Time, Condition, and the Seasonal Decline of Avian Clutch Size

Locke Rowe; Donald Ludwig; Dolph Schluter

The American Naturalist, Vol. 143, No. 4 (Apr., 1994), 698-722.

Vol. 143, No. 4 The American Naturalist April 1994

TIME, CONDITION, AND THE SEASONAL DECLINE OF AVIAN CLUTCH SIZE

LOCKE ROWE,* DONALD LUDWIG,† AND DOLPH SCHLUTER*‡

*Department of Zoology, University of British Columbia, Vancouver, British Columbia V6T 1Z4 Canada; †Departments of Mathematics and Zoology, University of British Columbia, Vancouver, British Columbia V6T 1Z4 Canada

Submitted September 14, 1992; Revised March 29, 1993; Accepted April 2, 1993

Abstract.—A seasonal decline in clutch size is typical of bird populations. This phenomenon may result from a conflict between the advantages of early breeding (greater offspring value) and the advantages of delay (greater accumulated condition and hence clutch size). We construct a dynamic model for adaptive seasonal decline in clutch size on the basis of these premises. The model requires a small number of well-supported assumptions; it is formulated and analyzed in both analytical and graphical forms. We outline some novel predictions and suggest tests of our conclusions. Initial comparisons of our predictions with results available from wild birds in the field are favorable. We briefly extend the model to consider the evolution of multiple clutches within a season and the effects of between-season costs of reproduction. Although this work focuses on avian clutch size, the analysis provides a general framework for studies of condition-dependent transitions in life histories. Such transitions between stages (e.g., maturation, metamorphosis, or reproduction) characterize the ontogeny of organisms. We expect that such conflicts between the advantages of early and late transitions are common to life-history decisions.

A seasonal decline in clutch size is common in bird populations (Klomp 1970; Drent and Daan 1980; Murphy and Haukioja 1986; Martin 1987; Daan et al. 1989). Individuals that nest early in the breeding season generally lay more eggs than those that nest later. Examples of this phenomenon include arctic nesting geese (Hamann and Cooke 1989), temperate raptors (Dijkstra et al. 1982), and many passerines (Murphy 1986*a*). A similar pattern is often observed between years: mean clutch size is usually larger in years of relatively early breeding than in years when the start of reproduction is delayed (see, e.g., Murphy 1986*a*; Perrins and McCleery 1989). The broad taxonomic and geographical distribution of birds exhibiting seasonal decline in clutch size argues for a simple and general underlying cause.

A seasonal decline in the value of offspring is typically associated with the seasonal decline of clutch size. Survival and probability of recruitment are usually lower for later-born fledglings than for those born earlier (see, e.g., Perrins 1966; Cooke et al. 1984; Newton and Marquiss 1984; Hochachka 1990). Birds that delay

---

‡ Present address for L.R.: Section of Ecology and Evolution, Storer Hall, University of California, Davis, Davis, California 95616. E-mail: L.R., szrowe@bullwinkle.ucdavis.edu; D.L., ludwig@bcu.ubc.ca; D.S., schluter@bcu.ubc.ca.

Am. Nat. 1994. Vol. 143, pp. 698–722.

reproduction consequently suffer a fitness cost per egg, an effect that makes it difficult to understand why some individuals delay. A variety of proximate mechanisms have been suggested to explain why some birds delay reproduction. For example, yearling females produce both smaller and later clutches than older birds (Klomp 1970; Askenmo and Unger 1986; Murphy 1986*b;* Hochachka 1990). Nevertheless, seasonal declines in clutch size are also seen within age-groups (Hochachka 1990). Others have postulated that parents that reproduce later reduce clutch size because reproduction is costly and offspring value decreases over the season (Hussell 1972; Murphy 1986*a;* Hochachka 1992). Finally, in some species, parents may reduce clutch size late in the year because of declining food supplies required for rearing young (Perrins 1970; Murphy 1986*a*). These mechanisms may help explain why smaller clutches of eggs are produced late in the breeding season, but they do not explain why some birds within a given cohort lay later than others.

Clutch size and timing of breeding are probably constrained by parental condition. In any one season, individuals in high condition typically produce both larger and earlier clutches (Askenmo 1982; Newton et al. 1983; Dijkstra et al. 1988; Hörnfeldt and Eklund 1990). Similarly, in years of high food abundance clutch size increases and/or lay date is advanced (Dijkstra et al. 1982; Jarvinen and Vaisanen 1984; Murphy 1986*a;* Perrins and McCleery 1989). The most compelling evidence that parental condition is a determinant of clutch size and lay date comes from experiments in which food was supplemented prior to egg laying. In 10 such experiments, as reported in Daan et al. (1989), lay date was advanced by food addition (usually by a statistically significant amount), and clutch size increased (usually by a statistically insignificant amount) for the seven species that produce a single clutch per season. There have since been several more food-supplementation experiments with similar results (reviews in Davies and Lundberg 1985; Arcese and Smith 1988; Daan et al. 1989; Meijer et al. 1990).

On the basis of such observations, Drent and Daan (1980) identified the primary benefit of delaying lay date to be the further accumulation of condition (e.g., nutrients) required for egg production. They suggested that the timing and number of eggs laid was the resolution of a conflict between the advantages of early breeding (greater offspring value) and the advantages of delay (greater accumulated condition and hence potential clutch size). With a graphical model they showed how birds in poor condition might have more to gain from delay than birds in good condition, and that this would lead to the observed pattern of seasonal decline in clutch size. Drent and Daan (1980) did not give a formal treatment of their model, and therefore emergent predictions and tests are lacking. Loman (1982) derived a special (linear) case of their model and confirmed that a seasonal decline in clutch size could be adaptive.

Our purpose is to formalize and generalize the arguments of Drent and Daan (1980), so that testable predictions can be derived. We construct a dynamic model for adaptive seasonal decline in clutch size with a small number of well-supported assumptions. This model is based on earlier theory for adaptive seasonal variation in the emergence of mayflies (the mayfly model; Rowe and Ludwig 1991). The model predicts optimal norms of reaction for the life-history transition between accumulating condition required for egg formation and laying the clutch. We outline predictions of the model and suggest some tests of these predictions. Where data are available, we compare our predictions to the qualitative results of previous experiments on birds. In Appendix A we extend the model to consider the evolution of multiple clutches within a single breeding season. Finally, the effects of between-season costs of reproduction are considered in Appendix B. It is not our purpose to review the vast amount of data or theory relevant to the evolution of clutch size (reviews in Murphy and Haukioja 1986; Martin 1987; Daan et al. 1989; Price and Liou 1989). We present our theory as a framework for studying adaptive seasonal variation in clutch size. Although we emphasize the application to avian clutch size, the theory and analysis are applicable to condition-dependent life-history transitions in a variety of taxa.

THE MODEL: CONFLICT BETWEEN EARLY LAY DATE AND LARGE CLUTCH SIZE

Intuitive Development

We are concerned with the prediction of optimal lay date, when lay date is subject to conflicting selection pressures. The two fitness components under conflicting selection are offspring number and offspring quality: fitness of any female is assumed to be the product of these factors. We assume that birds accumulate condition at rate $g(C)$ prior to producing a clutch and that the size of clutch produced, $N(C)$, is an increasing function of accumulated condition: with each delay in lay date, T, $N(C)$ increases. However, we also assume that the value of offspring, $V(T)$, is a decreasing function of lay date: with each delay in lay date, T, $V(T)$ declines. The optimal lay date is that one in which the marginal benefit of delaying further (increased clutch size) is equal to the marginal cost of delaying further (decreased offspring value). Note that, by determining optimal lay date, optimal clutch size is also determined.

To illustrate this point, consider a hypothetical season that is 10 d long (table 1). The recruitment probability of an egg, $V(T)$, laid on day 1 is 1.0. Each 1-d delay in lay date results in a 0.1 decrease in recruitment probability, so that, by day 10, $V(T)$ has declined to 0.0. Consider an individual (A) that is accumulating condition, C (potential clutch size, let $N = C$), such that one additional egg can be produced with each day that lay date is delayed in the season, so that by day 10 enough condition has been accumulated to produce 10 eggs. To find the lay date that maximizes fitness of individual A (F_A), we calculate the product of the two functions, $V(T)$ and $N(T_A)$. In this case the optimum occurs on the fifth day in the season, with a clutch size of five eggs (table 1).

