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# Food Supply and the Annual Timing of Avian Reproduction

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## Abstract

Avian breeding generally coincides with seasonal peaks in food supply, but detailed studies suggest that birds may breed on either the rising or the declining slopes of food availability. Nonetheless, a seasonal decline in clutch size appears general for single-brooded altricial species, except those laying only one or two eggs. Surplus-feeding experiments suggest that food in spring affects laying date and thereby clutch size in those species in which there is a decline. Survival indices for offspring, both in the nest and after fledging, generally decline with the progress of season. These effects of date of birth can be summarized in the reproductive value of eggs as a function of date of laying. It is shown that with constraints on parental investment, optimal clutch sizes should decline with season when egg reproductive value declines, independent of assumptions on the nature of the constraining and proximate control mechanisms. Experimental approaches outlined to evaluate the theory include brood-size reduction, selection experiments, and release of birds reared in captivity on different dates.

## Introduction

Food availability is the principal ultimate factor that has shaped the timing of breeding seasons in birds. Lack's (1950, 1968) theory postulated that the timing of breeding has a genetic basis, and that seasonal variations in food supply select genotypes of birds laying eggs so that the nestling stage coincides with the peak in food availability. On average, both early- and late-laying pairs would leave fewer offspring than birds laying at the average date. This theory received its main support from interspecific comparison of food sources and laying dates. Population studies subsequently revealed that clutches laid at the average time yielded fewer surviving offspring than the earliest clutches (Perrins 1965, 1966; Cavé 1968). This result implied that the majority of the population behaves suboptimally, but was reconciled with the optimal-timing theory by the sugges-

tion that energy requirements for egg formation prevent most female birds from laying at the optimal date (Perrins 1965, 1970; Lack 1968). This modification of the theory thus predicts that most young are in the nest *after*, rather than *during*, the food peak.

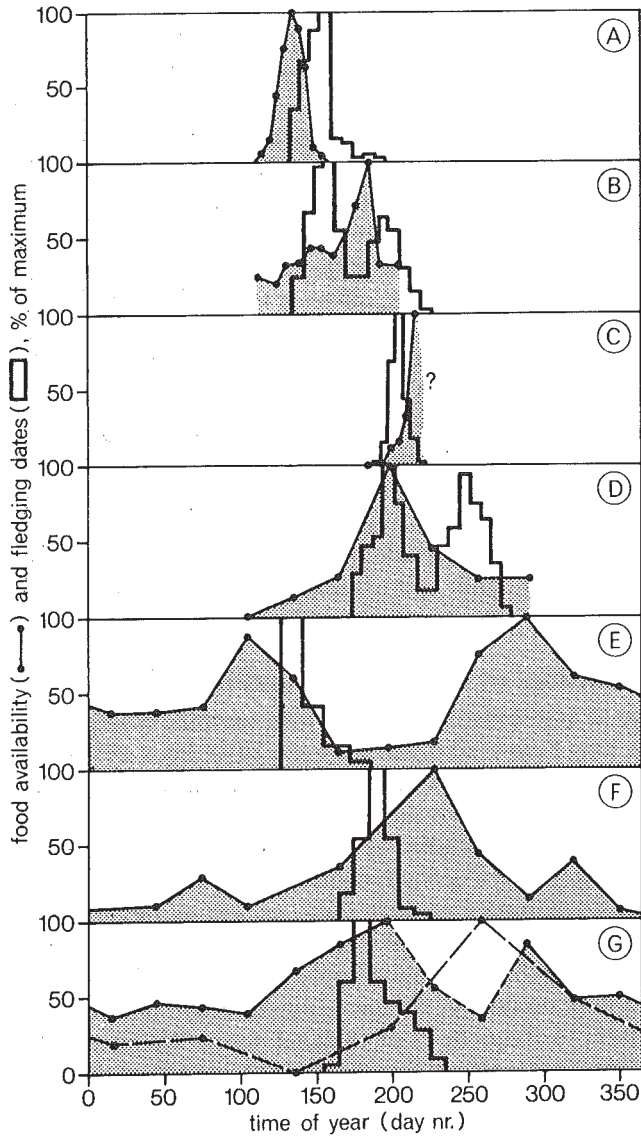
The predicted downward trend in food availability for the nestlings from the earliest to the latest broods was consistent with the well-known seasonal decline in clutch size, as this would be predicted on the basis of Lack's other theory of adaptation of clutch size to the number of nestlings that parents can maximally raise. However, the egg-laying constraint gives rise to a theoretical dilemma. It moves the role of food from the ultimate to the proximate causation of reproductive timing. It is further inconsistent with a primarily genetic determination of laying date, as genotypes with average or late laying dates are continuously at a selective disadvantage. Finally, the progressive deterioration of food supply remains to be established as a general phenomenon.

The work of Lack and Perrins has inspired many recent studies, and a review of the evidence pertaining to the main tenets of their theory is now appropriate. We shall consider (a) phase relationships between seasonal cycles in food availability and breeding; (b) seasonal variations in clutch size; (c) experimental evidence for a proximate role of food; and (d) seasonal variations in survival of eggs.

