

Presidential Address

THE EVOLUTION OF REPRODUCTIVE RATES: ARE THERE NO RULES?

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During the past 20 years animal ecologists have spent much time trying to understand population processes, the practical implications of which are vastly more important for our survival on earth than are all our extravagant efforts to leave it with a safe return ticket. In this period a handful of authoritative books has appeared, each to do with animal populations but having little else in common (Andrewartha and Birch 1954; Lack 1954, 1966; Wynne-Edwards 1962; Elton 1966). A layman reading these would be quite justified in concluding that "There appear to be no rules". Indeed, this phrase seems to reflect Elton's attitude: "The whole field of population control in nature and theories about how it works has got into a rather peculiar state where a number of strongly held views exist that are at first sight incompatible with one another. . . . For, if one fact is certain, it is that somewhere at some time in some species every one of these processes will be found acting as the chief or only limit to numbers. Similarly, somewhere at some time in some species, almost every conceivable combination of these factors will be operating in complex interaction" (Elton 1966, pp. 380-1).

I believe this is an over-tolerant attitude to adopt towards the two contrasting views on the evolution of reproductive rates, which is, after all, part and parcel of population control.

THE CONFLICT

In New Zealand it is easier than elsewhere to forget that, in the short term, relative stability is the normal state for most populations. Even when they are changing quite markedly, the magnitude of the change from one year to the next is usually small compared with what is theoretically possible from the species' intrinsic rate of increase. Although stability is so commonplace, we cannot explain how or why it prevails, and we tend to concentrate unduly on changing populations, which are the exceptions.

Stability implies that rates of mortality and of reproduction are equal; but there is disagreement about which is the main variable, and how this

balance comes about. On the one hand, Lack (1966, p. 280) maintains that "the reproductive rates of birds have been evolved through natural selection and so are, in general, as rapid as the environment and the birds' capacities allow" and that ". . . mortality rates balance reproductive rates because bird populations are controlled by density-dependent mortality". Wynne-Edwards (1962), on the other hand, considers that reproductive rates are restrained so as to compensate nicely for mortality, and that this must have come about by group selection.

FOR NATURAL SELECTION

Lack's argument is clear. Since reproductive rates are a product of natural selection which favours individual genotypes, animals are selectively obliged to contribute as much as they individually can to the immediately succeeding generations. Thus, the most frequent family-size in nature will be the most productive one; and extra-large families will be so penalised that they give rise to fewer survivors, not more, than do families of average size. (See also Lack 1967, for the significance of clutch-size in waterfowl.)

TABLE 1. *Breeding success of swifts (Apus apus) at Oxford, related to brood-size. (After Perrins 1964.)*

Brood size	No. of broods studied	Percent young fledged	No. of fledged young per brood
2	72	96.50	1.93
3	20	85.00	2.55
4	16	43.75	1.75

NOTE. Broods of 1 are omitted because they were almost always successful. Broods of 4 were made up by adding a small young from another nest, though elsewhere in their range swifts occasionally lay clutches of 4 eggs.

In birds, this specially heavy mortality in large families may happen to the embryos, the nestlings, or to the fledged young and juveniles; though it is easier to measure when it happens in the nest than when it happens later, as Lack found with swifts (*Apus apus*) breeding in the University Museum tower at Oxford. In Table 1 several

years' records are pooled to show the crucial point that extra-large broods of four young apiece each gave rise to fewer fledged young than did the commoner broods of two or three young. Admittedly, on average, broods of three each produced more fledged young than did the commoner broods of two; but most clutches of three were laid in fine, warm summers, with good feeding conditions. There may also have been additional mortality to broods of above average size after the young left the nest, but this was not measured.

Large families of some other species are penalised mainly after the young leave the nest, though the predisposing causes of this mortality are present beforehand (Lack, Gibb and Owen 1957). Using mechanical counters, I found, as shown in Table 2, that nestling great tits (*Parus major*) in large families were each fed less often than were those in small families, and that they left the nest under-weight. Since then, intensive trapping of young previously banded in the nest has disclosed relatively fewer survivors from the large families than from the small ones (Table 3).

TABLE 2. *Feeding visits and nestling weights of great tits (Parus major) according to brood-size, at Oxford. (After Gibb 1950, 1955 and unpubl.)*

Brood size	No. of broods	Daily feeds per nestling	No. of broods weighed	Nestling weight on 15th day
Small	—	—	9	19.6 g
Medium	21	65	129	18.5 g
Large	16	54	10	16.9 g

TABLE 3. *Survival of young great tits (Parus major) after leaving the nest, related to brood-size; as determined by trapping at Oxford. (After Perrins 1965.)*

Brood size	No. of broods studied	Percent of young recovered per brood	Number of young recovered per brood
Small	180	15.5	0.63
Medium	500	14.9	1.25
Large	116	10.1	1.33

Large families of tits were additionally penalised in the nest because, being under-fed, they called very loudly for food; and presumably as a result (see Table 4), they were twice as likely to be found and killed by weasels than were the better fed and less rowdy, smaller families. Weasels sometimes killed the parent birds at these nests as well.