We now introduce variation among individuals in their condition on any date and show that the optimal strategy differs between individuals. Consider a second individual, B, that differs from A only in that it reaches a given condition later. This may result from individual B arriving at the breeding site at a later date than individual A (day 4 rather than day 0; table 1) or because B begins the season (day 0) at a poorer condition (-4) than A (0). Both individuals accumulate condition at the same rate, $C(T)$, and both experience the same seasonal decline in offspring

TABLE 1

AN EXAMPLE OF HOW OPTIMAL COMBINATIONS OF CLUTCH SIZE, $N(C)$, AND LAY DATE, T, ARE CALCULATED

T	$V(T)$	$N(C)_A$	$N(C)_B$	F_A	F_B
0	1.0	0	. . .	.0	. . .
1	.9	1	. . .	.9	. . .
2	.8	2	. . .	1.6	. . .
3	.7	3	. . .	2.1	. . .
4	.6	4	0	2.4	.0
5	.5	5	1	2.5	.5
6	.4	6	2	2.4	.8
7	.3	7	3	2.1	.9
8	.2	8	4	1.6	.8
9	.1	9	5	.9	.5
10	.0	10	6	.0	.0

NOTE.—The rate of decline in probability of recruitment, $V(T)$, is 0.1 per day. The rate of increase in accumulated condition, $C(T)$, is 0.1 per day. These rates are the same for all individuals. We let clutch size, $N(C)$, equal accumulated condition, $C(T)$, for this example. Individuals A and B differ only in the date on which they reach a given condition. Individual A has condition 0 on day 0, whereas B reaches condition 0 on day 4. Fitness, F, of each individual is calculated as $V(T) \times N(C)$ for all possible lay dates. Optimal clutch size and lay date (the combination maximizing F) are underlined.

value, $V(T)$. Optimal clutch size and lay date for individual B are computed as three eggs on day 7, where fitness, F_B, is maximum at 0.9 (table 1).

Three central points are apparent from this numerical example, each of which will be developed further in subsequent sections. First, the optimal strategy of an individual is condition-dependent (sensu Andersson 1982; Nur and Hasson 1984) or state-dependent (sensu McNamara and Houston 1986; Mangel and Clark 1986). Individual A, in high condition, maximizes fitness by laying five eggs on day 5, whereas B, in lower condition, should lay three eggs on day 7 to maximize her fitness. Second, optimal clutch size declines as the season progresses: later breeding individuals should lay fewer eggs. Third, individuals in higher condition at any time in the season attain higher fitness: individual A attains higher fitness than individual B (2.5 and 0.9, respectively).

In the following section we formulate an analytical and graphical solution to the conflict between the advantages of early lay date and large clutch size, in a species that produces a single brood in a breeding season. Our purpose is to illustrate a minimal set of principles that underlie adaptive seasonal variation in clutch size. Hence, the model will be presented in its simplest form; we assume no cost of reproduction and no seasonal variation in food available to parents. Consideration of multiple clutches within a season and the addition of reproductive costs is postponed to the appendixes. The model is similar to previous formulations of condition-dependent traits, such as attractive male traits (Nur and Hasson 1984; Grafen 1990) and life-history traits such as age and size at sex change (Fernandes 1990) and age and size at maturity (Rowe and Ludwig 1990). Therefore, our conclusions are applicable to the evolution of an array of condition-dependent traits.

Basic Assumptions

We assume that individuals maximize their reproductive success in a single season. Fitness depends on the number of eggs laid and the time at which incubation of the clutch of eggs commences. The total number of eggs produced is a function of parental condition (accumulated nutrient reserves) at the time the clutch is produced. Condition of the parent at this time is a function of both her condition at the start of the season and her rate (and duration) of nutrient intake since then. We assume that individuals vary in their condition at the start of the breeding season (as in table 1). This is equivalent to assuming that all individuals can attain a given condition but will do so at different times during the season (i.e., individuals beginning the season in the poorest condition will attain this condition latest in the season). Further, we assume that food availability is constant over the season. Finally, we assume that the condition required for egg production includes both that for forming and that for rearing the eggs. The relative allocation of condition devoted to eggs prior to and subsequent to laying would vary with degree of precocity of offspring of the species.

Throughout our analysis, we assume that all eggs are laid on the day that incubation commences. Condition gain ceases on this day. This assumption simplifies the model and does not alter qualitative conclusions. Seasonal declines in offspring value are usually reported with respect to the date that the first egg is produced. If the value of eggs were reported with respect to the onset of incubation (date of last egg) then seasonal declines in egg value would be steeper: early broods are larger and the difference between the date of the first egg and date of incubation is greater for eggs laid early in the season. Our assumption that condition accumulates in the female soma prior to egg laying is similarly made for convenience. The model also applies to species that shunt nutrients directly into eggs.

The Single-Clutch Model

We make use of the following symbols:

$C(T)$	Condition (accumulated nutrient reserves), an increasing function of time
$V(T)$	Egg value, the probability that an egg laid at time T yields a recruit to the next breeding population
$N(C)$	Clutch size, an increasing function of condition
F	Fitness (output of a reproductive bout)
$g(C)$	Rate of condition accumulation, a function of current condition
T_S	Time of start of season (ordinarily the same for all individuals)
C_S	Condition at start of season (may vary between individuals)
C_C	Minimum condition to lay eggs (ordinarily the same for all individuals)
T_C	Time at which condition C_C is reached (may vary between individuals)

In general, the rate of condition gain may depend upon current condition.

$$\frac{dC}{dT} = g(C) \,. \tag{1}$$

However, for simplicity, we illustrate the case in which the rate of condition gain is constant (independent of current condition).

Relationship (1) does not uniquely determine the condition, $C(T)$, of an individual at time T: a starting condition must be specified. This could take several forms. If T_S is the start of the season when condition is accumulated for breeding, then the subsequent condition of a given individual is determined by her initial condition, C_S, at that time:

$$C(T_S) = C_S . \tag{2}$$

Ordinarily we assume that T_S is the same for all individuals: it is a property of the environment. But C_S may vary between individuals. Alternatively, we may specify C_C as a minimum condition required to produce eggs, which is the same for all individuals. In such a case T_C is defined as the time at which condition C_C is reached. This time may vary between individuals.

The Optimality Condition

We assume that the fitness of a given individual is the product of recruitment probability per egg and the clutch size:

$$F = V(T)N(C) . \tag{3}$$

The fitness in equation (3) is to be maximized as a function of the lay date, T. Consequently the derivative of F with respect to T must vanish:

$$\frac{dV}{dT}N(C) + g(C)\frac{dN(C)}{dC}V(T) = 0 . \tag{4}$$

The factor $g(C)$ is a consequence of the chain rule of calculus and equation (1). Equation (4) may be rearranged in the form

$$-\frac{1}{V(T)}\frac{dV}{dT} = g(C)\frac{1}{N(C)}\frac{dN(C)}{dC} . \tag{5}$$

This equation is a relation between the optimal combination of laying condition, C, and lay date, T. The left-hand side of equation (5) is the relative loss in fitness resulting from a decrease in probability of egg recruitment with a delay in lay date. The right-hand side of equation (5) is the relative gain in fitness resulting from the increase in clutch size permitted by the same delay in lay date. Henceforth, dV/dT will be denoted by $V'(T)$, and $dN(C)/dC$ by $N'(C)$ (prime indicating derivative). The preceding assumptions and the consequent optimality condition are generalized in Appendixes A and B.

Why Should Individuals That Lay Later Produce Fewer Eggs?

It is commonly observed that individuals that lay later (larger T) are in poorer condition (lower C) and lay fewer eggs then those laying earlier (see the introduction). This pattern is a consequence of equations (1), (2), and (3) when individuals begin the season at different conditions, under the following additional assumptions:

1. The left-hand side of equation (5), that is, $-V'(T)/V(T)$ (the relative cost of delay), must increase as lay date increases. This means that the rate of decline in offspring value, as a proportion of existing value, must increase with increasing lay date. All functions $V(T)$ that decline toward zero as the season progresses will satisfy this assumption in the latter part of the season. For example, in table 1 the relative cost of a 1-d delay is 0.1/1 at day 0 but increases to 0.1/0.5 by day 5. If $V(T)$ is a function that increases initially and then decreases as time progresses, then optimal lay date will always occur when this proportion is decreasing. For example, if eggs laid very early in the spring are at risk to lingering poor winter weather (see, e.g., Perrins and McCleery 1989), then offspring value may increase early in the season before declining. In such a case, optimal lay date must fall on the declining portion of the curve, because on the increasing portion of the curve both clutch size and offspring value are increasing, thus there are benefits to delay and no cost.
2. The right-hand side of equation (5), that is, $g(C)N'(C)/N(C)$ (the relative benefit of delay), must decrease as condition increases. This means that gain in clutch size (with accumulated condition) resulting from delay, as a proportion of existing clutch size must decrease with increasing condition. For example, in table 1 the relative benefit of a 1-d delay is 0.1/2 at the two-egg stage but declines to 0.1/3 at the three-egg stage. All functions $N(C)$ that vanish for small C will satisfy this assumption. Most functions in which condition increases with time prior to egg laying will also satisfy this assumption: only in unusual cases (e.g., an exponentially increasing rate of condition gain) will this assumption be violated.
3. The rate of condition gain is positive ($g(C) > 0$).

