On the relationship between avian clutch size and life span

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The negative correlation between avian clutch size and life span is usually explained on the basis of trade-off between fecundity and survival. The main difficulty in such explanations, as in evolutionary ecology in general, lies in the obscurity of the criterion of fitness. Our analysis produced the following *a posteriori* goal for organisms: maximal probability of bridging gaps in time. This makes it possible to see longevity and fecundity as equal components of fitness. Our interpretation does not demand selection above the level of the individual, but we point out that theories based on the benefit of individuals and of genes produce different measures of success for individuals.

The evolution of low reproductive rates is not in itself a problem, but the reasons for it have not been adequately studied. Variation in the ratio clutch size/life span obviously largely depends on differences in the intake of resources. The observation of trade-off between avian fecundity and survival is complicated by some special features of birds, such as potentially high life span and parental care. Due to the former it may not be adaptive to endanger adult survival for the sake of reproduction. And, since the young are dependent on parental care, a high reproductive effort leading to the death of an adult, obviously kills the whole brood. Some difficulties encountered in empirical testing of avian life history theories are discussed.

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"Most trees, if they bear too much fruit, wither away after the crop when nutriment is not reserved for themselves, and this seems to be what happens to annuals, as leguminous plants, corn, and the like. For they consume all their nutriments to make seed, their kind being prolific. And some fowl after laying too much, so even to lay two eggs in a day, have died after this. For both the birds and the plants become exhausted, and this condition is an excess of secretion of residual matter" (Aristotle in De Generatione Animalium).

Introduction

In birds, clutch size, i.e. number of eggs produced in a breeding attempt, varies between one and about twenty. Evolution of clutch size by natural selection is a general biological problem. Research and speculation on the subject go farthest in the field of ornithology (see Klomp 1970 for a review), and here, too, the greatest theoretical advances were made in the 1940s and 1950s (Lack 1947, 1948, 1954, Skutch 1949, v. Haartman 1954, Wynne-Edwards 1960).

Clutch size shows an overall negative correlation with life span which is especially clear in nidicolous birds. Annual production of eggs has an even stronger correlation with life span, because only short-lived species tend to lay more than one clutch per season. The evolution of the combination low reproductive rate — long life span has been found hard to explain. Lack's answer was the same for all cases: birds reproduce as efficiently as they can and long-lived birds are not able to rear more than small broods. But he ignored the core of the problem — how low rearing capacity of adults has evolved. Wynne-Edwards' answer was totally different and suggested an explanation for the overall negative correlation of fecundity and longevity: reproduction needs to be just high enough to balance mortality. Higher clutches are not only unnecessary but also deleterious.

The most remarkable theoretical advance in the explanation of low reproductive rates took place when Williams (1966) concluded that reproductive rates should not be seen as separate problems but are connected with adult survival. If efficient reproduction increases adult mortality, i.e. there is a trade-off between survival and fecundity, then lower than maximal reproductive rates may maximize the total lifetime fitness of parents. Many variations of and slight improvements on this explanation were presented later (e.g. Cody 1966, Haukioja 1970, Hussell 1972, Charnov & Krebs 1973, Goodman 1974, Anderson 1978). Murphy (1968) emphasized the role of the environment, showing that adult survival over reproductive failures is a way which may lead directly to the fixation of iteroparity with accompanying lower reproductive rates. When defining K-selection, Mac Arthur & Wilson (1967) also suggested a hypothetical way in which reproductive capacity could be compromised for adult survival.

Thus there is no shortage of potential explanations for the evolution of low reproductive rates. All of them assume that when the reproductive capacity decreases something else is won. This other thing is the direct or indirect improvement of adult survival. But what is the role of survival in the theory of evolutionary ecology? Research has traditionally been based on population genetics and demography, where the rate of change (in gene frequencies or in population size) has been emphasized. Consequently, the fitness measure, r_m or the innate capacity of increase, has been adopted in evolutionary ecology, too. But if r_m is the sole measure of success, it leaves little space for trade-off between fecundity and survival, because an increase in survival is inefficient in increasing the value of r_m.

