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FOOD AS A LIMIT ON BREEDING BIRDS: A LIFE-HISTORY PERSPECTIVE

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INTRODUCTION

Food limitation is an important issue in ecology because it can influence life history traits, population sizes, and community structure (through effects of competition). Work at the level of populations and communities has led to arguments that food limitation and competition are more important in winter than during the breeding season (e.g. 1, 2, 7, 8, 83, 85, 211, 234). In fact, it is commonly argued that food is superabundant during the breeding season (7, 8, 161, 213, 246, 250, 251, 308–311). However, such arguments are based on indirect rather than direct evidence of the effects of food on reproduction and survival (fitness) (149). Direct evidence for food limitation and competition in winter exists when survival is affected, and some experimental evidence suggests such effects (e.g. 75, 113, 122, 132). However, if current or future reproductive success is limited by food, then food limitation will also exist during the breeding season.

Reproductive ecologists historically have argued that food limits reproductive success (e.g. 13, 297). Yet, even this school has included recent arguments against food limitation. For instance, Ettinger & King (77) think that perching time of birds commonly reflects loafing time because birds set their clutch and brood sizes based on years and periods of stringent (low food) conditions. However, perching time may not reflect loafing but rather an important time commitment to reproductive success (T. Martin, unpublished ms.) Thus, the status of food limitation in breeding birds is not clear.

Here, I review evidence for food limitation in the context of life history theory because it provides a fundamental framework from which to interpret

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food limitation based on reproductive success and survival. I examine evidence on the existence and consequences of food limitation, not the factors causing food limitation; I address these issues in more detail elsewhere (149, 150). I focus on birds with altricial young, although I include some comparative information on semi-precocial and precocial birds. Owing to time and space constraints, I mostly ignore the vast literature on seabirds.

An Energy Allocation Framework Based On Life-History Theory

Individuals of a genotype must reproduce at a rate, on average, that allows replacement with offspring that replace themselves, or else the genotype will be selected against over evolutionary time. Given that birds incur mortality no matter what level of breeding effort they provide (i.e. nonreproductive mortality), they always face some absolute lower limit on the annual fecundity necessary to balance mortality and achieve replacement. This annual fecundity should be distributed among more than one breeding attempt, if breeding failure increases disproportionately with increases in brood size above some limit and minimum fecundity exceeds this limit. On the other hand, season length may limit the number of breeding attempts and thereby place a lower limit on clutch size. Moreover, these lower limits on clutch size and fecundity are raised by the additional mortality of young and adults that is associated with the breeding effort (i.e. reproductive mortality) (53, 314, 315). To understand the extent to which individuals should sustain such reproductive mortality in their reproductive strategy requires an understanding of the trade-offs in adult and juvenile survival resulting from differential energy allocation by parents. Survival and longevity of parents are often thought to be inversely related to reproductive effort, where reproductive effort is the proportion of total energy and nutrients that an organism devotes to reproduction (see 281, 282a). The energy and nutrients not used for reproduction are incorporated in somatic effort (SE), used for maintenance and survival. Reproductive effort can be subdivided into mating effort, which I am going to ignore, and parental effort (PE) which is the sum of expenditures of nutrients, or effort, or taking of risks in the production and raising of young or other kin (144). Parental investment (cf 288) is the portion of PE received by each offspring (144).

I consider total energy (TE) to be energy and nutrient reserves stored prior to the reproductive event, plus those acquired by feeding during the reproductive event. TE represents the amount available for reproduction and survival (TE = PE + SE). Note that this definition does not focus solely on energy; nutrients, such as protein, can equal or exceed energy in importance (6, 81, 119, 120, 130, 216, 243). Energy may be drawn largely from endogenous fat reserves, while protein may be accumulated mainly through exogenous re-

sources (71, 76, 120, 129, 130, 287). However, both fat and protein are accumulated by feeding either prior to or during the reproductive event. Consequently, the time spent feeding relative to the availability of protein and energy in foods will determine their rate of intake and storage. Thus, TE reflects food availability relative to available foraging time before and during a reproductive event, as appropriate to an analysis of food limitation.