### Phase Relationships of Food Supply and Breeding

The general coincidence of bird breeding seasons with seasonal highs in their specific food supply has long been established (Moreau 1950; Lack 1950). Only a few studies provide answers to specific questions as to whether birds breed on the upward slope, at the peak, or on the downward slope of food supply. Some of the most accurate data are compiled in Fig. 1. The nine species involved are not by any means sufficient for a definitive answer, but may serve to illustrate the problems involved in obtaining such data, as well as the variability in reproductive adjustment to food. We have expressed the original data on number of birds breeding, as well as on food-supply indices, in percentages of the maximum values. Where necessary, we have transformed the frequencies of laying or hatching dates to frequencies of fledging dates. We have chosen this point because fledging is nearly always somewhere in the middle of the period in which parents feed their brood, including the often neglected but intensive postfledging period of parental care.

The first problem with such data is that they deal primarily with indices of food abundance rather than food availability. For instance, caterpillar frass fall (Fig. 1A), as measured in the pioneering studies of Gibb (1950), reflects the abundance of the primary food source for nestling Great Tits (*Parus major*) and Blue Tits (*Parus caeruleus*) in deciduous woods in England. It is unknown how the growth of caterpillars and their changing detectability with the spring deployment of leaves modify the seasonal curve of availability (i.e., of food biomass obtained per unit of effort by tit parents). The same problem is inherent in studies on the Buzzard (*Buteo buteo*) (Fig. 1F) by Mebs (1964), who painstakingly established Common Vole (*Microtus arvalis*) densities by excavating their



**Figure 1.** Seasonal variation in reproduction and food abundance. Histograms: frequency of fledging dates in percentage of the annual maximum. Shaded areas: food in percentage of the annual maximum. (A) Great Tit and Blue Tit; caterpillar frass fall (Gibb 1950). (B) Coal Tit (Lack 1950); mg caterpillars/m<sup>2</sup> (Gibb and Betts 1962). (C) Snow Bunting and Lapland Longspur; chironomid midges (Hussell 1972). (D) House Martin; aerial insects (Bryant 1975). (E) Rook, Cambridgeshire (Murton and Westwood 1977); foraging yield (cal·min<sup>-1</sup>), Scotland (Feare *et al.* 1974). (F) Buzzard; Common Vole density (Mebs 1964). (G) Eurasian Kestrel; foraging yield (voles per hour). Dashed line: vole trapping index (D. Masman *et al.*, unpublished data).

burrow systems. This estimate, although far better than trapping indices, does not consider seasonal variations in vole surface activity in daytime (Hoogenboom *et al.* 1984) and changing detectability of active prey due to vegetation cover. Such problems are overcome when the food biomass obtained per unit of foraging time is directly established from behavioral observations. We know of only two such studies. In one (Fig. 1D), food availability to foraging Rooks (*Corvus frugilegus*) was measured in Scotland in  $J \cdot \text{min}^{-1}$  year-round (Feare *et al.* 1974). Unfortunately, laying dates for the Rook population concerned have not been published, and data for England (Cambridgeshire) have been entered for comparison in Fig. 1E. The other study gives data on Eurasian Kestrel (*Falco tinnunculus*) flight-hunting yield collected by our group (Fig. 1G). Here the problem is that hunting yield is reduced by molt, and the yield data for August and September are therefore not strictly comparable with those of the rest of the year—although the curve of Eurasian Kestrel hunting yield (voles per hour flight-hunt) is more realistic than that of the trapping index (voles per 1500 trapnights). Further problems in the interpretation arise when there are two peaks either in breeding (Fig. 1D) or in food supply (Fig. 1E). Although finer analysis solving the methodological problems might later alter the conclusion, at present we conclude from Fig. 1 that the majority of broods may fledge either during the increase phase (Coal Tit (*Parus ater*), Lapland Longspur (*Calcarius lapponicus*), Snow Bunting (*Plectrophenax nivalis*), Buzzard, Eurasian Kestrel) or on the downward slope of food supply (Great Tit, Blue Tit, House Martin (*Delichon urbica*), Rook).

### Seasonal Variation in Clutch Size

Variations in clutch size with date of laying have been documented for numerous altricial bird species. The trends have been summarized in a review by Klomp (1970), whose main conclusions are still valid. The majority of single-brooded species show a monotonic decline in clutch size, such that the earliest breeders produce the largest clutches. Double- and triple-brooded species often have an initial shallow rise of clutch size, followed by a decline. Few species in both the single- and multiple-brooded group have a seasonally constant clutch size, especially those with small clutches (e.g., Procellariiformes, Columbiformes). Klomp (1970) stated that "nothing is known about the proximate factors determining the seasonal trends in clutch size" and that "the adaptive significance of the seasonal decline of clutch size is still very vague . . . , and the question may be raised as to whether the downward trend of the clutch cannot be due to a proximate effect without having any ultimate adaptive significance."