Birds are characterized by low reproductive rates — lower, presumably, than in their reptile ancestors. Hence evolution towards lower reproductive capacity and r_m has taken place. Trade-off between fecundity and survival gives the only orthodox explanation and birds should be excellent study objects for testing the prediction experimentally. Some attempts have been made in ornithology — mainly as by-products of population studies. To our knowledge unambiguous results are lacking which conclusively prove that efficient reproductive performance means higher mortality among adults. Earlier studies have given only weak indications that this is the case (e.g. Snow 1958, Perrins 1965, v. Haartman 1971, Hussell 1972) or failed to show it (e.g. Kluyver 1963, Haukioja 1970, Ricklefs 1977). Yet, if we cannot demonstrate trade-off, how can the evolution of low reproductive rates be understood? What are the consequences of neglecting r_m as the only measure of success? Is the theoretical basis sound? Are there possible biases in the empirical procedures? These types of questions are treated in this paper.

Two views of the same theoretical basis

The central difficulty in evolutionary ecology is that the term fitness is not clear. However, fitness is what natural selection is said to favour, and high fitness is often, although anthropomorphically, called the ultimate goal of an organism. But what does fitness mean for the ecologist? Is the concept of natural selection of population genetics ("differential reproduction of genotypes") relevant for ecologists trying to explain how certain characteristics have evolved in relation to certain environmental factors?

First we must analyse the basic nature of the term natural selection. When studying the use of natural selection in different types of life history models, Tuomi & Haukioja (1979) proposed that the process of natural selection must include two levels: *selection 1,* survival and reproduction of *individuals* as the function of their phenotypes and the environmental factors encountered, and *selection 2, characters* (and *genes* behind them) becoming frequent in a population due to selection 1 and the mode of heredity. Let us study these different levels separately.

Natural selection as differential reproduction of genotypes is the equivalent of selection 2. Now the whole process of natural selection is easily seen only as a statistical phenomenon. This line of reasoning regards the population as an evolutionary unit, because the change in the constitution of the population is studied. Here fitnesses are end products of phenotypes and environments, i.e. they inform us of realized success, or probability of realized success. However, fitnesses without environments can be used productively in genetic models, because stochastic variation and the mode of heredity also modify the final result, change in gene frequencies. This kind of approach does not need individuals: "The individual is simply a device constructed by genes to ensure the production of more genes like themselves" (Maynard-Smith 1977). But, strangely enough, the widely accepted ultimate goal of an organism is produced by such reasoning neglecting individuals: maximal genetic representation in a population. If this goal is taken literally — and it generally is — only traits leading to high r_m and to an asexual type of reproduction are features which natural selection should favour. In our opinion, however, producing "more genes like themselves" is simply a description of a tactic to produce surviving individuals when successive generations of organisms tend to meet similar environmental conditions. We see no reason why genes should be "less willing" to form new types of genes, if this solution would lead to phenotypes which were better in contests with environments, i.e. in selection 1.

An *a priori* fitness can be used productively in studying selection 2 but it is totally unsuitable in studying selection 1, where fitness is the end product and not the starting point. In selection 1 we have no *a priori* fitness for certain types of organism, but fitness is always the result of contests between the phenotype and the environment. Now the ultimate goal of an organism can be seen from a different angle. The traits of organisms do not have their present constellation because genes in their ancestors strove to ensure production of genes similar to their own. Rather, particular genes exist now, and may even be common, because they happened to enable individuals to function in agreement with the environment.

Taking the above view, let us now proceed from the following axiom: each ancestor of present organisms has produced at least one replacement for itself. This is an *a posteriori* outlook, and it yields an *a posteriori* goal for an organism: *to maximize the probability of bridging gaps in time.* It is the uninterrupted continuity of generations up to the moment of study which determines the individuals that can be studied, and it is their characters that we are trying to explain.

We wish to empasize that the above "goal" should not be interpreted as meaning acceptance of group selection. Continuity of a particular chain of generations is quite different from avoidance of extinction by populations or species. But, of course, solutions enabling a chain of generations to bridge gaps in time also lead to survival of populations and species, because these are collections of surviving individuals.