We expect that most biologically realistic relationships between time, condition, and offspring value will meet these criteria, at least in the vicinity of an optimal combination of lay date and clutch size. As a consequence, clutch size in single-brooded species is generally expected to decline with increasing lay date. More formally, if equations (1)–(3) are satisfied, and if $V(T)$, $g(C)$, and $N(C)$ satisfy assumptions 1–3 above, and if a solution of equation (5) exists, then the optimal clutch size must decrease as lay date increases. A graphical demonstration is given below. The graphical argument can be made rigorous, but that argument will be omitted. The conclusion does not depend upon the linearity of any of the postulated relationships, although such assumptions are used to simplify the illustrations.

The preceding assumptions are illustrated in figures 1 and 2. Figure 1*A* shows the relationship between $-V'(T)/V(T)$ (the relative cost of delay) and T and figure 1*B* shows the relationship between $g(C)N'(C)/N(C)$ (the relative benefit of delay) and C. Optimal clutch size for any lay date occurs when the relative cost in delaying lay date (fig. 1*A*) is balanced by the relative benefit of delay (fig. 1*B*). For simplicity we illustrate the simplest case in which both $C(T)$ and $V(T)$ are linear. Further, we let

$$N(C) = C - C_{\mathrm{C}}, \tag{6}$$

so that values of condition above C_{C} (the minimum needed to produce eggs) correspond to clutch size. *Horizontal segments* in figure 1 connect points at which

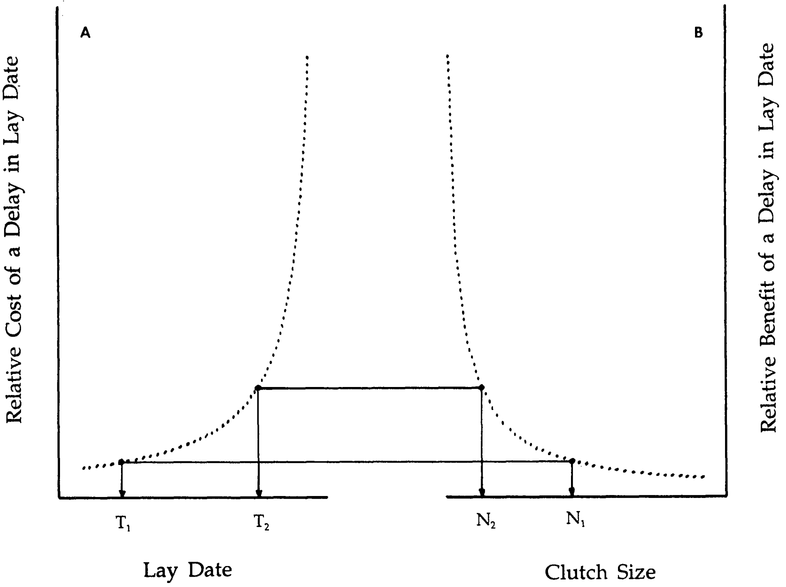

FIG. 1.—*A*, The relative loss of fitness with a delay in lay date, $-V'(T)/V(T)$ (the relative cost of delay); *B*, the relative gain in fitness with increasing condition at the time of laying, $g(C)N'(C)/N(C)$ (the benefit of delay), which is equivalent to clutch size in this example. Costs and benefits increase vertically on the Y-axes. These two quantities must be equal at the optimum combination of clutch size and lay date. *Horizontal lines* connect points of equal losses and gains. A raising of the horizontal segment corresponds to a decrease in the optimal clutch size at laying from N_1 to N_2 and an increase in the optimal lay date from T_1 to T_2. Therefore, a seasonal decline in clutch size is expected.

the two quantities are equal; these are the optimal combinations (C, T) according to our equation (5). A *higher horizontal segment* corresponds to a later lay date, which in turn corresponds to a lower value of condition and thus a smaller clutch size. Thus, optimal clutch size is expected to decline as the breeding season progresses.

By connecting all optimal combinations of condition and lay date (fig. 1) we generate a "switch curve," as is shown in figure 2. This curve represents an optimal norm of reaction of clutch size and lay date for birds varying in condition. We expect an individual's clutch size and lay date to lie on this curve, the exact point depending on her starting condition. A variety of possible trajectories for condition gain of individuals is illustrated by the *dashed lines* (fig. 2). The different growth curves represent differences among individuals in the times at which the minimum baseline condition is attained or in their condition at the start of the breeding season. In this example, note that all individuals accumulate condition at the same rate. According to the theory presented above, an individual should accumulate condition until her trajectory crosses the switch curve, at which time she should produce her clutch of eggs. At that point the relative cost of further delaying lay date equals the relative benefit of delay. Under the three assumptions

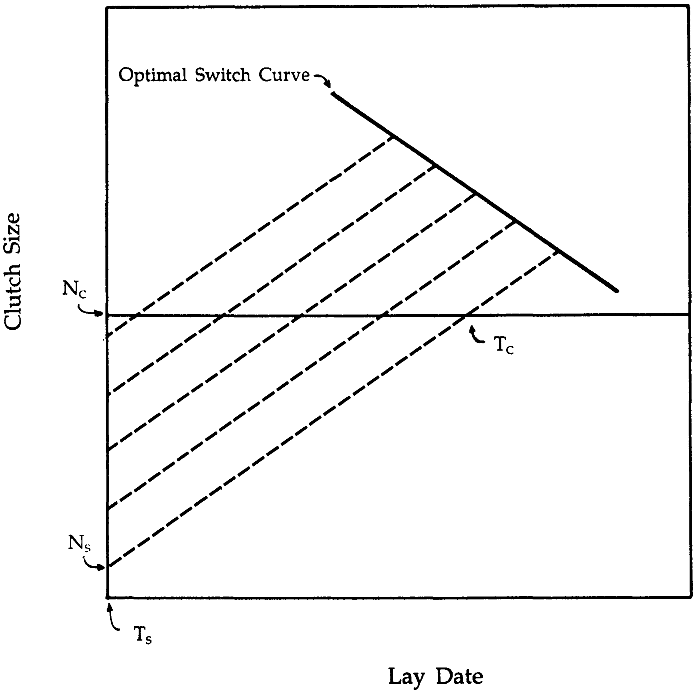

FIG. 2.—The switch curve connecting optimal combinations of clutch size and lay date (*solid*). *Dashed lines* are trajectories of condition gain by individuals, in which higher condition translates into a higher clutch size (N). In this and following examples we let $N = C$. Individuals are assumed to accumulate condition at equal rates. A bird should delay laying until the switch curve is crossed. The designation N_S denotes an individual's condition at the beginning of the season, T_S, when resource accumulation begins; N_C denotes the minimum condition for production of a clutch and each individual reaches N_C at a different time T_C depending upon its starting condition N_S. See text for further details.

given above, figures 1 and 2 show that the switch curve will have a negative slope: individuals that begin the season in relatively poor condition breed later and lay fewer eggs than those that start in higher condition.

Fitness (eq. [3]) as a function of condition at the start of the breeding season is shown in figure 3. The contours demonstrate that an individual's optimum combination of lay date and clutch size is condition-dependent: fitness is maximized at different lay dates and corresponding clutch sizes, depending on starting condition. Individuals that start the breeding season in high condition maximize fitness by laying larger and earlier clutches than individuals starting in poor condition. The contours also show that individuals in best condition always have highest fitness. The optimal strategies for individuals starting the season in less than the highest condition may be thought of as the "best of a bad job."

In summary, our model predicts seasonal declines in clutch size under the simplest set of assumptions: the only assumed difference between individuals is their condition at the start of the breeding season. It is important to note that we

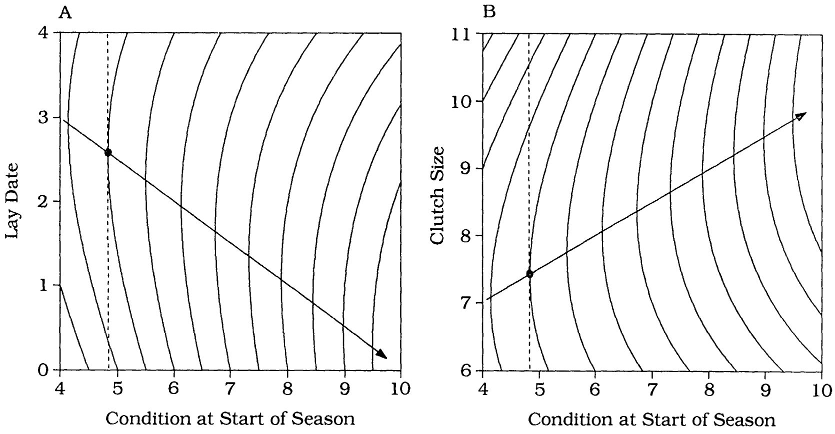

FIG. 3.—Fitness contours for lay date (*A*) and corresponding clutch size (*B*) as a function of condition at the onset of the season, C_S. Fitness was calculated with equation (3) and on the assumption that $N(C) = C = C_S + T$ and $V(T) = 1 - T/10$. Fitness increases from left to right in both panels, as indicated by *arrows*, in increments of 0.5. *Dashed line* in *A* shows the range of lay dates available to an individual starting with condition $C_S = 4.8$. Fitness is maximized at lay date $T = 2.6$, indicated by the *dot*. The *dot* in *B* indicates the clutch size produced on this date (7.4). Other points along the *arrows* are optimal lay date (*A*) and clutch size (*B*) for other values of starting condition.

held the rate of condition gain constant for all individuals regardless of date (i.e., we incorporate no seasonal variation in food supply) or current condition (females in higher condition accumulate condition at the same rate as females in lower condition). The model thus illustrates the effect of time per se on optimal clutch size and lay date. Since our conclusions depend only upon the qualitative features of the graphs (fig. 1), the qualitative behavior of the model illustrated here will remain when more complex assumptions are added to better represent the biological realities of specific situations.