In the present context, it is important to note that the seasonal decline in clutch size holds for all of the nine species illustrated in Fig. 1: for these species we know that laying dates are all distributed on the upward slope of food supply, whereas fledging dates may be centered before, at, or after the annual food peak. The paradoxical decline in clutch or brood size coinciding as it often does with a rising food supply poses a problem in devising an explanation either in proximate terms or in an ultimate sense.



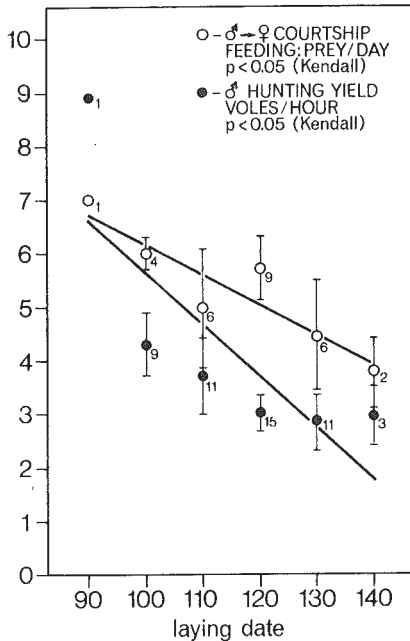
This paradox, which has puzzled many ornithologists, calls for a general explanation. In fact, the decline is not restricted to birds, but occurs also in mammals (Myers and Poole 1962; Kott and Robinson 1963), reptiles (Nussbaum 1981), and invertebrates (Turnbull 1973). Perrins (1970) explained the seasonal decline by assuming that the food supply surpasses a threshold, required to initiate laying, at different times of year for different females. The late pairs have their broods in the nest at a time when food is declining again, and the reduced clutch size is an adaptation to this deteriorating food supply. Perrins' explanation thus focused on species for which food declines during the nestling period.

Toft *et al.* (1984) emphasized the genotypic rather than phenotypic contributions to laying date/clutch size variations. They suggested that early and late reproducers are extremes of a continuum of reproductive strategies, late birds being those whose low annual reproductive output is compensated by a longer life expectation. Higher survival rates of late breeders, however, remain to be documented. Evidence for a strong genetic basis of variations in laying date is based on parent-offspring correlations in laying date and related variables in the Great Tit (Perrins and Jones 1974; van Noordwijk *et al.* 1981). The interpretation of such correlations as "heritability" of the traits underestimates the phenotypic effect which birth date of a young bird may have on its own date of reproducing the next year. In any breeding season, a recruit born early in the previous year has had more time to develop foraging skills and compete for territorial establishment than one born late. The early recruit might be expected to breed earlier than the late-born conspecific, independent of a genetic component to reproductive decisions.

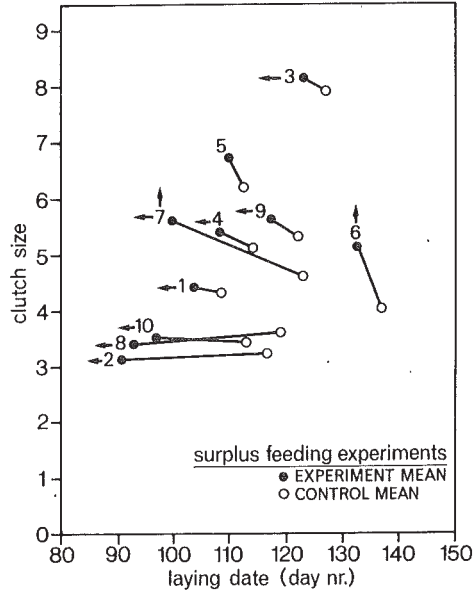
We have emphasized elsewhere (Drent and Daan 1980) the phenotypic adjustment of laying date and clutch size to food conditions as an optimization problem with different solutions for individuals in a population. For a generalization of this approach, it is necessary to consider the evidence for effects of food supply and the seasonal variation in the prospects of eggs laid.

### **Proximate Effects of Food in Reproductive Timing**

Variations in food abundance have often been found to be correlated with reproductive behavior of altricial birds. The general trend is one of earlier and larger clutches in better food conditions. This holds both for comparisons between years and between habitats (e.g., Klomp 1970) and for interindividual comparisons. The latter have been less frequently documented, and Fig. 2 shows our data for the hunting yield of male Eurasian Kestrels during courtship feeding and the frequency of prey transfer to the female. Both are negatively correlated with the date on which the female lays her first egg. The negative seasonal trend is solely due to interindividual differences. In individual male Eurasian Kestrels, observed repeatedly, hunting yield *increased* significantly from courtship to nestling phase. In accordance with the seasonal trend in Fig. 2, male hunting yield and rate of prey delivery are positively correlated with female clutch size (S. Daan *et al.*, unpublished data). It is important to note that early-laying females received more food and ate more per day during courtship than late-



**Figure 2.** Hunting yield (Common Voles obtained per hour of flight-hunt) of male Eurasian Kestrels and delivery rate (voles transferred to female per day) in Eurasian Kestrel pairs in The Netherlands during courtship phase as a function of laying date.