The above reasoning closely agrees with the phrase used by Darwin (1859): struggle for existence. Note that he did not use phrases like struggle for reproduction, struggle for evolution or struggle for rapid evolution. The "goal" presented above also accords with the possible evolutionary goal given by Stearns (1977) — following Mountford (1973): to minimize the probability of leaving no young. We prefer the version of the present paper, because Stearns' definition easily overlooks a very important point: *the time period within which an adult produces a replacement for itself may be of any length.* In theory survival without reproduction is also a possible tactic.

A gap in time can be bridged by longevity of the particular organism or/and by reproduction and survival of the young. The longer the time interval, the greater will be the probability that reproduction is involved. The importance of reproduction is clear, because it also permits rapid evolution. What is not so generally understood is that longevity *per se* is of similar inherent value. This is because longevity is not a tactic for rapid evolution but to keep organisms existing. But when tactics based on fecundity fail, longevity may also help to make a type of organism frequent in a population — even to replace other types of organisms.

The above rationale relaxes the assumption that natural selection "maximizes" only r_m. Natural selection as a process "maximizes" everything that keeps organisms existing. Adaptations leading to high r_m are one path to survival. Another, but equally good, path is longevity. Which tactic gives a phenotype a higher rate of actual increase (r) depends on the phenotype, the environment and heredity. No explanation neglecting one of these can be sufficient.

Hence we have no difficulty in explaining why natural selection has produced low reproductive rates or long life spans or iteroparity. They accord well with the original Darwinian theory. Difficulties are created by models which replace the dynamic effects of environmental factors by the basically static concept of *a priori* fitness.

Reproductive effort — definitions

Not only production of the clutch, but also pairing, nest-building, incubation and rearing the young make demands on the adult bird. All these activities may be characterized by the term reproductive effort (RE). It is usually defined as the part of resources which the adult directs towards reproduction instead of towards maintenance and growth. The following three related aspects of RE are separated in the present paper:

(1) The *proportion* of resources which the parent uses for reproduction (REp). If REp is high, the proportion of total resources used for adult maintenance and/or growth is low.

(2) The *absolute amount* of resources used for reproduction (REa). REa gives the limits within which the reproductive processes are realized, but it does not inform us how many offspring (small and many or large but few) are produced.

(3) The *stress* of reproduction on the adult (REs). REs should not be confused with high mortality. A high REs will make organisms less resistant to environmental challenges, but environmental factors determine whether higher mortality results or not, i.e. high REs *may* lead to high mortality. In our opinion REs can replace REp in most theoretical predictions concerning the behaviour of RE.

Empirical determination of the above parameters is tedious. REp and REa can be measured from detailed time and energy budgets. REs can be measured indirectly from evidence of the strain of reproduction on breeding adults.

Trade-off between fecundity and survival

Comparison of fecundity and survival is complicated due to the different factors contributing to them. Both of them are based on a certain design and it is only in the design that evolution can occur. As used here the term design does not bear any teleological label. Survival is a product of the design in relation to resources used and in relation to potentially fatal environmental factors (predation, diseases, competition, accidents, etc.). Fecundity, on the other hand, is a product of the design for reproduction and the amount of resources processed through that design. Within certain limits, fecundity can be increased simply by processing more resources through the existing design, but survival is no longer enhanced if more resources are processed than are demanded for performing the vital activities. Hence, fecundity may depend more directly on resources than survival.

Theories of trade-off between fecundity and survival often include the tacit assumption that the intake of resources is fixed. This would mean that when REp is high the amount of resources available for maintenance is low. But the intake of resources may be increased tremendously during the breeding season in birds. Hence high

REa or REp need not imply a decrease in the amount of resources available for adult survival.

Realization of trade-off. Reproduction may lead to the death of an adult in three different ways:

(1) Reproduction drains resources so much that REs increases to dangerously high values and a higher mortality results during the breeding season or immediately after it. This is the classic basis for trade-off in the theory of life histories. But REs can obviously be regulated by the parent. We can predict that those birds will manage better — have a greater probability of bridging gaps in time — that can limit REa when REs threatens ot increase too much, if adult survival is high and juvenile survival low. The central question thus is: what is limited when resources are in short supply, investments in reproduction or survival? If investments in reproduction are limited, high REs will not be observed to cause trade-off between fecundity and survival.

