influences can be examined by comparing time energy budgets of young and old breeders. Pugesek (1983, 1984) applied this method to the reproductive success of different-aged California Gulls (*Larus californicus*) and found evidence for reproductive restraint among young breeders, but no evidence for increases in parental ability or efficiency with age.

Another, more simple, method for distinguishing between the two hypotheses has been suggested by Curio (1983). He argues that if the variance in reproductive success among young and among old breeders is compared, a greater variance among young breeders will support the constraint hypothesis. However, we believe that this leads to equivocal conclusions. Curio's argument assumes a greater variance in skills among young birds than among the same individuals when they are older. This may not always be true. Some may learn early how to exploit a particular resource (*e.g.* food type, nesting situation), and may, as they develop skills, increase their relative advantage over others which have not had the same opportunities. So variance in breeding success could also increase with age.

GENERAL APPLICATION OF CONSTRAINT AND RESTRAINT

Constraint and restraint arguments can be extended to explain the variation in reproductive success among conspecifics of the same age which experience different conditions such as weather or territory quality. Traditional ecological explanations for reduced success, such as bad weather, poor habitat, and an unavoidable lack of skill describe the *constraints* on current reproduction. But a bird may also *restrain* its reproduction in these conditions, especially where the chances of future reproductive success are relatively better. The bird would thereby enhance its survival and general health in order to breed successfully in the future. Different degrees of restraint among birds may be due to genetic differences, to different effects of the immediate environment (*i.e.* non-genetic

influences), or to both. The following discussion deals only with the environmental influences on an individual's behaviour.

Restraint in *any* activity (and hence extra effort in others) can be identified when its rate is *reduced* despite the bird receiving either *more* or *the same amount* of a limiting resource (Atkinson 1985). Conversely, extra effort in an activity (and hence restraint in others) will be seen when its rate is increased despite the bird receiving either less or the same amount of limiting resource. Instances of such extra effort include:-

(a) The proximate effects of long days, which in temperate regions can initiate breeding activities. The birds therefore use daylength to anticipate future conditions, and this extra effort should decrease the amount of limiting resources directed to their own survival. However, this would not be extra effort if initiation of reproduction were due solely to the increased time spent feeding during the longer days (a constraint).

(b) The effect of removing eggs from a nest, which can increase the total numbers laid and thus reduce the amount of resources for other activities. In this case, the birds receive no additional resources but they nonetheless increase the effort directed to egg production.

(c) The effects of artificially adding chicks to a brood, which can increase the amount of time the parents spend feeding the brood and hence decrease the amount spent on feeding themselves. In this case too, the parents receive no additional resources, but with more chicks to feed will put more effort into rearing the brood.

An important point is that the degree of restraint in current reproduction in response to environmental conditions will depend on how much information about the future the bird perceives in those conditions. Current reproduction will be more restrained, for example, if poor feeding success is perceived by the bird as temporary (*e.g.* a poor season for insect food) rather than as an indication of a longer term threat to future reproduction (*e.g.* a severe wound). This point is important because it implies that different environmental stresses, even if they reduce a bird's current abilities by the same amount, may not have equivalent effects on current reproductive output.

We think that the use of constraint and restraint arguments will help clarify the interpretations of reproductive variation. In particular, they should help researchers avoid overlooking the effects of present environmental conditions on the bird's future. For instance, the recent manipulations of brood size in the House Wren *Troglodytes aedon* (Fincke *et al.* 1987) provided no evidence for an adaptive clutch size, and the authors suggest that clutch size may be limited by the ability of females to produce eggs (*i.e.* females are constrained). However, another alternative is that some females restrain egg production because they anticipate problems in the future (*e.g.* when feeding the chicks). Whilst such arguments can be applied to most bird groups, we believe that there are good opportunities for tackling relevant issues in waders. To date, this has not been attempted.

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