TABLE 4. *Predation by weasels on broods of great tits (Parus major) related to brood-size at Oxford. (After Perrins 1965.)*

Brood size	Number of broods studied	Percent of broods killed by weasels
Small	195	10.3
Medium	330	9.1
Large	186	20.4

There is thus good evidence for Lack's hypothesis, founded on natural selection, that the most frequently occurring family size is indeed the most productive. Not every situation is immediately explicable, of course: North Atlantic gannets (*Sula bassana*) apparently can raise twins as successfully as the single chick that is their rule; whereas white boobies (*Sula dactylatra*) in the Galapagos Islands invariably rear just one of the two chicks that usually hatch (Nelson 1966). Such apparent exceptions may seem to support Elton's (1966) view quoted in the opening paragraph, but much more contrary evidence than this would be needed to refute Lack's hypothesis.

FOR, AND AGAINST, GROUP SELECTION

The alternative notion, that reproductive rates are adjusted to compensate for mortality, seemed to be dying until Wynne-Edwards (1962) gave it a new look and an air of authority that it previously lacked.

Wynne-Edwards was specially impressed with the low reproductive rate of sea-birds, which he regarded as a "prudential restraint" evolved by group selection to prevent "over-fishing". Whilst agreeing with Lack that the food supply sets an upper limit to population density, Wynne-Edwards believed (p. 11) that "... population density must at all costs be prevented from rising to the level where food shortage begins to take a toll of the numbers"; and hence, as a rule, that "Food may be the *ultimate* factor, but it cannot be invoked as the *proximate* agent in chopping the numbers, without disastrous consequences" (p. 11). Instead of competing directly for food, Wynne-Edwards maintains that most animals compete, ceremonially, for space; and (p. 12), "... once they have established their claim to the ground they can do the actual food-getting in perfect

peace and freedom, entirely without interference from rivals". Finally (p. 11), "Most important of all, we shall find that self-limiting homeostatic methods of density regulation are in practically universal operation, not only in experiments, but under 'wild' conditions also."

These are sweeping assertions, to be challenged on three counts: (a) that group selection is not a proven force; (b) that reproductive rates are not restrained; and (c) that animals do not feed in perfect peace and freedom, nor is "over-fishing" always prevented.

On the first count, the real objection to Wynne-Edwards' hypothesis is not just that it relies on the unproven force of group selection; but much more importantly that this postulated group selection is both opposed to, and incompatible with, the natural selection of genotypes leaving the most survivors. "There is currently no mechanism known whereby something can be evolved for the good of the species unless it also benefits the individuals concerned" (Orians 1962); and with this I entirely agree.

On the second count, I have already shown that tits, like swifts, are raising as many young as they profitably can. If they try to raise more, the survival of the whole family is endangered; so that on average fewer, not more, young actually survive. Even if reproductive rates were restrained, it is very dubious if population density would be affected.

On the third count, I find Wynne-Edwards' views at variance with my own experience. Whether or not food shortage is more or less directly responsible for "chopping the numbers" of animals, and whether or not animals forage "in perfect peace and freedom, entirely without interference from rivals", are questions to be decided from field observation. My experience comes mainly from about ten years' study of several species of tits (Paridae) in broadleaved and coniferous woodland in Britain, followed by a similar period studying wild rabbits (*Oryctolagus cuniculus*) here in New Zealand. Are these animals really so insulated from the effects of food shortage?

In the breeding season and in mid-winter tits spend up to about 90% of the day foraging, which is much more than at other seasons. In mixed flocks in winter, inter- and intra-specific attacks among them become increasingly common as the days shorten, and almost all of these are attacks

to obtain food. Coal tits (*Parus ater*), the smallest and most submissive species in the flocks, are robbed of food on the average about 20 times an hour, and submissive individuals more often still (Gibb 1954). In 20-year-old pine plantations each bird visits more than 1,000 trees daily in its search for food in winter and must find an insect of average size about every $2\frac{1}{2}$ seconds of the day in order to obtain enough calories for maintenance. The dry weight of insects and spiders in the pine foliage fell at one time in winter to about 200 g. per hectare, yet the tits could find and eat up to 70% of the stocks of certain preferred foods hidden in the vast mass of foliage (Gibb 1958, 1960, 1966).