(2) Although not increasing REs to a dangerous level, REa may make adults susceptible to predation and accidents. Here the adult has less control than in the previous case. But two lines for adaptation exist: a lower REa and/or a better design for survival. Both may decrease potential fecundity.

(3) Designs demanded by high fecundity may decrease adult survival even outside the breeding season. For instance, brilliant colours, which are important in pairing, may help predators to locate such individuals more easily than birds with duller colouring.

What is the degree of freedom in evolution of fecundity and longevity? In most evolutionary analyses the tacit assumption is that organisms can adapt in various directions to an almost unlimited extent. But the whole animal kingdom manifests strong correlations between, for example, body size and other measures important in life history (see Blueweiss et al. 1978). Such correlations may indicate that there are perhaps only one or a few very general laws, which determine what can be combined in a single individual.

Longevity is a trait of life history which is strictly determined by other traits and can occur only in certain combinations. Sacher (1978) demonstrated that mammalian longevity is explained well ($r^2 = 0.85$) by the ratios brain size/body size and body temperature/metabolic rate. Further he found that the higher longevity of small birds when compared with small mammals having a corresponding cephalization coefficient and metabolic rate, agrees nicely with the mammalian equation due to the higher body temperature in birds. Sacher concluded that "the fact that mammalian longevity increases by only one path, in an invariable association with four other constitutional parameters, clearly implies that the set of genetic mechanisms regulating these constitutional characters is a tightly linked system that all mammals have in common".

Because the same conclusion is obviously also true in birds, our attempts to understand variation in life history traits may suffer severely from lack of understanding of the innate restrictions. We simply do not know how much the lower fecundity of long-lived organisms results from environmental influences and how much from internal limitations.

Stearns (1976, 1977), especially, has emphasized the role played by design constraints in hindering the arrival of predicted optimum points. We agree with this but at the same time wish to point out that design constraints may also be caused by natural selection. For instance, if a trait favouring longevity is easily evolved again and again, and if an organism with this trait less often bridges gaps in time than an alternative type with a trait favouring fecundity, design constraints which hinder the birth of long-lived types will probably evolve. Conversely, design constraints which make high fecundity impossible may evolve if individuals bearing them are more successful in bridging gaps in time than individuals with high fecundity.

As regards avian reproduction, Case (1978) called attention to the large minimum size of bird eggs as compared with the eggs of reptiles of corresponding size. He concluded that it is the development of the nervous system that determines the minimum size of bird eggs. Thus the potential number of eggs which can be formed from a certain REa is not high. Another factor contributing to the same direction is the habit of birds to lay, at the most, one egg per day. This is obviously necessary to maintain flight ability, but it also limits the size of a clutch, because the interval between the first and the last egg cannot be increased indefinitely. A factor restricting clutch size still further is the incubation capacity of the parents (e.g. Anderson 1976).

Trade-off in birds. Birds have a well-developed nervous system and high metabolic rate. Besides they are flexible in their reactions due to their high nervous development. Their mobility enables them to select and move to a suitable environment (see Wolsky & Wolsky 1976), which increases the importance of sensory abilities and nervous development. Due to such intercorrelated features birds are potentially long-lived and have a high probability of surviving till the next breeding season — adult mortality rates are seldom higher than 0.6 and may be much lower. Parental care, which is made possible by high nervous development, permits a large annual REa to be distributed over a long period so that REs does not increase to high values at any one time. Parental care also provides a highly predictable environment for the young and, consequently, these are adapted to take advantage of it. If an adult, especially a female, succumbs during the breeding attempt, the whole brood will probably perish, too. This increases the probability that the adult will die without leaving any young. Hence, in our opinion, no solutions in which REs will threaten adult survival are likely to evolve in long-lived birds. This means that trade-off between fecundity and survival due to high REs cannot be a characteristic feature in birds. This does not eliminate trade-off due to predation and accidents.

Empirical testing of trade-off between avian fecundity and survival is complicated by the phenotypic plasticity of clutch size, too. It is not too high an REa as such which leads to higher adult mortality, but more probably too high an REa under particular environmental conditions. Trade-off might be more clear in exceptional years than in normal years, but this is hard to prove. But it is clear that the longer the potential life span in adults, the more likely they will be to meet bad years, and, if they are not able to predict bad years (see Hirschfield & Tinkle 1975), the less they can afford to endanger survival.