**Figure 3.** Mean clutch size and laying date in control pairs and pairs receiving additional food. (1) Carrion Crow (*Corvus corone*) (Yom-Tov 1974). (2) Song Sparrow (*Melospiza melodia*) (Smith *et al.* 1980). (3) Willow Tit (*Parus montanus*) (Von Brömssen and Jansson 1980). (4) Crested Tit (*Parus cristatus*) (Von Brömssen and Jansson 1980). (5) Magpie (*Pica pica*) (Högstedt 1981). (6) Sparrowhawk (Newton and Marquiss 1981). (7) Eurasian Kestrel (Dijkstra *et al.* 1982). (8) Red-winged Blackbird (*Agelaius phoeniceus*) (Ewald and Rohwer 1982). (9) European Starling (Karlsson 1983). (10) Dunnock (Davies and Lundberg 1985). Arrows show directions of statistically significant effects.

laying birds. If there is a nutritional threshold for breeding, it is apparently lower in the late-laying females.

Correlative indications for a causal role of food in reproductive timing have been supported by a number of surplus-feeding experiments in the past decade. The evidence is summarized in Fig. 3. At least eight species—in addition to Källander's (1974) initial demonstration of a food effect in the Great Tit—have shown significantly earlier breeding in experimentally fed birds than in nonfed controls. Effects on clutch size were either absent (three multiple-brooded species) or positive (Sparrowhawk (*Accipiter nisus*), Eurasian Kestrel); most species showed insignificant increases in clutch size. The experimental

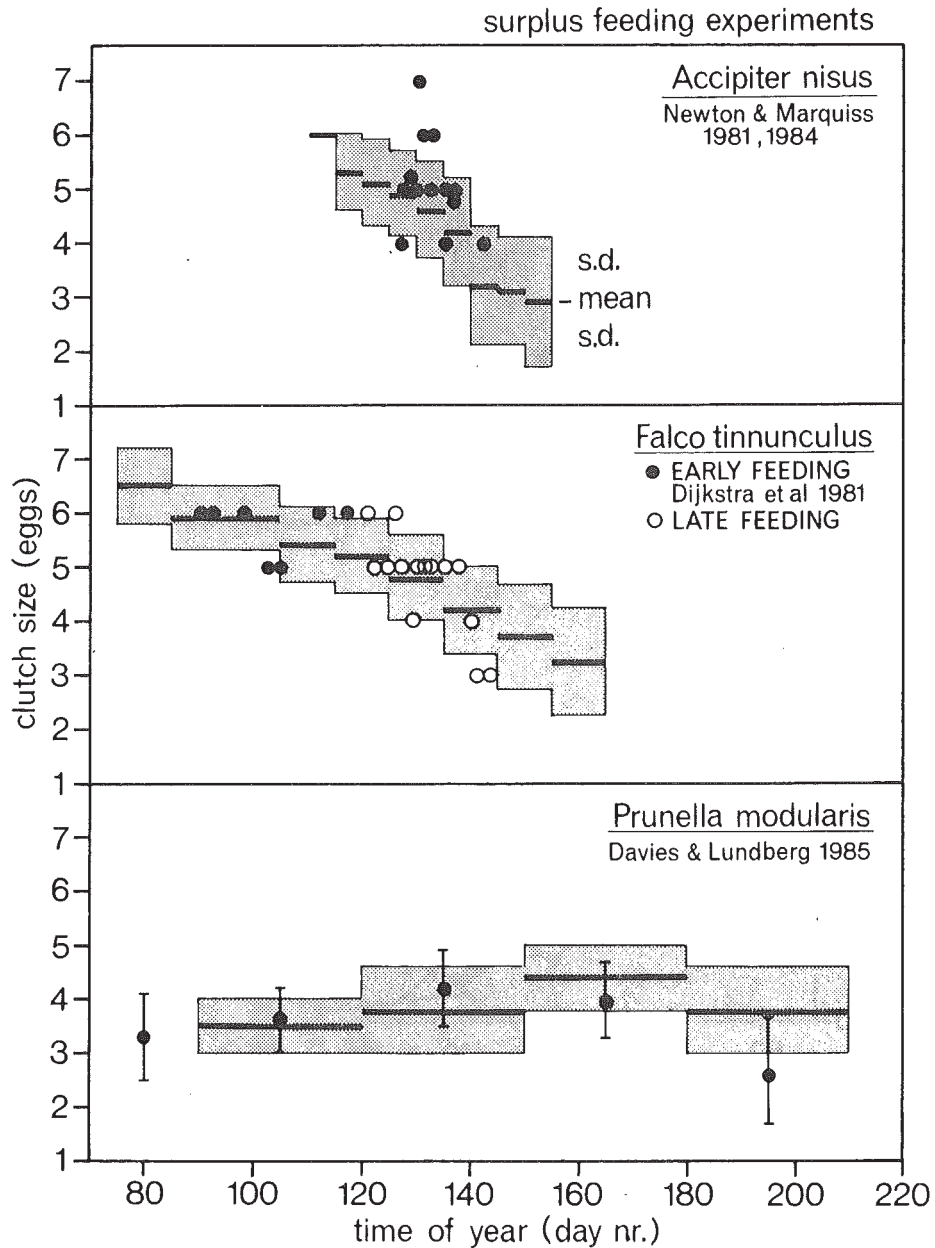
clutches were not significantly larger than the control clutches produced at the same time of year. Figure 4 illustrates the array of responses found. The Dunnock (*Prunella modularis*) represents those multiple-brooded species with little seasonal variation in clutch size for which food advances laying and does not affect clutch size (Davies and Lundberg 1985). The Sparrowhawk has a steep decline in clutch size, and the food effect is primarily in a "vertical" direction (Newton and Marquiss 1981). The Eurasian Kestrel, with its broad natural range of clutch size and laying date, showed significant effects in both directions. Presumably, clutch size increased only by as much as appropriate to the advance in date. The experimental data are thus all consistent with the proposition that food affects laying date, whereas clutch size is independent of food supply. Additional evidence for this proposition comes from late-feeding experiments in the Eurasian Kestrel (Fig. 4), a protocol suggested by Drent and Daan (1980) to distinguish between their "capital" and "income" models of reproductive adjustment to food. Eurasian Kestrel pairs that had not yet started to breed in our study area on April 30 (day 120) were divided into control and experimental groups. The experimental group received surplus food (120 g dead white laboratory mice per pair per day) from day 120 till clutch completion. The experimental group laid significantly earlier than the control group. Experimental clutch sizes were not different from sizes of control clutches laid at the same date and were significantly smaller than clutches of the early-fed pairs—in spite of the same amount of food being available to the laying female (S. Daan *et al.*, unpublished data). The data are hence at variance with the "income" model of Drent and Daan (1980).