MODEL PREDICTIONS

The assumptions of our model are well supported by data (see references above), and the model predicts the familiar seasonal decline in avian clutch size. Support for the model, however, requires that its emergent predictions be tested in the field. In this section we manipulate the model to produce testable predictions for clutch size and lay date. Our manipulations and predictions are not exhaustive. We highlight those that we believe elucidate the mechanics of our model and that will be most useful to the field biologist. Subtleties of the responses of individual birds to manipulation often depend upon subtleties of their position in time/condition space, and our figures are used to illustrate this point. We also continue to use linear functions (e.g., accumulation of condition) for simplicity; however, the qualitative predictions are not dependent upon linearity.

Where possible, we compare predictions to the data that are available from wild birds. These data were collected for a variety of purposes other than those to which we now put them. For example, experimental additions of food are often carried out to test whether food limitation affects lay date and clutch size. Yet, these data also prove to be useful for addressing more specific predictions outlined below. Our tests assume that the proximate cues used by birds when making reproductive decisions are linked to the factors underlying the theory. This assumption is inherent to all manipulative tests of adaptive hypotheses. For example, variation in the fitness value of eggs is central to our theory and could potentially be manipulated, but birds may not be able to assess this value directly. Instead, they may use more distant cues (such as photoperiod) that indicate time remaining in the season and thus egg value. A field test in this case would require manipulating photoperiod and not $V(T)$ itself.

Onset of Condition Gain (Season Length)

Onset of the breeding season probably differs between years for a number of reasons. For example, a cool spring, prior food shortage, or late migration may delay onset of the period of condition gain. In our model any such delay is represented by a shift to the right in the growth trajectories of individuals (fig. 2), such that birds reach a baseline condition at the same rate as before but at a later T_C. We intuitively expect that a later start to the breeding season will result in birds' laying smaller, later clutches; conversely, an early start should mean earlier, larger clutches. Our model makes a more specific prediction: if the start of the breeding season is experimentally advanced or retarded, but rate of condition gain is not altered by the manipulation, then manipulated birds will alter their clutch size and lay date, but the clutches will be equal in size to unmanipulated birds laying on the same date.

The logic behind this prediction is evident in figure 2 (see also table 1), which shows the switch curve that governs clutch size and lay date for all individuals having the same rate of condition gain but differing in timing, T_C (or, equivalently, starting condition, C_S). If a change in season length adjusts only the T_C of individuals, then their new clutch sizes and lay dates will lie on the same switch curve as before (fig. 2). In this case they would be producing as many eggs as control individuals with the same T_C. Birds that achieve baseline condition late, for whatever reason, should produce smaller, later clutches. They should also have a contracted period between the time, T_C, at which baseline is reached and eventual lay date (fig. 2). Conversely, advanced birds should lay larger, earlier clutches of eggs and have an expanded interval between T_C and eventual lay date.

Several tests of this prediction are possible. First, comparative studies of populations in different years or locations show the predicted effect of season length on clutch size and lay date. Large clutches are generally produced in years of early breeding (Murphy 1986*a;* Perrins and McCleery 1989; Daan et al. 1990; Korpimaki and Hakkarainen 1991). However, such tests are unlikely to be conclusive because other variables may change with season length, such as the rate at which condition is accumulated. There are fewer confounding effects if individuals within a single population and season are compared, and such data provide a

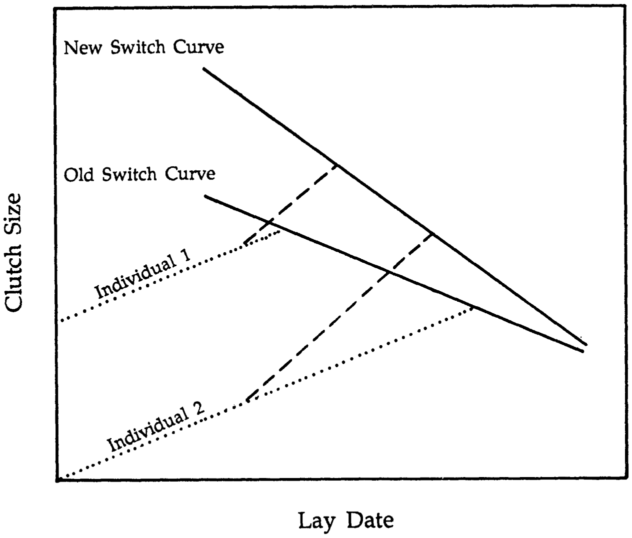

FIG. 4.—The effect of supplementing food during the breeding season, when rates of condition gain are affected. The *solid lines* show the switch curve before and after food supplementation. *Dotted lines* show condition trajectories of individuals prior to food supplementation; *dashed lines* show trajectories at the elevated rate. Comparison between individuals 1 and 2 shows the effect of duration of food supplementation on optimal clutch size and lay date.

second line of evidence. For example, birds may arrive at breeding sites at different times but all in similar depleted condition. Those arriving early start to gain condition sooner than those arriving later, and they should therefore produce earlier and larger clutches. The interval between arriving at the breeding site (T_C) and production of the clutch will be correlated. This effect has been observed in pied flycatchers (Lundberg and Alatalo 1992, p. 64): birds arriving late at the breeding site had a shorter prelaying period and produced a smaller clutch than birds arriving early. A stronger test would be to experimentally retard arrival of migratory birds, taking care to prevent any condition gain during the retarding period.

A third test would be an experimental manipulation of individual birds' perceived time remaining in the season. Such a test assumes that birds can assess their temporal position within the breeding season. For example, Meijer (1989) manipulated the photoperiod of captive kestrels. Birds exposed to a long photoperiod, mimicking a time late in the breeding season, produced their clutches sooner than birds subjected to an early spring photoperiod, as predicted by our model. However, the long-photoperiod birds did not produce a smaller clutch, contrary to our predictions.

A fourth test would be to advance the breeding season by supplementing food prior to the usual period of breeding. This shifts the T_C of affected individuals to the left (or, equivalently, elevates their condition at T_S). Our model predicts earlier and larger clutches for experimental birds (figs. 2 and 4). However, as in the previous example, we would expect no change in the clutch size of experimental birds relative to control birds laying on the same date. Most food-addition experiments in birds may be of this kind: food is usually supplemented well before the typical breeding season (Davies and Lundberg 1985; Arcese and Smith 1988; Meijer et al. 1990). The results from experiments with single-brooded species support our predictions in two ways: (1) experimental birds generally laid larger and earlier clutches and (2) clutch size was usually no larger than that for control birds that laid on the same date. The latter result is expected only if the primary effect of food supplementation is to advance the time at which birds reach a baseline level of condition. However, food additions may also elevate the rate at which birds gain condition. The predicted effects of rate manipulation are more complicated, and we consider them next.

Rate of Condition Gain

Our switch curve connects clutch size and lay date optima for birds that have equal rates of condition gain but different times at which they achieve baseline condition (fig. 2). To accommodate a change in rate of condition gain (a second possible outcome of food supplementation), we must introduce a second switch curve for affected birds, as shown in figure 4. The new curve corresponds to a higher rate of condition gain; it will always lie above the curve for birds with a lower rate. This effect can be deduced from figure 1*B:* an increase in rate of condition gain, $g(C)$, increases the value of $g(C)N'(C)/N(C)$ and hence shifts the curve for relative fitness gain upward. A *horizontal segment* corresponding to any given optimal lay date (fig. 1*A*) now extends further to the right (fig. 1*B*) and therefore corresponds to a higher C and higher clutch size.