Clutton-Brock (55) emphasized the importance of distinguishing between energetic costs of breeding (roughly equivalent to PE) and reproductive costs (costs affecting residual reproductive value, which is defined as future survival and reproductive potential). I assume that residual reproductive value increases with the somatic energy (SE) remaining at the termination of breeding events. I examine the validity of this assumption later. I also assume that physiological condition can only improve to some maximum such that residual reproductive value increases with SE only up to some limit (SE*). If PE is insufficient to reduce SE below SE*, then an energetic cost of breeding exists (i.e. PE), but there is no reproductive cost (Figure 1). A reproductive cost occurs whenever PE causes SE to decrease below SE* (i.e. $SE/SE^* < 1$). Consequently, if $SE/SE^* > 1$, then parents are obtaining or saving energy for themselves that will have no benefit (Figure 1). This extra energy could be allocated to PE to increase the number or probability of survival of offspring (Figure 1). Thus, strategies where $SE/SE^* > 1$ are selectively inferior to ones where PE is increased and $SE/SE^* < 1$ (also see 91), assuming that increases in PE do not cause disproportionate increases in mortality from predation or other sources. As a result, for birds that maximize fitness, there will, on average, be a reproductive cost ($SE/SE^* < 1$), which means that parents will be energy (food) limited. However, the extent to which birds should reduce SE below SE* will depend on the average survival schedules of adults versus juveniles (102, 139, 156, 168, 206, 230, 255, 256, 318).

Parents must also decide how to allocate PE among offspring and thereby determine the number and quality of young they will try to produce. Parents should provide sufficient energy per offspring to optimize the chances of survival of each young to achieve the maximum number of young possible. Such strategies should commonly result in offspring receiving less than the maximum energy they can use, creating a parent-offspring conflict (cf 289) and reflecting an energy cost (food limitation) to the juvenile.

In short, the average reproductive strategy of a species should reflect evolutionary selection pressures, and it should result in food limitation for both parents and young. However, responses should vary around these average strategies with variation in food in ecological time. This variation in food should be expressed in part by the physiological condition (energy reserves) of the parents at the beginning of the reproductive event. These energy reserves are critical to the reproductive strategy in ecological time because

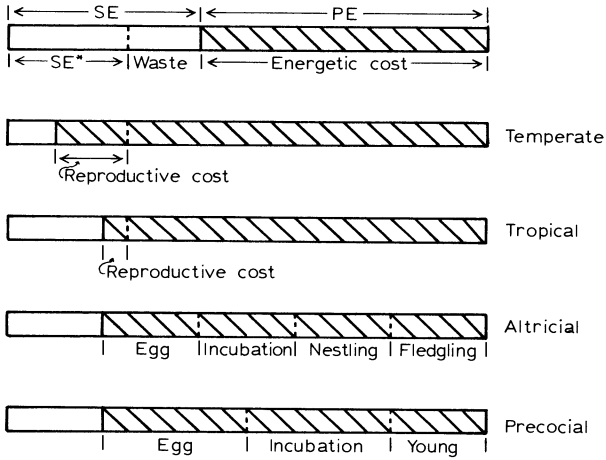

Figure 1 Qualitative illustration of partitioning of total energy (TE) for reproduction. PE (hatched areas) is parental effort (see text for definitions) and represents the energetic cost of breeding. SE (clear areas) is somatic energy and represents the energy left after reproduction is completed. SE* (represented by the dashed line) is the level of SE at which further increases in SE have no effects on residual reproductive value; increases in SE when it is less than SE* cause increases in residual reproductive value. If SE > SE*, then the difference is waste energy; and if SE < SE* then the difference is the reproductive cost (see text for full explanation). The reproductive cost incurred differs among species, such as temperate versus tropical, due to differences in mortality schedules. Also, partitioning of PE among the various activities of the breeding cycle differs among species, such as altricial versus precocial.

they must last through the entire reproductive cycle (egg laying to independence of young). Decreases in reserves at the beginning of the reproductive event must be met either by decreased investment in current offspring (fewer or lower quality) or increased dependence on exogenous resources, which takes time and energy away from caring for the young. Of course, the size of such reserves and the extent to which species depend on them will vary among species and ecological groups. Thus, I will explore this energy allocation perspective as I examine food limitation at the levels of both adults and young.