Pitfalls in empirical testing of avian life history theory

To our knowledge the material necessary for testing general theories of life histories does not exist, since the relevant parameters (adult mortality due to breeding and the remaining adult mortality, juvenile mortality, clutch size, available resources) have not been measured in several populations in any species of birds. But certain important points have been studied, especially on two fronts: the correlation between the number of young and their survival, and the correlation between brood and clutch size and adult survival rates.

Clutch and brood sizes have been manipulated in several species of birds to find out whether they have the largest clutches and broods that they are able to rear. Results from experiments where extra young or eggs have been added to nests have suggested that natural brood sizes are the same or smaller than the most productive brood size (see Klomp 1970). The latter conclusion, especially, is uncertain due to the following potential sources of error:

(1) The fate of the young can usually be followed only up to their leaving the nest. However, clutch size-dependent differences in the mortality of the young may become evident just at the time they become independent (Haukioja 1970).

(2) The probability that an egg will produce a fledgling may depend on the order in which it is laid in the clutch (e.g. Nisbet 1973, Antikainen 1978). If an egg chosen randomly from another clutch is added to an experimental clutch, it may be more likely to produce a fledgling than a further egg laid by the female.

(3) Parents which are physiologically ready to rear their natural brood may not be able to adapt to the demands of an artificially increased brood (Wynne-Edwards 1964).

(4) If parents belonging to a potentially long-lived species cannot predict the availability of resources during the breeding season, their best tactic for bridging gaps in time is obviously to lay smaller clutches than they can rear under good conditions. If in a good year they are able to rear extra young, this is of limited value as a proof of general theories.

(5) When egg numbers are manipulated, the survival of the adults is seldom measured at the same time.

The best way to demonstrate possible trade-off between fecundity and adult survival would probably be to decrease the size of a clutch or brood, and to monitor the survival of the parents. If they survive better, this can be taken as evidence of trade-off. But even such a result must be inspected with caution. Kluyver (1966) artificially halved the production of young by the Great Tit *Parus major*, which improved both adult survival and juvenile survival. But the goal of the study was to examine regulation of density and hence the whole population was treated. Thus the decisive factor may have been decrease in density rather than trade-off between fecundity and survival. A more informative test would be to manipulate a small proportion of broods, so that the total density of the population was not significantly affected. However, one difficulty remains: if birds with low reproductive success are more apt to change nesting sites, their movements may mask the trade-off.

It is difficult to obtain reliable data on survival rates e.g. for correlation analyses. Potential life spans can, at least in theory, be determined by rearing birds in captivity under optimal conditions. Actual survival rates, reflecting the influence of environmental factors, are easier to obtain. Ringing data provide abundant material, but must be used with caution. Common sources of error are loss of rings in older age classes due to ring metal wearing away, and bias introduced by greater vulnerability of young birds to hunting by man (see Haukioja 1969). More difficulties are encountered when ringing files are used to examine adult mortality rates in relation to breeding. To us it seems useless to compare ringing recoveries during and outside breeding seasons (Ricklefs 1977), because recovery rates may be different at different times of the year, and for other reasons than breeding.

Birds are excellent objects for studying the heritability of clutch size in natural environments. However, besides heritability, phenotypic plasticity is also of the utmost importance, and it can be revealed by detailed studies of individually marked birds. Actually what should be known is heritability of susceptibility to environmentally induced variation in clutch size. Unfortunately, the chances of obtaining such material are very slight.

Discussion

The original theory of evolution by natural selection contains nothing which disagrees with evolution of low reproductive rates, longevity or iteroparity. The obscurity surrounding the question comes largely from traditions in other fields of biology, which have produced models valid in their original fields but not always applicable in evolutionary ecology.