The only other bird I have known so well was a rock pipit (*Anthus spinoletta*), living on a rocky shore in Cornwall (Gibb 1956) and vigorously defending its individual territory in which it fed in winter. Others, possibly first-year birds, were in free-ranging flocks. The amount of food available in the territory was apt to vary greatly with every tide. When many isopods (mostly *Idotea* spp.), a prized food, were stranded in the pipit's territory, it had to repel a poacher on average 17 (max. 45) times an hour all through the day. When, more often, there was little or no stranded food, it resorted to less desirable, reserve foods, and had to defend its then less attractive territory only about twice an hour. Under these circumstances it had to spend $8\frac{1}{4}$ hours of the 9-hour day (cf. $6\frac{1}{2}$ hours with much food available) collecting its daily requirement of roughly 14,000 *Littorina neritoides* and 4,000 chironomid larvae. Demonstrably, since the bird defaecated about 60% of the 30 odd kcals. ingested, this was an unsatisfactory diet; and the pipit was often distinctly short of food.

Turning briefly to mammals; for about ten years we watched a population of rabbits living more or less natural lives, except that they were confined in a 21-acre enclosure. They were given no extra food, nor did we interfere in other ways with their numbers (Gibb and McIlwaine in prep.).

Rabbits are not renowned for exercising "prudential restraint" on their reproduction; theirs is a "boom and bust" economy, a predictable succession of the "disastrous consequences" abhorred by Wynne-Edwards. Time and again we saw them go on breeding until their young starved, giving birth to litter after litter so long as the pasture could stand it — but without regard to its future productivity.

Inevitably, this gay abandon was followed by a retrenchment in numbers in late summer when the pasture dried out, and again in mid-winter when the grass stopped growing. Food shortage slashed the numbers of rabbits drastically, and the pasture was kept permanently depleted. This is commonplace with rabbits, of course, and not just a consequence of having the population enclosed. When pinched for food, as Table 5 shows, these rabbits fed actively almost all night; and instead of resting by day in the safety of cover, as at low density with plenty of food, they stayed dispersed on the feeding grounds, alternately resting and feeding and vulnerable to predation.

TABLE 5. *Time budget and dispersal from warrens of rabbits (Oryctolagus cuniculus) during 12-hour day in winter, according to density; New Zealand. (After Gibb and McIlwaine, in prep.)*

Density	Time spent by day: hours-mins.		
	Above ground	Dispersed from warrens	feeding
Low	5-39'	3-00'	2-02'
High	10-42'	5-46'	4-34'

To summarise, I fail to see either these birds or rabbits exercising those "prudential restraints" on their reproduction that might have allowed them to feed "in perfect peace and freedom, entirely without interference from rivals"; nor do I find that "self-limiting homeostatic methods of density regulation are in practically universal operation, not only in experiments, but under 'wild' conditions also" (Wynne-Edwards 1962, pp. 11-12). Instead, as a rule, the supply of food immediately to hand is inclined to set the pace for reproduction and for mortality. "What I have seen of Nature's way, in this respect, is the ruthless way, little resembling any mysteriously benign process of falling birth rates" (Errington 1957).

FAMILY-SIZE RELATED TO MORTALITY

Moreau (1944) and then Lack (1947-48) pointed out that as a rule, the clutch-size of birds of the same or allied species increases with increasing latitude; and Lack attributed this to the increasing hours of daylight, from the tropics towards the poles, which allow diurnal birds to feed larger families. This explanation is certainly not complete, "... since in various passerine

families the temperate-zone species lay clutches of twice the size of their tropical congeners" (Lack and Moreau 1965; see also Cody 1966).

Lord (1960) then discovered a similar relationship between litter-size and latitude among North American mammals, which held for most non-hibernating and prey species but not for hibernators and predators. We may notice in passing that, within New Zealand, hares (*Lepus europaeus*) have larger litters in the south than in the north (Flux 1967), and that lambing percentages of sheep are highest in the south of the country.

Lord discounted Lack's explanation in terms of day-length, because many of the mammals are nocturnal. Instead, he suggested that large litters are associated with heavy mortality; not in order to compensate for it, but because populations subjected to heavy mortality are further below the carrying capacity of their environment at next breeding than are those with lighter mortality, and so are free to raise larger families. Understandably in this context the numbers of non-hibernating mammals and of prey species may be more directly affected by reduced primary production in winter than are those of hibernators and predators. Supporting Lord's suggestion is the fact that birds and mammals are known to raise larger families in years of low than of high density, other things being equal (Kluijver 1951, Lack 1958, and references in Lord 1960).