The surplus-feeding experiments force us to accept a causal role of food in the timing of reproduction. However, food availability in spring may act as a proximate cue aiding in the fine-tuning of reproductive decisions without posing energetic constraints on egg formation. It is our contention that food availability in spring primarily affects laying date, and that laying date in turn determines clutch size, either via an internal annual program or via some external variable independent of food (e.g., day length). Fitting with this view—which has been advanced by other authors (Klomp 1970; Perrins 1970)—is the fact that clutch sizes produced at the same date in years with different food availability are not different (e.g., von Haartman 1967a; S. Daan *et al.*, unpublished data).

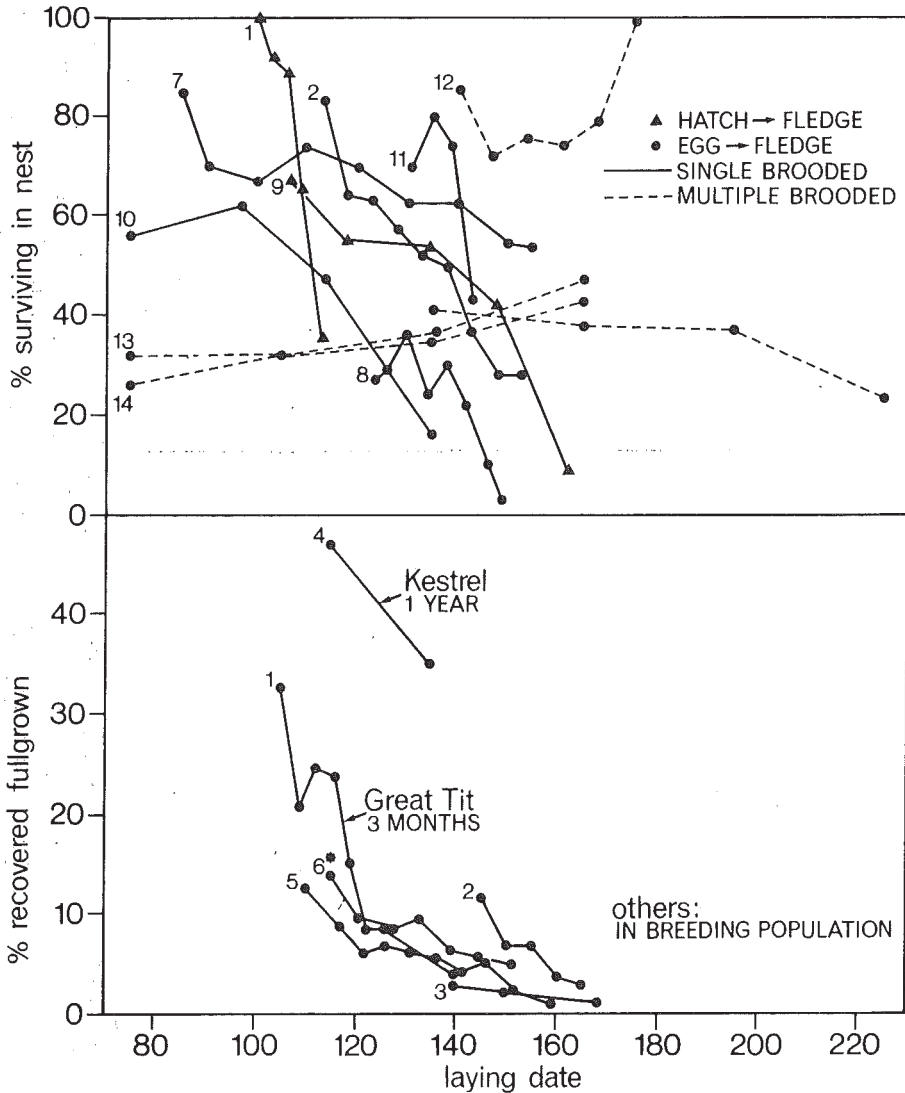
### Seasonal Change in Reproductive Value of Eggs