EGG PRODUCTION

Egg formation is the first process in the nesting cycle that requires energy and nutrient output (not counting the energy required for gonadal hypertrophy). The amount of energy and nutrients invested in egg production varies with the size, quality, and number of eggs, but this is as modified by the need for energy for stages after egg production. For example, the daily energy ex-

penditure for production of clutches increases from altricial to galliform to anseriform species (124), a progression of increasing precocity that follows Nice's (180) classification. Precocial parents can allocate a greater proportion of PE to egg production than do altricial parents (Figure 1) because care of their young requires less energy (136). Such comparisons of precocial and altricial birds provide a convenient starting point because they highlight the functional effects of differences in egg size and quality.

Egg Size and Quality

In general, egg size increases with body mass, but not at a proportional rate; egg size increases proportional to adult metabolic rate (15, 215). When these allometric effects are corrected, relative egg size increases with precocity—precocial birds lay larger eggs that produce larger hatchlings (214).

The energy content (caloric density) of eggs, determined by egg composition, also varies between precocial and altricial birds. The caloric density of an egg increases with the yolk content because yolk contains higher levels of lipids and proteins than of albumen. In general, yolk content and caloric density tend to increase with degree of precocial development of hatchlings (15, 50, 180, 204, 228, 230, but see 313). Thus, larger eggs with greater energy content produce young that are larger and more developed at hatching and are supplied with more energy reserves.

The same relationship exists within species; hatching success, maturity, weight, growth rate, and survival of young from large eggs are typically greater than from small eggs (5, 22, 40, 62, 107, 128, 145, 164, 173, 185, 189, 193, 196, 253, 257). However, effects of egg size and quality can be modified by parental care; in a series of experiments on European starlings *(Sturnus vulgaris),* Ricklefs (237) found that differences in parental care could override effects of egg size on growth rate, but egg size did affect the plateau size of the nestling. This latter result is still significant because larger plateau size can confer an advantage on young birds; larger nestlings have a higher probability of survival after fledging (60, 64, 65, 69, 87, 135, 178, 188, 200, 258, 297; but see 16, 249).

Trade-off Between Egg Quality and Number

Assuming that offspring survival is higher, on average, from higher quality eggs, then under ideal conditions, birds should produce such eggs. I will assume that the survival probabilities of young birds vary as a logistic function of egg size because egg size influences nestling size and the logistic function appears to be a reasonable explanation of nestling survival relative to nestling size (see 187 and later). Consequently, above some size threshold, changes in egg size and quality will have negligible impact on subsequent

survival, but reductions below this size threshold will have increasingly costly repercussions on nestling survival (Figure 2a).

Although the proportion of PE allocated to egg production is set by the energy demands of egg production relative to later stages, the actual quantity of energy allocated will depend on the magnitude of PE as determined by TE (Figure 1). This quantity may be limited in such a way that the number of eggs laid is limited (13, 119, 172). On the other hand, given that the energy cost of producing an egg depends on the energy content of the egg, then the number

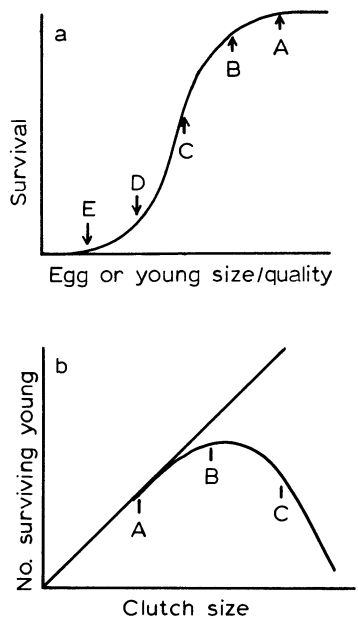

Figure 2 (*a*) Survival probability of eggs or young as a function of their size/quality. Survival probability is maximized if size of eggs or young is A or larger. Decreases in egg or young below A has increasingly negative repercussions on survival. (*b*) Number of surviving young, relative to clutch or brood size. The straight line represents maximum survivorship (approaching 100%) where all eggs or young of a clutch are of quality A. For a given level of energy, the maximum number of young that can be produced of quality A is represented by A. Increases in quality of young above A do not increase their probability of survival (see upper figure), but the greater energy cost of producing those young reduces brood size, in such a way that the number of surviving young decreases. Decreases in quality reduce survivorship below maximum but allow increased clutch size that compensates for the reduced survivorship and yields a net greater production of surviving young. The optimum allocation of energy among eggs or young lies between B and C. The degree of compromise that can be sustained while still obtaining an increase in number of surviving young depends on the shape of the survival curve (see upper figure); steeper curves allow less compromise and more gradual curves allow greater compromises in egg and young size for obtaining positive benefits.

of eggs produced from a limited amount of energy will also be influenced by the quality (size and composition) of the eggs.