The predicted outcomes are illustrated in figure 4. The *dotted trajectories* and lower switch curve indicate growth, clutch sizes, and lay dates expected at the initial (control) rate. The *dashed trajectories* and the *upper curve* indicate the values expected from an experimentally increased rate of condition gain that begins midway through the breeding season. Three results are evident. (1) An increase in rate of condition gain always increases the optimal clutch size. (2) Affected birds should lay more eggs than control birds laying on the same date. This is in contrast to the result expected from a mere advancement of the breeding season. (3) Lay date may be advanced, unchanged, or delayed, depending on the starting condition of individual birds. If a bird experiences an elevated growth rate long before her otherwise predicted lay date, then lay date should be advanced (trajectory for individual 2 in fig. 4). If the growth rate is advanced immediately prior to the predetermined lay date, the bird should slightly delay breeding (trajectory for individual 1 in fig. 4). This seemingly paradoxical result can be intuited: an elevated growth rate always makes it advantageous to lay a larger clutch. If only a short time remains before the optimal lay date, this lay date must be delayed. In this case there is a partial trade-off between an elevated clutch size and a later lay date. However, if there is more time available, the higher growth rate makes it possible to achieve both a larger clutch and an advanced lay date.

Most food manipulations on single-brooded species have added food well before the typical breeding season and have, as expected, resulted in earlier lay dates.

In some cases clutch size was increased relative to control birds laying on the same (advanced) date, but this effect was rarely statistically significant (Davies and Lundberg 1985; Arcese and Smith 1988; Daan et al. 1989; Meijer et al. 1990). The pattern suggests that the primary effect of most manipulations has been to advance the time at which birds begin gaining condition for breeding, without greatly increasing the rate of condition gain during the breeding season. Such a result would be expected if the primary period of food limitation precedes the breeding season.

In order to disentangle effects of condition gain from those of season onset, food should be added after the breeding season has begun. Under these conditions we expect an increased clutch size relative to control birds laying on the same date but variable effects on lay date depending on the duration of exposure of individuals to additional food. A few recent studies have supplemented food during the breeding season. In general these show a stronger effect on clutch size and a weaker effect on lay date than the previously cited studies. In two recent cases in which food was added very late, lay date was not affected or was actually delayed and clutch size increased significantly above that of control birds laying on the same date (Carlson 1989; Nilsson 1991). Carlson (1989) experimentally increased courtship feeding to red-backed shrikes about 10 d prior to laying. There was no significant effect on lay date but a 20% increase in clutch size. Nilsson (1991) supplemented food to individual marsh tits once they had started laying and observed a significant increase in clutch size relative to control birds. The latter two studies are significant in that they show a direct effect of food on clutch size, disproving the possibility that clutch size is determined solely by lay date. In contrast, late food addition to kestrels resulted in earlier lay dates and larger clutch sizes, but experimental females had body masses indistinguishable from those of earlier layers (Meijer et al. 1988). The latter result suggests that clutch size may be fixed by lay date in this species. Further studies of this type would be valuable, particularly if growth rate can be monitored directly.

Egg Value

The model also predicts responses to changes in perceived egg value (probability of recruitment), through its effects on the relative cost of delay ($-V'(T)/V(T)$) (fig. 1*A*). When offspring value at a given date (i.e., $V(T)$) is decreased, individuals are expected to lay earlier and to produce smaller clutches. This is because $-V'(T)/V(T)$ rises with a decrease in $V(T)$, its denominator, pushing the curve in figure 1*A* upward. A horizontal segment corresponding to a given clutch size would now intercept the new curve to the left of the previous value (i.e., at an earlier date); conversely, a given lay date is now associated with a lower condition (and hence clutch size). The result is a new switch curve for clutch size and lay date to the left and below the previous curve. An individual encounters the new curve at an earlier time and a lower condition than before, and thus produces a smaller clutch.

An additional alteration is to increase the rate at which offspring value is declining with advancing lay date (i.e., $V'(T)$). In this case, optimal clutch size will decline more steeply with optimal lay date than before, because the numerator of $-V'(T)/V(T)$ is increased at the same time as its denominator is decreased. This result predicts that among populations or years the steepness of the switch curve for clutch size and lay date should be positively correlated with the steepness of the decline in egg value.

It is difficult to test these predictions by experimental manipulation of egg value for two reasons. First, one must manipulate egg value without affecting condition gain rate in the parents (ruling out a simple food addition). Second, one must ensure that the new egg values are detectable by parents prior to egg laying. Comparative data may provide a suitable test. For example, if parents are capable of predicting the relationship between lay date and egg value in any given year (e.g., using environmental cues at the start of the season) then we expect a positive relationship among years between the steepness of this relationship and that of the observed curve of clutch size and lay date. Korpimaki and Hakkarainen (1991) have found such a positive relationship in Tengmalm's owl. Survival of young owls was largely determined by vole abundance. Vole populations follow a regular cycle and conceivably parents can foresee declines in the food supplies for their offspring (Korpimaki and Hakkarainen 1991). We would also expect the steepness of the two curves to be positively correlated among populations and perhaps species that have evolved under different regimes of $V(T)$. The slope of the egg value versus lay date curve indeed varies between populations and species (see, e.g., Perrins and McCleery 1989; Korpimaki and Hakkarainen 1991), but its relationship to the slope of the clutch size versus lay date curve has not been investigated.

Individual Variation in Condition Accumulation Rates

There is growing evidence that breeding individuals differ in their ability to acquire resources (Murphy and Haukioja 1986; Martin 1987; Daan et al. 1990). The variation may result from differences in age (and hence experience) or territory quality. Hence individuals in a population probably vary not only in the times at which they achieve condition C_C, but also in rates of condition gain. For instance, suppose that there are three types of individuals in the population that differ in their rates of condition gain. In such a case we expect there to be three optimal switching curves, one for each such rate. Figure 5 shows such switch curves as *solid lines*. Individual growth trajectories are shown as *dashed lines*. If all individuals have the same T_C (shown as "late T_C" in fig. 5), then the observed pattern of clutch size and lay date would be the *dotted curve* to the right in figure 5. On the other hand, there may be several different values of T_C represented in the population, as illustrated by the two groups of trajectories in figure 5. Such a combination produces a "smeared" overall pattern of clutch sizes and lay dates among all individuals in a population.

The change to be expected in response to a food addition thus depends on the amounts of variation present among individuals in both starting times and growth rates and on which of these two variables the experiment itself perturbs. For example, consider a population in which all individuals have the same starting time, T_C, but vary only in gain rates. The natural pattern of clutch size and lay date might then be similar to that shown by the *dotted curve* to the right in figure 5.

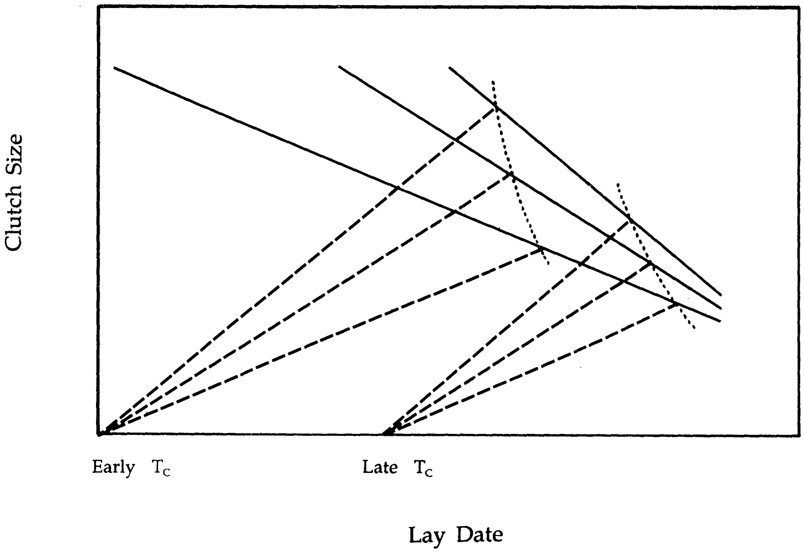

FIG. 5.—The effects of variation among individuals in both starting time and rate of condition gain. Each *solid line* is the optimal switch curve of clutch size and lay date for all individuals having the same rate of condition gain but different starting times, T_C. *Higher lines* correspond to higher rates of condition gain. *Dotted lines* connect optimal clutch sizes and lay dates of individuals starting at the same time but having different gain rates.

If this hypothetical population is subjected to a food addition that advances the onset of breeding but does not alter growth rate, then every individual should lay more eggs earlier, according to the switch curve that corresponds to her rate of gain of condition. The result would be a wholesale shift to the left in the observed pattern of clutch sizes and lay dates (fig. 5). Conversely, if the food addition only affects rates of condition gain during the breeding season, then each individual should move to a higher switch curve. The result would be a new pattern of clutch sizes and lay dates that is only an extension upward and to the left of the previous pattern (i.e., along a *dotted curve* in fig. 5). Thus, a comparison of control birds to experimental would reveal no difference in clutch size for any given lay date. Clearly, when carrying out a food-addition experiment, attention should be paid to the sources of natural variability in clutch size and lay date.