Evaluation of the ultimate aspect of reproductive timing requires that we establish the chances of eggs laid at different times of year becoming recruits in the next breeding generation. In many population studies, the percentage of offspring fledged has been analyzed. Our compilation (Fig. 5A) illustrates the well-known general pattern of a monotonic decline in fledging success for single-brooded species. In multiple-brooded birds, the seasonal variation is much less pronounced. The chances of survival after fledging vary again with date of birth, although this has been documented in far fewer instances. The available data (Fig. 5B) usually concern local survival in the study population, either from





**Figure 4.** Clutch size and laying date for pairs receiving surplus food (open circle) compared with mean clutch size ( $\pm$  s.d.: shaded areas) of control birds per laying-date interval. In the Eurasian Kestrel, symbols refer to surplus food from day 71 (shaded circle) and from day 120 (open circle) until clutch completion.



**Figure 5.** Seasonal variation in survival indices of offspring in the nest (upper panel) and after fledging (lower panel). (1) Great Tit (Perrins 1965). (2) Sparrowhawk (Newton and Marquiss 1984). (3) Pied Flycatcher (*Ficedula hypoleuca*) (von Haartman 1967b). (4) Eurasian Kestrel, percentage after first year of all recoveries (Cavé 1968). (5) Manx Shearwater (*Puffinus puffinus*) (Perrins 1966). (6) Herring Gull (*Larus argentatus*) (Nisbet and Drury 1972). (7) Eurasian Kestrel (S. Daan *et al.*, unpublished data). (8) Herring Gull (Parsons 1975). (9) Oystercatcher (*Haematopus ostralegus*) (Harris 1967). (10) Rook (Murton and Westwood 1977). (11) Common Guillemot (*Uria aalge*) (Birkhead 1977). (12) House Martin (Bryant 1975). (13) Blackbird (*Turdus merula*) (Snow 1955). (14) Song Thrush (*Turdus philomelos*) (Snow 1955).

fledging till the autumn, or till recruitment in the breeding population. Such variations may deviate more or less from true survival by differential migration. The general trend is one of a decline in survival rates with a progressively later birth date, as demonstrated originally by Perrins (1965) for the Great Tit. These seasonal variations in survival are the consequence of variations both in food supply to the brood and in chances for the offspring when independent.

For nestlings surviving till the next breeding season, there may be further dependence of the chance to participate in breeding on birth date. This has been documented for the Eurasian Kestrel (S. Daan *et al.*, unpublished data). For this species, we have combined data on nest survival, birth-date-specific first-year survival, and expectation of egg production by offspring to calculate Fisher's (1958) reproductive value  $V_o(i)$  of Eurasian Kestrel eggs as a function of the laying date  $i$ :

$$V_o = \sum_{x=1}^{\infty} \lambda^{-x} \cdot l_x \cdot b_x \quad (1)$$

where  $i$  = day no. (121 = May 1)

$\lambda$  = innate rate of population increase, determined by setting  $V_o = 1$  for the population as a whole

$l_x(i)$  = probability of survival of eggs laid at date  $i$  till age  $x$

$b_x(i)$  = expected number of eggs produced by a bird surviving from an egg laid at date  $i$  till age  $x$  ( $b_x(i) = 5.2$  for all  $i$  when  $x > 1$ , and varies with  $i$  only at age  $x = 1$ ).

$V_o$  data points were obtained for Eurasian Kestrel eggs laid in The Netherlands in nine 10-d intervals from day 75 (March 16) till day 165 (June 14). The points can approximately be described by the linear regression  $V_o = 2.42 - 0.0142 \cdot i$  ( $r = 0.939$ ;  $n = 9$ ;  $P < 0.001$ ), which predicts a decline towards zero reproductive value at day 170. This measure of egg fitness as determined by laying date will allow us to model the optimization of clutch size and date at least for the Eurasian Kestrel. A fitness measure such as the frequently used "lifetime reproductive output" (identical to  $V_o$  when  $\lambda$  is unity) is invalid because it neglects the fact that breeding early in life increases the rate of gene propagation more than breeding late in life. In the Eurasian Kestrel, an important contribution to the large reproductive value of early eggs is their high probability of reproducing as yearlings, in contrast with late-born birds.