Parents have four possible responses to limited energy reserves. First, for any set level of energy expenditure, parents can increase the number of surviving young by compromising offspring quality (egg size), within limits, to allow production of a greater number of offspring (Figure 2b; also see 270). The degree to which egg size should be compromised is influenced by the amount of energy that can be allocated to egg production relative to the need to achieve minimum clutch sizes set by mortality levels (see earlier), but as modified by the relationship between egg size and subsequent survival of young (Figure 2). Note, then, that the form of the size/survivorship function is important; the steeper the slope, the greater the cost of compromising egg size. Thus, I use the logistic form to allow presentation of the argument here, but the actual function needs study.

Second, parents can potentially increase the number of surviving young by investing additional energy in egg production (Figure 2b). However, by allocating more energy to egg production, parents must either reduce energy for themselves (SE) or energy for young in stages after egg production (Figure 1). Reductions in SE can reduce residual reproductive value. Yet, reduction in energy for young at later stages can increase mortality probability of the young. Thus, parents should allocate more energy to egg production only if current reproductive success is increased and if this increase is greater than the reduction in residual reproductive value.

Third, parents can increase the quantity of reserves available for egg production by delaying until more reserves are stored. However, this advantage is offset if delayed egg production increases mortality probability from other sources or reduces the number of nesting attempts.

Fourth, some species may not breed at all in that season. This response is only profitable for long-lived birds that have a reasonably high probability of breeding in the future. It is typically seen in precocial birds (136) but also in altricial raptors (e.g. 86, 98, 205, 271).

Moreover, clutch size is only mutable within limits. Heredity, in some cases, may place genetic constraints on the adaptability of clutch and egg size (e.g. 194, 202, 291–293). In addition, clutch size can only increase to some upper limit dictated by parents' physiological capabilities relative to the energy requirements for care of the young after egg production; increases in energy output from increased foraging must eventually reach a level where intake cannot meet expenditure (e.g. see 219). Thus, species may evolve average strategies of egg quality and number, with individuals modifying egg quality and number around this mean response as a function of food abundance and energy reserves at the time of egg production.

Evidence For Food Limits On Egg Production

TIMING OF EGG PRODUCTION Food abundance may often rapidly decline and approach a minimum during the late nestling and fledgling stages (periods of greatest food demands of young—discussed later). Perrins (200) noted that tits fledged approximately 10–12 days after the peak abundance of winter moths, a favored food. Similarly, examination of numbers of lepidopteran larvae (favored nestling food) relative to the timing of production of young in Hubbard Brook forest (i.e. 106) shows that fledglings are produced during the period of lowest abundance. Data in Wittenberger (316) and Sealy (260) also show that lepidopteran abundance peaked before, declined rapidly, and/or approached minimum levels during the late nestling and fledgling periods. This pattern of declining or minimal food abundance has the potential to explain seasonal patterns of reproductive success; broods often are larger and more successful early in the season than late (49, 79, 88, 110, 135, 170, 200, 201, 266, 278, 304, 305), but this is not always so (26, 92, 275). However, all three latter studies occurred in a northern clime, which may offer better thermal and food conditions later in the season. Indeed, Bedard & La Pointe (26) found that late broods occurred during a period of warmer temperatures and more food.

Because earlier clutches often are larger and more successful, altricial birds in most cases should lay eggs as early as they can store sufficient reserves (200, 201). Earlier clutches have been observed in favorable food conditions (Table 1a,b). More convincingly, almost all supplemental feeding experiments have resulted in earlier laying (Table 1c).

On the other hand, egg laying is only advanced to a limited extent. Initiation of egg laying may also be constrained by heredity (i.e. 291, 294), thermoregulatory costs associated with cold temperatures early in the season (78), and predator pressure (e.g. 48). Yet, earlier breeding due to supplemental feeding documents the fact that food often limits initiation of egg production before thermoregulatory costs and predation do. The higher reproductive success often obtained by earlier breeding may force a compromise between optimal laying date and maximal clutch quality; if birds delay egg production until they store enough food to produce the best eggs possible, the increased egg quality may be offset by a lower probability of the young surviving later in the season or by a reduced ability to renest. Thus, altricial birds may often produce eggs before they can produce the maximum number of eggs of maximal quality.