Constraints on Clutch Size

Conceivably, a threshold body condition may need to be surpassed in order to produce a single egg, imposing a constraint on minimum clutch size. This minimum can be represented by the baseline C_C in equation (6). It is interesting that varying the height of the threshold (see fig. 2) only alters the proportion of individuals reproducing in a season but has no effect on the position of the switch curve above the minimum. The effect on the proportion of individuals breeding will depend on the fraction of individuals in low condition near the end of the season.

For example, if the onset of the breeding season is delayed, those individuals that surpass the threshold will decrease the period of resource accumulation and produce a lower subsequent clutch size (as in fig. 2). The proportion of individuals that do not surpass the threshold (and thus will not reproduce) will simply increase.

A maximum clutch size may be imposed by loading constraints on the reproductive tract, or space restrictions in the nest. Constraints on maximum clutch size, or diminishing returns accompanying large clutches, are interesting because they can lead to the evolution of multiple clutches within a season. We develop this theory in Appendix A.

DISCUSSION

We have focused on the transition from a prereproductive to reproductive stage in birds. However, we believe that a similar framework would be useful for predicting norms of reaction for many other life-history transitions in other taxa. The ontogeny of all organisms is characterized by developmental shifts involving transitions in niche use, morphology, function, and sexual stage. Both the time at which the transition occurs and the condition of individuals at that time are typically related to fitness. Commonly, there is a fitness advantage to early transition from one life-history stage to the next (Forrest 1987; Fernandes 1990; Ludwig and Rowe 1990; Rowe and Ludwig 1991). In addition, fitness gains following a life-history transition usually increase with condition or size, which takes time to accumulate (see, e.g., Forrest 1987; Smith 1987). Thus, we expect that a conflict between the advantages of early life-history transition (e.g., higher offspring value, lower prereproductive mortality) and late transition (higher fecundity) is common. For example, theory presented here may be useful for predicting optimal reaction norms for age and size at maturity in a variety of taxa (Rowe and Ludwig 1991; Kozlowski 1992). As predicted from theory presented here, temporal declines in the condition of individuals at the time of life-history transitions are common (see, e.g., Forrest 1987; Daan et al. 1989; Ydenberg 1989; Fernandes 1990; Reznick 1990; Rowe and Ludwig 1991; Schultz et al. 1991).

We have provided a theoretical basis for Drent and Daan's (1980) hypothesis that the conflict between the advantages of early breeding and of high condition explains the commonly observed pattern of seasonal decline in avian clutch size (see also Loman 1982). Moreover, manipulation of model parameters leads to novel predictions that are testable in the field by both comparative and experimental methods. Results of our initial comparison of these predictions with available data are usually favorable. For example, the theory predicts that food supplementation should advance lay date and increase clutch size, a result supported by experiments (reviews in Davies and Lundberg 1985; Martin 1987; Arcese and Smith 1988; Daan et al. 1989; Meijer et al. 1990). The effect on clutch size was usually weaker than on lay date (and not statistically significant), but an increase in clutch size has been noted in virtually every study involving a single-brooded species. Such a result would be highly improbable if there were no effects of food supplementation upon clutch size.

However, we show that the consistency of these field observations may obscure a number of different underlying processes. Our model may aid in the resolution of those differences. We also identify situations in which food additions should and should not result in a change in clutch size at a given lay date. Finally, we indicate how the expected results of food manipulations depend on natural sources of variability in clutch size and lay date (starting time vs. rate of condition gain) and on the manner in which the experiment alters these sources.

Price et al. (1988) recently emphasized the effects of condition (nutrition) on lay date and fitness and incorporated the idea into a genetic model for the evolution of lay date. Their analysis was based on the assumption that birds in good condition lay earlier, although they did not offer a model to explain this assumption. Our model shows how optimal lay date should decrease with increasing condition (fig. 3*A*), and hence it identifies the selective forces that favor the evolution of a negative correlation between condition and lay date. Similarly, we show how selection is expected to produce a positive correlation between condition and clutch size (fig. 3*B*), as assumed by Price and Liou (1989).

The central conclusion of Price and colleagues is that the dependence of clutch size and lay date on condition leads to a persistent association between each of these traits and fitness, without necessarily producing an evolutionary response. Birds adhering to our formulation would also appear to be under persistent directional selection: individuals in high condition have the earliest and largest clutches and attain highest fitness (fig. 3). Apart from the genetic component, phenotypic variation in clutch size and lay date is maintained by variation in nutritional condition. We connect the ideas of Price et al. (1988) and Price and Liou (1989) by demonstrating a condition-dependent norm of reaction (switch curve) for optimal clutch size and lay date, rather than independent optima for both clutch size and lay date. Thus, our theory identifies the condition-dependent switch mechanism as a target of natural selection.

There is increasing evidence of between-year costs of reproduction in birds: reproductive effort in one breeding season has a direct negative effect on future fecundity or survival (see, e.g., Williams 1966; Gustafsson and Sutherland 1988; Nur 1988). Some have suggested that a cost of reproduction may account for the seasonal decline in clutch size (Hussell 1972; Murphy 1986*a;* Hochachka 1992). According to this argument, if offspring value declines seasonally, then parents should be less willing to pay the cost of producing an egg late in the season when the contribution of that egg to fitness is low. Hence, optimal clutch size is expected to decline through the breeding season. However, this scenario does not explain why some individuals delay reproduction until late in the season; therefore it does not provide a full explanation for seasonal declines in clutch size. Our theory shows that variation among individuals in condition, combined with a seasonal decline in offspring value, can explain both the delay of some individuals and their subsequent small clutches without invoking a cost of reproduction.

Although we have not included between-year costs of reproduction in our basic model, the theory presented here is similarly based on trade-offs among fitness components in a single breeding season. Optimization of such trade-offs among fitness components is the essence of earlier ideas on individual optimization of clutch size in birds (see, e.g., Lack 1954; Drent and Daan 1980; Hogstedt 1980; Pettifor et al. 1988). Nevertheless, addition of between-season costs of reproduction is possible without qualitative change to our predictions. Appendix B contains an expansion of our model to include reproductive costs that are paid in subsequent years. In the presence of such additional costs, clutch size is reduced to some extent and this effect increases as the season progresses: parents will be less willing to pay reproductive costs as the benefits of reproductive effort decrease.

ACKNOWLEDGMENTS

This research was supported by Natural Sciences and Engineering Research Council grants to G. G. E. Scudder, D.L., and D.S. and by an I. W. Killam Fellowship to L.R. We thank C. Adkins, S. Daan, W. Hochachka, M. Kirkpatrick, C. Perrins, T. Price, D. Repasky, J. Tinbergen, and D. Winkler for their comments on an earlier draft.

APPENDIX A

Multiple Clutches

The previous theory concerns individuals that reproduce only once per breeding season. In this appendix we indicate how the analysis can be extended to include multiple clutches per breeding season. Our formulation is limited to two clutches per breeding season, but a similar treatment is possible for more than two clutches.

PROBLEM FORMULATION

The model is the same as that described in equations (1)–(3), except that we modify it to include the fitness payoff from producing a second brood. We shall assume that the clutch size associated with condition C is $N(C)$ as in our earlier formulation. Furthermore, the probability that an egg laid yields a recruit is given by $V(T)$, and the growth rate for condition is given by $g(C)$ as was assumed before.

We assume that, after an individual lays her first clutch of size C_1, there is a time lag, l_1, before she can start to accumulate condition for the second clutch. During this time interval her condition is assumed to drop to a fixed level, C_3. The loss of condition is assumed to be that required to produce and rear the clutch. The time lag may be thought of as the time required to rear the first clutch: it is proportional to the difference between C_1 and C_3. If we denote the date of first laying by T_1 and the time at which condition begins to be accumulated for the second brood by T_3, then

$$T_3 = T_1 + l_1, \qquad \text{(A1)}$$

where

$$l_1 = \gamma(C_1 - C_3). \qquad \text{(A2)}$$

According to equations (A1) and (A2), all individuals lose condition at the same rate, γ; during incubation, for example, loss rates are independent of clutch size. However, the incubation period l_1 depends upon clutch size in a linear fashion.

Suppose that a given individual starts at condition C_S at time T_S, produces her first clutch at time T_1, when she has attained condition C_1, and produces her second clutch at time T_2 and condition C_2. The problem is to find T_1, C_1, T_2, and C_2 in order to maximize fitness. That is, we wish to maximize

$$F(C_1, T_1, C_2, T_2) = V(T_1)N(C_1) + V(T_2)N(C_2), \tag{A3}$$

in analogy with equation (3). The first term in equation (A3) is the contribution of the first clutch to fitness, and the second term is the contribution of the second clutch. These four variables to be determined are not independent, since they are connected by growth assumption (1). An equivalent form of equation (1) for the period between T_3 and T_2 is

$$T_2 - T_3 = \int_{C_3}^{C_2} \frac{dC}{g(C)}, \tag{A4}$$

and for the period between T_S and T_1 the requirement is

$$T_1 - T_S = \int_{C_S}^{C_1} \frac{dC}{g(C)}. \tag{A5}$$

Equations (A1), (A2), (A4), and (A5) are constraints to be satisfied in maximizing F.