On the basis of the data summarized in Fig. 5, we expect that in other single-brooded species the reproductive value of eggs will decline the later they are produced in the season. The postfledging period in most species coincides with the seasonal decline in food resources (Fig. 1), although the food curves measured may not always be relevant for the diet of fledglings.

### On the Optimization of Reproductive Decisions

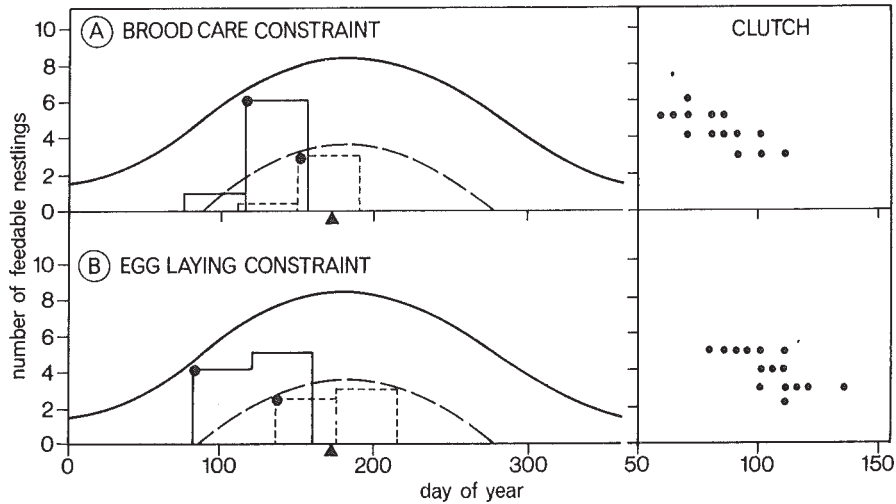
Two seasonally changing variables are thus important in the annual organization of reproduction: food availability and reproductive value of eggs. Food availability can be expressed in the number of feedable nestlings. This is not an imaginary parameter. Altricial birds during parental care work at a level of

daily energy expenditure that is reasonably predictable on the basis of their basal metabolic rate (Drent and Daan 1980; Bryant and Tatner, this publication) and which is close to the physiological maximum energy intake (Kirkwood 1983; D. Masman *et al.*, unpublished data). If the energetic yields and costs of foraging are known, the net energetic gain of birds foraging at this level can be calculated. For instance, male Eurasian Kestrel parents on average have 4.6 h of flight + flight-hunt per day, corresponding with a daily energy expenditure of  $\sim 400 \text{ kJ}\cdot\text{d}^{-1}$  (D. Masman *et al.*, unpublished data). This expenditure is independent of brood size in parents feeding complete broods. The net energy gained with this daily foraging effort can be quantified from behavioral observations (D. Masman *et al.*, unpublished data) and is a straightforward measure of environmental food availability. On the other hand, when energy requirements of nestlings are known ( $\sim 186 \text{ kJ}\cdot\text{d}^{-1}$  per Eurasian Kestrel nestling), the maximum energy gain can be expressed in maximum feedable nestlings (MFN).

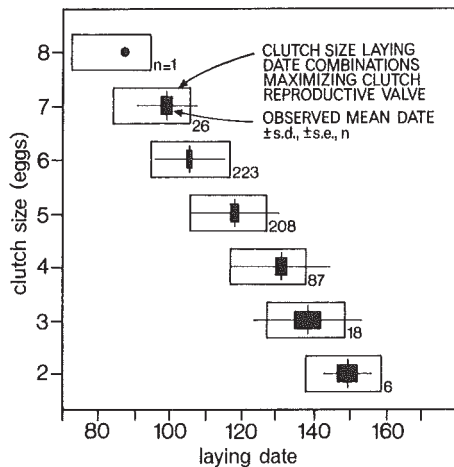
Whereas MFN will go up and down with time of year and energy availability, reproductive value of each egg declines with the progression of laying date. In a simple algorithm we can ask, for any combination of MFN and  $V_o$  functions, which is the optimal combination of clutch size (C) and laying date, i.e., the combination maximizing  $C\cdot V_o$ . This was done for two arbitrary situations: one in which energy requirements for formation and incubation of an egg are small (one-sixth) compared with the energy required by a nestling (Fig. 6A), and one in which this ratio is large (five-sixths; Fig. 6B). In both cases, the optimal solutions were calculated for 15 parallel sinusoidal MFN curves, representing different habitat or parental qualities. The optimal solutions in both cases lie on a declining slope. This result is independent of phase and amplitude of the MFN curves, of the average time of fledging, on either the rise or fall of MFN, of the precise  $V_o$  function as long as  $V_o$  declines monotonically, and of energetic constraint by egg or nestling requirements.