EGG SIZE AND QUALITY Birds should only reduce egg quality if energy constraints make it necessary, since egg quality can affect hatching success and survival of young. However, food constraints on egg production should

Table 1 Effects of natural and artificial increases in food on breeding performance of birds.

Food Availability	Earlier Laying	Clutch Size	Reproductive Success	Sources
a) More favorable food years				
Falco tinnunculus	+	+		66
Coccyzus erythropthalmus		+		259
Coccyzus americanus		+		80
Tyrannus tyrannus	+	+		171
Tachycineta bicolor		+	+	112
Delichon urbica		+	+	38, 39, 40
Parus major	+[a]	+	+	200
Campylorhynchus brunneicapillus	+	+		148
Ficedula hypoleuca	+	+	+	114, 115
Dendroica caerulescens	0	0	+[b]	244
Seiurus aurocapillus		+		319
Agelaius phoeniceus		0	+	284
Passer domesticus		0	+	9
Spizella arborea		+		9
b) Territories or habitats with more food				
Accipiter nissus	+	+	+	175, 177
Tyrannus tyrannus	+	+	+	35
Pica pica	+	+	+	217
Ficedula hypoleuca	+	+	+	146
Zosterops lateralis			+	52
Hemignathus virens	+	+		295
Tachycineta bicolor		+	+	112, 212
Pipilo erythrophthalmus	+	+		94
Cardinalis cardinalis		0	+	56
c) Artificial increases in food				
Accipiter nisus	+	+		176
Falco tinnunculus	+	+		66
Pica pica	+	+	+	104
Parus major	+			121
Parus montanus	+	0	+[b]	37
Parus cristatus	+	0	+	37
Prunella modularis	+	0		61
Sturnus vulgaris			+	58
Corvus corone	+	0	+	317
Agelaius phoeniceus	+	0		78
Melospiza melodia	+	0	0	276

[a] A "+" indicates an increase; a "−" indicates a decrease; a "0" indicates no difference; and a blank indicates the response was not reported.

[b] Increased frequency of second clutches.

first be expressed by reduced egg size rather than egg number, because changes in clutch size represent major stepwise changes in reproductive potential. Thus, egg quality should increase with food abundance if food limits egg production. Indeed, egg size and quality have been found to increase with food abundance in some altricial species (e.g. 40, 78, 104, 115, 170, 171).

Correlation of egg quality with food abundance is an indirect measure of energy limits. Presumably, increases in food availability enhance egg quality through enhanced parental condition (i.e. increased TE). Unfortunately, parental condition is rarely examined relative to egg size. Yet, egg weight was, indeed, correlated with parental condition in house sparrows *(Passer domesticus)* (167) and eastern kingbirds *(Tyrannus tyrannus)* (171). Thus, food can limit egg production in terms of egg size and quality. However, egg size and quality relative to food conditions and parental condition need much greater attention in more species and habitat conditions.

EGG NUMBER Continued reductions in egg size eventually cause an increase in mortality probabilities of young to a point where birds may better optimize their reproductive success by reducing clutch size (Figure 2). Circumstantial evidence that food can limit the number of eggs that can be laid is provided by observations that clutch sizes are larger in more favorable food years or habitats (Table 1a, b). However, most food supplementation experiments have not produced an increase in clutch size (Table 1c). This seeming contradiction suggests an important insight. Most studies comparing reproduction among years are based either on comparisons among very different years or on relatively long-term data. Long-term studies increase the chances of including very different years. Thus, such studies should have a high probability of finding clutch size responses to food if they exist. Food supplementation studies, on the other hand, are typically conducted over one or a few years, so that they may commonly encompass more average years. In such years, clutch size may already be at or near the maximum number of young that parents are physiologically capable of raising. Thus, instead of increasing clutch size, parents may divert the additional energy provided by supplemental food into higher quality eggs and greater reserves for later stages, as well as somatic energy for themselves. Such responses should cause increased reproductive success. Indeed, six of the seven supplemental food studies that examined reproductive success found an increase (Table 1c, also see later).