Examples of trade-off between fecundity and survival are surprisingly scanty in the literature (see Stearns 1976, Calow 1977). Although such trade-off is the most probable reason for the evolution of low reproductive rates and for the failure of more fecund types to replace the present ones, we are somewhat sceptical about the possibility of verifying this conclusion empirically, especially among potentially long-lived species of birds. If adults do not invest in reproduction more than remains after their needs for maintenance have been satisfied, trade-off between fecundity and survival is not easy to demonstrate. Potentially short-lived species are obviously more likely to give positive results. A further complication is that parents which are able to rear the largest broods, for example experienced ones, are the most likely to do so, and the survival of such individuals need not to be threatened at all.

As regards the classic explanations of low reproductive rates offered by Lack and Wynn-Edwards, we must point out that both concentrated on one side of the coin. Lack's explanation has proved to be very successful for clutch sizes in populations following the same design for longevity, but in our opinion he overemphasized the role of fecundity and basically had a narrower view of the whole problem than Wynne-Edwards. Unfortunately, however, the latter applied selection above the individual as an explanation. We do not see any difficulties in explaining the same traits — e.g. those preventing overexploitation — on the basis of the benefit of the individual. The measure of success, however, should not be increased frequency as such but continuity of generations. At the same time we can discard the unrealistic conditions for the evolution of low reproductive rates demanded by group selection: existence of small semi-isolated populations which become extinct after destroying their resources through overpopulation. The same end result can be achieved if longevity is a better tactic in bridging gaps in time than fecundity and if the goal of organisms is simply to bridge gaps in time.

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Selostus: **Lintujen pesyekoon ja eliniän välisestä suhteesta**

Negatiivinen korrelaatio lintujen pesyekoon ja eliniän välillä selitetään tavallisesti siten, että linnun keskittäessä resurssejaan lisääntymistoimintoihin, niitä jää vähemmän aikuisen omaan ylläpitoon. Näin voidaan traditionaalisen kelpoisuuskäsitteen (fitness) pohjalta selittää, miksi linnuilla tavataan myös erittäin pieniä pesyekokoja. Kuitenkaan kelpoisuus evolutiivisen menestyksen mittana ei kirjoittajien käsityksen mukaan kerro koko totuutta, kun tarkastellaan miksi tietyt elinkiertojen piirteet ovat kehittyneet suhteessa tiettyihin ekologisiin ympäristötekijöihin. Kelpoisuuden mittana evolutiivisessa ekologiassa käytetään usein suoraviivaisesti populaatiogenetiikasta ja demografiasta tuttuja populaation kasvunopeuden kuvaajia, esimerkiksi populaation sisäistä kasvunopeutta, johon lisääntymiskapasiteetti luonnollisesti vaikuttaa nopeuttavasti. Pitkän eliniän merkityksen ymmärtäminen tulee kuitenkin vaikeaksi, koska se ei juuri nosta populaation sisäistä kasvunopeutta. Kirjoitus rakentuu käsityksen varaan, jonka mukaan organismin menetyksen mitta tietyllä hetkellä on vain sen olemassaolo. Ts. kaikki sellaiset ominaisuudet ovat edullisia, jotka yksilöiden kohtaamissa ympäristötilanteissa minimoivat sukupolvien ketjun katkeamistodennäköisyyttä. Korkea populaation sisäinen kasvunopeus osoittaa yhden taktiikan ko. ongelman ratkaisemiseksi, pitkä elinikä toisen. Tältä pohjalta voidaan pitkäikäisyyttä pitää yhtä taseveroisena kelpoisuuden osatekijänä kuin lisääntymistehokkuuttakin.

Alhaisen lisääntymiskapasiteetin kehittyminen ei siis sinänsä ole ongelmallista, ongelmat on luotu lähinnä biologian teoreettisten mallien kehittelyn yhteydessä, sovellettaessa muiden alojen teorioita suoraan ekologisiin probleemoihin. Luonnollisesti syyt ja ympäristötekijät, jotka ovat johtaneet alhaisten pesyekokojen kehittymiseen ovat paljolti selvittämättä.

Ornitologian alalta ei vielä mistään lintulajista ole selvitetty useasta eri populaatiosta kaikkia niitä parametreja (esim. pesyekoko, sen vaihtelu, nuorten kuolevuus, pesinnästä johtuva aikuiskuolevuus, muu aikuiskuolevuus, saatavilla olevat resurssit), jotka olisi tunnettava yleisten elinkiertoteorioiden testaamiseksi.

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