DETERMINATION OF C_1 AND C_2

One might eliminate some of the preceding variables by use of the constraints, but it is simpler to perform the differentiation first: we can obtain the necessary requirements for a maximum of F from the differential forms of equations (A1), (A2), (A4), and (A5). These are

$$dT_3 = dT_1 + \gamma dC_1, \tag{A6}$$

$$dT_2 - dT_3 = \frac{dC_2}{g(C_2)}, \tag{A7}$$

$$dT_1 = \frac{dC_1}{g(C_1)}. \tag{A8}$$

Note that differentials of T_0, C_3, and C_0 do not appear in equation (A8), since these variables are fixed during the optimization. At the optimum

$$\begin{aligned} dF = {} & V'(T_1)N(C_1)dT_1 + V(T_1)N'(C_1)dC_1 \\ & + V'(T_2)N(C_2)dT_2 + V(T_2)N'(C_2)dC_2 = 0, \end{aligned} \tag{A9}$$

where the prime symbol indicates the derivative.

If we eliminate three of the differentials from equation (A9) by means of equations (A6), (A7), and (A8), there will remain two independent differentials in (A9). We choose to eliminate all others in terms of dT_1 and dT_2. Note that we can eliminate dC_1 and dT_3 by using equations (A6) and (A8). If these substitutions are made in equation (A7), the result is

$$\frac{dC_2}{g(C_2)} = dT_2 - [1 + \gamma g(C_1)]dT_1. \tag{A10}$$

This equation is a crucial one, and it differs from the corresponding equation (A8) by the term involving dT_1. After the appropriate substitutions have been made into equation (A9), the result is

$$\begin{aligned} 0 = {} & \{V'(T_2)N(C_2) + V(T_2)g(C_2)N'(C_2)\}dT_2 \\ & + \{V'(T_1)N(C_1) + V(T_1)g(C_1)N'(C_1) - V(T_2)g(C_2)N'(C_2)[1 + \gamma g(C_1)]\}dT_1. \end{aligned} \tag{A11}$$

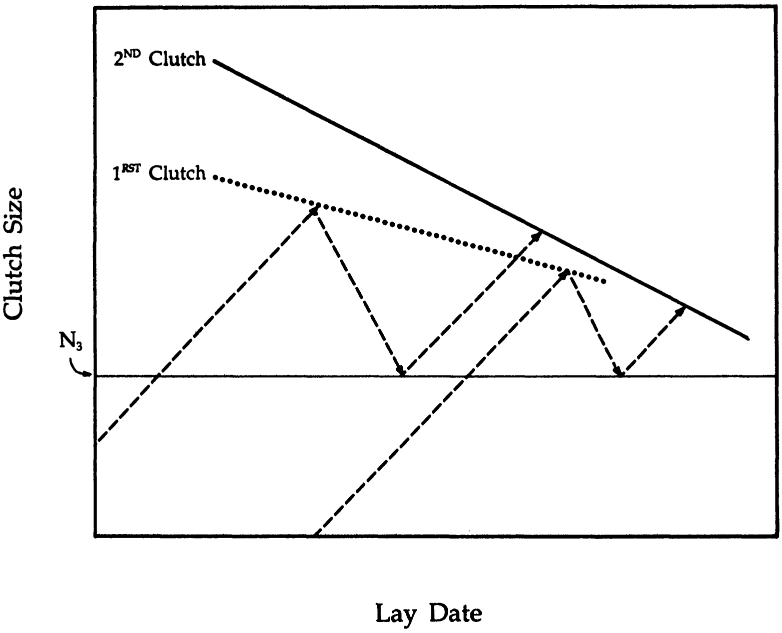

FIG. A1.—Clutch size vs. lay date for the case of two clutches. The *dashed curves* show the trajectories of condition with time for two individuals that begin the season at different condition. Each trajectory depicts the initial gain in condition, laying of the first clutch (and the accompanying loss of condition), a lag before condition again begins to accumulate, and finally the laying of the second clutch. The *solid line* shows the optimal combination of lay date and clutch size for the second clutch. The *dotted line* shows the optimal combination of lay date and clutch size for the first clutch. It lies below the *solid curve:* hence the size of the first clutch is reduced and its lay date is advanced when individuals lay two clutches.

By setting the coefficient of dT_2 equal to zero and simplifying, we obtain an equation that specifies the optimal timing and size of the second clutch,

$$\frac{V'(T_2)}{V(T_2)} + g(C_2)\frac{N'(C_2)}{N(C_2)} = 0\,. \tag{A12}$$

Note that equation (A12) is the same equation derived in the single-clutch model, corresponding to equation (4). By setting the coefficient of dT_1 equal to zero, we obtain an equation specifying the optimal size and timing of the first clutch

$$\frac{V'(T_1)}{V(T_1)} + g(C_1)\frac{N'(C_1)}{N(C_1)} - \frac{V(T_2)}{V(T_1)}\frac{N'(C_2)}{N(C_1)}g(C_2)[1 + \gamma g(C_1)] = 0\,. \tag{A13}$$

The optimality equations (A12) and (A13) can be put into a form corresponding to equation (5):

$$-\frac{V'(T_2)}{V(T_2)} = g(C_2)\frac{N'(C_2)}{N(C_2)}, \tag{A14}$$

$$-\frac{V'(T_1)}{V(T_1)} = g(C_1)\frac{N'(C_1)}{N(C_1)} - \frac{V(T_2)}{V(T_1)}\frac{N'(C_2)}{N(C_1)}g(C_2)[1 + \gamma g(C_1)]\,. \tag{A15}$$

Actually equation (A14) is identical to equation (5). Each side may be graphed as in figure A1. Since the second term on the right-hand side of equation (A15) is positive and is subtracted from the first term, the curve in the *right-hand side* of figure A1 is lowered compared with the unaltered form. This fact implies that the first clutch will be laid earlier and be smaller if a second clutch is anticipated. Some of the resulting life histories are shown in figure A1. An individual female accumulates condition with time until the first switch curve is crossed, at which time she produces her first clutch. After the lag period, l_1, given by equation (A2), she begins accumulating condition for the second clutch, which is laid when the second switch curve is reached. These two switch curves may be nearly the same if the second term on the right-hand side of equation (A15) is small. This is to be expected when the value of the second clutch is small relative to the first clutch, which corresponds to a steep decrease in recruitment probability as the breeding season progresses.

APPENDIX B

EFFECT OF A COST OF REPRODUCTION

The earlier discussion dealt only with reproductive output for a single season. Here we describe some modifications to that development that account for the effects of later reproductive bouts.

We denote the residual fitness resulting from subsequent reproduction by $R(C)$. This quantity is assumed to depend upon the clutch size in the initial season. If R does not depend upon C or T, there is no effect upon our earlier results. But if the residual fitness is included, equation (3) becomes

$$F = V(T)N(C) + R(C), \tag{B1}$$

and consequently equation (5) becomes

$$-\frac{1}{V(T)}\frac{dV}{dT} = g(C)\frac{1}{N(C)}\frac{dN(C)}{dC} + \frac{dR}{dC}\frac{1}{V(T)N(C)}. \tag{B2}$$

Equations (B1) and (B2) are analogous to equations (A3) and (A13), respectively. That is, the possibility of laying a second clutch is analogous to a cost of reproduction as far as the timing of the first clutch is concerned: a large first clutch results in a reduced second clutch. As a consequence of this analogy, we expect that the effect of the additional cost term in equation (B2) will be to produce earlier, smaller clutches.

We shall characterize both the direction and magnitude of the changes in the optimal switch curve induced by the additional term in equation (B2). The expression $R(C)/[V(T)N(C)]$ is the ratio between the residual fitness and the fitness associated with the current season. The final term in equation (B2) has a corresponding interpretation of the change in residual fitness associated with a clutch of size C, divided by the fitness for the current season. The sign of the final term in equation (B2) will be negative as long as higher clutches in the current season depress the residual fitness. Hence the curve in figure 1*B* is lowered. A consequence is that smaller clutches are laid at a given time T, as was pointed out in Appendix A.

In order to assess the magnitude of such changes, we examine the ratio of the two terms on the right-hand side of equation (B2). To facilitate this procedure, we may rewrite equation (B2) in the form

$$-\frac{1}{V(T)}\frac{dV}{dT} = g(C)\frac{1}{N(C)}\frac{dN(C)}{dC}[1 + Q], \tag{B3}$$

where

$$Q = \left[\frac{dR}{dC}\right]\left[\frac{dC}{g(C)dN(C)}\right]\frac{1}{V(T)}. \tag{B4}$$

The first two factors in Q may be interpreted as the per-egg decrease in residual fitness and the time required to produce an additional egg, respectively. It is plausible that these two factors will vary only slightly as the season progresses. Hence the variation in Q (and hence the relative importance of the residual fitness) will be influenced mainly by $1/V(T)$. This factor increases strongly as the season draws to its end. Hence we expect that the effects of postseason residual fitness will be expressed most strongly by the marginal (later, low condition) individuals during the first season. Their lay date (if any) will be advanced and their clutch sizes will be reduced, possibly to zero.