Using the same algorithm, it can easily be shown that multiple breeders optimally produce the smallest clutches early and late in the season, in agreement with empirical data. The earliest broods are produced far ahead of the seasonal optimum, but this head start allows time for second and third broods.

Theoretical games such as in Fig. 6 cannot replace real data, although they emphasize the kind of empirical data needed to define environment plus parent quality on the one hand and the prospects for offspring on the other. In a long-term project on the Eurasian Kestrel, we have been able to arrive at a more precise prediction of optimal date/clutch size combinations by observing hunting birds repeatedly throughout the spring. In 16 males, flight-hunting yields increased on average with 0.069 (s.e. 0.033) prey per hour per day, which is equivalent to an increase of 1 MFN per 10.7 d. In combination with the known decrease in egg reproductive value (eq. 1), this leads to precise predictions on optimal date/clutch size combinations indicated in Fig. 7. Observed distributions of laying dates per clutch size are somewhat broader than the predicted ranges, but their central tendency corresponds not unreasonably.



**Figure 6.** Model for the ultimate optimization of clutch size and laying date. Left panels: Sinusoidal seasonal variation in habitat and parent quality expressed as number of feedable nestlings with maximal effort for rich (solid line) and poor (dashed line) situations. Rectangles indicate energy requirements for egg laying and incubation (left) and nestling care (right) for the clutch size/date combinations maximizing clutch reproductive value when  $V_0$  declines linearly to zero at day 170 (rate of decline does not affect the solution). Right panels: 15 solutions for sine waves intermediate between the two extremes on the left. (A) Egg requirements one-sixth of nestling requirements. (B) Egg requirements five-sixths of nestling requirements.



**Figure 7.** Rectangles: clutch size/laying date combinations maximizing clutch reproductive value for the Eurasian Kestrel, calculated on the basis of increasing number of feedable nestlings (1 per 10.7 d) and declining egg reproductive value ( $V_0 = 2.42 - 0.0142 \cdot \text{day no.}$ ). Solid symbols: mean laying dates per clutch size.



### Perspective

The theory outlined in the above section is a general theory for single-brooded species: as long as the reproductive value of an egg declines with season (i.e., as evolution puts a premium on earliness), it is better for animals in the best conditions (parent or habitat) to advance laying date with respect to the same date when the maximum number of young could be raised, than for those in the poorest conditions. The theory extends Perrins' (1970) view of individual variations in clutch-size optima to the simultaneous optimization of clutch size and laying date. The prediction of a seasonal decline is independent of any assumptions on: (a) whether the peak in viable offspring production is due to high food abundance or low parental cost; (b) whether birds breed on the upswing or downswing of food availability; (c) whether egg production or nestling care constrain the maximum number of raisable offspring; (d) how inter-individual variation in viable offspring production is partitioned in parental quality and environmental variation; and (e) the proximate control mechanism and its genetic and environmental components.

The theory will be useful when it incites experiments aimed at showing where it is wrong. We conclude by outlining some potential areas for experimentation. We have not explicitly taken into account the fact that natural selection acts on parental and clutch fitness simultaneously (Charnov and Krebs 1974). Implicit in the concept of a maximum level of parental energy expenditure is that birds will generally accept the same parental investment. This need not be generally true. Available evidence suggests, however, that parental energy expenditure does not vary systematically with natural brood size (Bryant and Tatner, this publication). This holds also for the Eurasian Kestrel (D. Masman *et al.*, unpublished data), which might explain why in this species, clutch size/date combinations fit the quantitative predictions based solely on egg reproductive value. In contrast, we suspect that in multiple breeders parental investment will vary between successive breeding attempts (Bryant and Westerterp 1980) and hence needs to be measured before application of the model. Experimental brood manipulations will be the key to the estimation of parental investment. Brood enlargements have shown negative effects on parental fitness (Askenmo 1979; Röskaft 1985). However, brood reductions so far failed to demonstrate that naturally chosen brood sizes already entail any parental investment (Tinbergen and van Balen, this publication).

The proximate mechanism by which a bird chooses one from the set of optimal date/clutch size combinations should presumably depend on the predictability of food supply. Primarily genetic variation may be expected when food availability constrains parental effort in the nestling phase and is unpredictable from the situation during egg laying. Environmental variability will be more pronounced when proximate cues can be used as predictors. Food manipulations and selection experiments seem to offer the best prospects for establishing environmental and genetic control.

Finally, the key assumption in our theory is that the declining reproductive value of eggs derived from population data would also hold for an individual egg: that, everything else being equal, its chances would diminish the later it

were laid. No experimental data are at hand to test this assumption. We have recently started to manipulate laying date in captive Eurasian Kestrels by photoperiod and to release offspring at 8 weeks of age in the natural population at different times of year. The evaluation of their survival and recruitment probabilities provides another avenue for the experimental analysis of reproductive timing strategies.

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