Ashmole (1961) independently proposed a similar explanation for the relatively small clutch-size of tropical birds. Lack and Moreau (1965) tested this within tropical Africa by comparing the clutch-sizes of passerine birds living at similar latitudes, (a) in equable evergreen forest, and (b) in the seasonally more variable savanna; it being supposed that mortality between breeding seasons might be heavier in the savanna, thereby allowing the birds to raise larger families. Only those bird families with at least five species living in each of the two habitats were included. Though the average differences were small, the savanna species did indeed lay larger clutches than did the forest species. This adds weight to Ashmole's suggestion, in effect that the bigger the reduction in the food supply—and hence the heavier the mortality between one breeding season and the next, the larger the families that can be raised.

I now suggest that the small family-size of sea-birds, which first attracted Wynne-Edwards, as well as of birds and mammals generally in the tropics, may all be explicable on this same argu-

ment. For sea-birds, like tropical birds, also live in a relatively equable environment with a rather steady food supply through the year — though this is sometimes contrived by long distance migration, as in the muttonbirds *Puffinus tenuirostris* studied by Serventy (1953). The constancy of the marine as opposed to the terrestrial environment for birds is reflected in the regularity of laying dates exhibited by some sea-birds. For example, in Australia 80% of the muttonbirds laid between 23 and 28 November each year (Serventy 1953); the average laying date of yellow-eyed penguins (*Megadyptes antipodes*) in Otago, New Zealand, varied between 21 and 30 September during Richdale's (1957) 18-year study; and at a north of England colony of kittiwakes (*Rissa tridactyla*) the average laying date fell between 15 and 22 May in the years 1954–63 (J. C. Coulson quoted by Lack 1966).

Thus, sea-birds may have low reproductive rates partly because their relatively constant food supply may keep them permanently close to the carrying capacity of their environment, and partly because feeding may be specially difficult for them during the breeding season (the only time of year when they are tied to a land base). Their low mortality is well established: for example, royal albatrosses (*Diomedea epomophora*) nesting in Otago have a life expectancy estimated in excess of 30 years (Lack 1954); and the very long round trips undertaken by many petrels and shearwaters to procure food for their single young and the prolonged fasting of breeding penguins (e.g., Stonehouse 1952), illustrate the peculiar difficulties confronting sea-birds during the breeding season.

Recently, in an interesting paper, Cody (1966) has tried to rationalise the selective forces influencing the clutch-size of birds, and has developed further the ideas put forward earlier by Lord and Ashmole, supported here. Cody makes the points that the strength of selection for maximising reproductive rates will vary inversely with the stability of the environment; and that under equable conditions, as in the tropics, birds may devote less energy to rearing as many young as they can feed (because the population will be already close to carrying capacity) and more energy or attention to, for instance, avoiding predators. If this is so, Skutch (1949) may be, in a sense, right in doubting whether tropical land-birds rear as many young as they can nourish. This does not invalidate Lack's main hypothesis that reproductive rates are maximal, but shifts the emphasis from food shortage

to predation as perhaps the more important limiting factor. Predation on nests is much heavier in tropical than in temperate regions (see references in Cody 1966), which may be another reason why tropical birds lay small clutches (cf. Table 4, above).

Unfortunately, as an example of the small clutches supposedly laid by birds on oceanic islands, "well known for the great climatic stability they enjoy", Cody tabulates the mainland and island clutch-sizes of New Zealand birds, as documented by Oliver (1955). New Zealand ornithologists will appreciate that this is a perilous comparison, notwithstanding Cody's assertion that the differences revealed are statistically significant.

In this thumb-nail sketch of the evolution of reproductive rates, I have paid unavoidably scant attention to the very wide range of adaptive, phenotypic variations which are widespread and which at once confuse and enlighten the main issues. Thus, tits lay larger clutches in early than in late springs, in first than in second clutches, when they are more than one year old than at first breeding, in broadleaved than in coniferous woodland, and even in certain parts of a wood than in others; and kittiwakes lay earlier and larger clutches (and rear more young) when in established pairs than they do for a couple of years after a change of mate.

We have in New Zealand unique opportunities for research in evolutionary ecology — in our forests, on the islands, and at sea. Yet, with a handful of notable exceptions, virtually nothing is known of the comparative ecology (or ethology) of, for instance, our array of shags, penguins, and petrels. Are the stocks of foods available to insectivorous birds in the rain forests really so limited as the sparse populations of birds suggest, and how do both vary seasonally compared with tropical and temperate forests? And finally, among the introduced birds too, there are tremendous opportunities for studying the machinery of evolution working to accommodate them to new conditions, opportunities that are ours for the taking.

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