LITERATURE CITED

Andersson, M. 1982. Sexual selection, natural selection and quality advertisement. Biological Journal of the Linnean Society 17:375–393.

Arcese, P., and J. N. M. Smith. 1988. Supplemental food ameliorates the effects of high population density on reproduction in song sparrows. Journal of Animal Ecology 57:119–137.

Askenmo, C. 1982. Clutch size flexibility in the pied flycatcher *Ficedula hypoleuca*. Ardea 70:189–196.

Askenmo, C., and U. Unger. 1986. How to be double-brooded: trends and timing of the breeding performance in the rock pipit. Ornis Scandinavica 17:237–244.

Carlson, A. 1989. Courtship feeding and courtship in red-backed shrikes (*Lanius collurio*). American Naturalist 133:454–457.

Cooke, F., C. S. Findlay, and I. F. Rockwell. 1984. Recruitment and timing of reproduction in lesser snow geese (*Chen caerulescens caerulescens*). Auk 101:451–458.

Daan, S., C. Dijkstra, R. H. Drent, and T. Meijer. 1989. Food supply and the annual timing of avian reproduction. Pages 392–407 *in* H. Oullet, ed. Acta XIX International Congress of Ornithology. University of Ottawa Press, Ottawa.

Daan, S., C. Dijkstra, and J. M. Tinbergen. 1990. Family planning in the kestrel (*Falco tinnunculus*): the ultimate control of covariance of laying date and clutch size. Behaviour 114:83–116.

Davies, N. B., and A. Lundberg. 1985. The influence of food on the time budgets and timing of breeding of the dunnock *Prunnella modularis*. Ibis 127:100–110.

Dijkstra, C., L. Vuursteen, S. Daan, and D. Masman. 1982. Clutch size and lay date in the kestrel (*Falco tinnunculus* L.): the effects of supplementary food. Ibis 124:210–213.

Dijkstra, C., S. Daan, T. Meijer, A. J. Cave, and R. Foppen. 1988. Body mass of the kestrel in relation to food abundance and reproduction. Ardea 76:127–140.

Drent, R. H., and S. Daan. 1980. The prudent parent: energetic adjustment in avian breeding. Ardea 68:225–252.

Fernandes, D. M. 1990. Sex change in terrestrial slugs: social and ecological factors. Pages 155–182 *in* M. Mangel, ed. Sex allocation and sex change: experiments and models. Springer, Berlin.

Forrest, T. G. 1987. Insect size tactics and developmental strategies. Oecologia (Berlin) 73:178–184.

Grafen, A. 1990. Sexual selection unhandicapped by the Fisher process. Journal of Theoretical Biology 144:473–516.

Gustafsson, L., and W. J. Sutherland. 1988. The costs of reproduction in the collared flycatcher *Ficedula albicollis*. Nature (London) 335:813–815.

Hamann, J., and F. Cooke. 1989. Intra-seasonal decline of clutch size in lesser snow geese. Oecologia (Berlin) 79:83–90.

Hochachka, W. M. 1990. Seasonal decline in reproductive performance of song sparrows. Ecology 71:1279–1288.

———. 1992. How much should reproduction cost? Behavioral Ecology 3:42–50.

Hogstedt, G. 1980. Evolution of clutch size in birds: adaptive variation in relation to territory quality. Science (Washington, D.C.) 210:1148–1150.

Hörnfeldt, B., and U. Eklund. 1990. The effect of food on laying date and clutch-size in Tengmalm's owl *Aegolius funereus*. Ibis 132:395–406.

Hussell, D. J. T. 1972. Factors affecting clutch size in Arctic passerines. Ecological Monographs 42:317–364.

Jarvinen, A., and R. A. Vaisanen. 1984. Reproduction of pied flycatchers (*Ficedula hypoleuca*) in good and bad breeding seasons in a northern marginal area. Auk 101:439–450.

Klomp, H. 1970. The determinants of clutch size in birds: a review. Ardea 58:1–125.

Korpimaki, E., and H. Hakkarainen. 1991. Fluctuating food supply affects the clutch size of Tengmalm's owl independent of lay date. Oecologia (Berlin) 85:543–552.

Kozlowski, J. 1992. Optimal allocation of resources to growth and reproduction: implications for age and size at maturity. Trends in Ecology & Evolution 7:15–19.

Lack, D. 1954. The natural regulation of animal numbers. Clarendon, Oxford.

Loman, J. 1982. A model of clutch size determination in birds. Oecologia (Berlin) 52:253–257.

Ludwig, D., and L. Rowe. 1990. Life-history strategies for energy gain and predator avoidance under time constraints. American Naturalist 135:686–707.

Lundberg, A., and R. V. Alatalo. 1992. The pied flycatcher. Poyser, London.

Mangel, M., and C. Clark. 1986. Towards a unified foraging theory. Ecology 67:1127–1138.

Martin, T. E. 1987. Food as a limit on breeding birds: a life history perspective. Annual Review of Ecology and Systematics 18:453–487.

McNamara, J. M., and A. Houston. 1986. The common currency for behavioral decisions. American Naturalist 127:358–378.

Meijer, T. 1989. Photoperiod control of reproduction and molt in the kestrel, *Falco tinnunculus*. Journal of Biological Rhythms 4:351–364.

Meijer, T., S. Daan, and C. Dijkstra. 1988. Female condition and reproduction: effects of food manipulation in free-living and captive kestrels. Ardea 76:127–141.

Meijer, T., S. Daan, and M. Hall. 1990. Family planning in the kestrel (*Falco tinnunculus*): the proximate control of covariation of laying date and clutch size. Behaviour 114:117–134.

Murphy, E. C., and E. Haukioja. 1986. Clutch size in nidicolous birds. Current Ornithology 4:141–210.

Murphy, M. T. 1986*a*. Temporal components of reproductive variability in eastern kingbirds (*Tyrannus tyrranus*). Ecology 67:1483–1492.

———. 1986*b*. Body size and condition, timing of breeding, and aspects of egg production in eastern kingbirds. Auk 103:465–476.

Newton, I., and M. Marquiss. 1984. Seasonal trends in the breeding performance of sparrowhawks. Journal of Animal Ecology 53:809–829.

Newton, I., M. Marquiss, and A. Village. 1983. Weights, breeding and survival in European sparrowhawks. Auk 100:344–354.

Nilsson, J.-A. 1991. Clutch size determination in the marsh tit (*Parus palustris*). Ecology 72:1757–1762.

Nur, N. 1988. The consequence of brood size for breeding blue tits. III. Measuring the cost of reproduction: survival, fecundity, and differential dispersal. Evolution 42:351–362.

Nur, N., and O. Hasson. 1984. Phenotypic plasticity and the handicap principle. Journal of Theoretical Biology 110:275–297.

Perrins, C. M. 1966. Survival of young manx shearwaters *Puffinus puffinus* in relation to their presumed date of hatching. Ibis 108:132–135.

———. 1970. The timing of birds' breeding seasons. Ibis 112:242–255.

Perrins, C. M., and R. H. McCleery. 1989. Laying dates and clutch size in the great tit. Wilson Bulletin 101:236–253.

Pettifor, R. A., C. M. Perrins, and R. H. McCleery. 1988. Individual optimization of clutch size in great tits. Nature (London) 336:160–162.

Price, T., and L. Liou. 1989. Selection on clutch size in birds. American Naturalist 134:950–959.

Price, T., M. Kirkpatrick, and S. J. Arnold. 1988. Directional selection and the evolution of breeding date in birds. Science (Washington, D.C.) 240:798–799.

Reznick, D. N. 1990. Plasticity in age and size in maturity in male guppies (*Poecilia reticulata*): an experimental evaluation of alternative models of development. Journal of Evolutionary Biology 3:185–203.

Rowe, L., and D. Ludwig. 1991. Size and timing of metamorphosis in complex life cycles: time constraints and variation. Ecology 72:413–427.

Schultz, E. T., L. M. Clifton, and R. R. Warner. 1991. Energetic constraints and size-based tactics: the adaptive significance of breeding-schedule variation in a marine fish (Embiotocidae: *Micrometrus minimus*). American Naturalist 138:1408–1430.

Smith, D. C. 1987. Adult recruitment in chorus frogs: effect of size and date at metamorphosis. Ecology 68:344–350.

Williams, G. C. 1966. Natural selection, the costs of reproduction, and a refinement of Lack's principle. American Naturalist 100:687–690.

Ydenberg, R. C. 1989. Growth-mortality trade-offs and the evolution of juvenile life histories in the Alcidae. Ecology 70:1494–1506.

Associate Editor: Mark Kirkpatrick