If egg production is influenced by parental condition, and variation in body weight among conspecifics reflects parental condition, then the number of eggs produced should vary with body weight. Jones & Ward (119) documented that loss of protein reserves of red-billed quelea *(Quelea quelea)*

during egg formation increased with clutch size. Moreover, birds with larger clutches completed egg production at a weight similar to birds with smaller clutches, indicating that the larger clutches were produced by a greater initial reserve. Ankney & MacInnes (13) showed similarly that differences in weight of lesser snow geese *(Chen caerulescens)* on arrival on their breeding grounds were correlated with follicle development (potential clutch size). These effects are not limited to precocial birds; clutch size increased with body weight and condition in the altricial pied flycatcher (20, 262), European sparrowhawk *(Accipiter nisus)* (178), and hooded crow *(Corvus corone)* (143). Moreover, the rate of supplementary food acquired by the female, or supplied by the male in species that provision their mates, can influence energy stores and egg production. For instance, Nisbet (181, 182) showed that the rate of provisioning by the male common tern *(Sterna hirundo)* influenced female body weight and subsequent clutch size (also see 81, 131, 252). Thus, egg production can increase with increases in TE as indexed by body weight.

The extent to which birds depend on endogenous reserves (versus exogenous feeding) for meeting energy and nutrients demands of breeding varies among species (6, 12, 13, 71, 76, 130, 287), and body size may be one determinant. Larger birds have metabolic demands relatively lower than smaller birds (299), so that, compared to small birds, they can store relatively more energy for the same proportion of body weight. Moreover, an upper limit on stored reserves may exist due to effects of extra weight on flight efficiency (e.g. see 82, 186). As a result, small species may depend on exogenous resources more than do larger species (14, 120), and thus the clutch sizes of small species depend, in part, on the anticipated availability of food at later reproductive stages (190). Yet, as I will show, endogenous reserves are used to some extent throughout the reproductive cycle, even for small birds. Consequently, food constraints on egg production are imposed in part by energy reserves needed for later stages (see Figure 1). This perspective seems to be commonly overlooked. For example, Murphy (171) argued that egg production was not constrained by food in eastern kingbirds because birds could produce an additional egg from reserves. This argument fails to consider the need to maintain reserves for later stages.

INCUBATION

Incubation may be energetically costly, with larger clutches costing more energy (29, 30, 96, 155). Females commonly lose weight during incubation (10, 13, 82, 101). However, this weight loss does not necessarily reflect the stress of incubation. Instead, it may reflect limited time for foraging (300), which can arise due to an antagonistic interaction between parental condition

and nest attentiveness. The duration of incubation may be reduced as adults spend more time on the nest, but time available for foraging is reduced by spending more time incubating.

Shorter incubation can be beneficial because the probability of predation on both eggs and young increases with exposure time (225, 226). However, the extent of reserve depletion during incubation will vary among groups of birds, depending on how they allocate energy and nutrients among the different reproductive stages. Birds with precocial young that do not need to use energy to feed their young after hatching may deplete their energy reserves during egg production and incubation much more than birds with altricial young (Figure 1). As a result, parents of precocial young may make themselves more vulnerable to mortality during incubation. Indeed, abandonment of nests by emaciated females and mortality due to starvation by incubating females are generally reported for precocial rather than altricial birds (e.g. 13, 117, 164).

Yet, in both groups of birds, attentiveness to the nest during incubation should increase with increases in body reserves or greater provisioning by mates in such a way that incubation is shorter and hatching success is higher. Indeed, Aldrich & Raveling (4) showed that in the precocial Canada goose *(Branta canadensis moffitti),* older females began incubation at a heavier body weight than birds nesting for the first time. Heavier females were able to lose more weight, allowing them to spend more time incubating the eggs. The greater attentiveness to the nest by older females reduced the duration of incubation, thereby reducing risk of predation. Furthermore, the greater weight loss of heavy females caused heavy and light females to end incubation with similar body weights, suggesting they invested maximum reserves during the incubation period, as would be expected for precocial birds.

Transplant experiments showed that altricial starling parents had a significant effect on duration of incubation independent of variation in egg size and composition (241). Such effects may arise because of differences in endogenous reserves of parents, but greater body weights and fat reserves were not measured. On the other hand, female condition and nest attentiveness is influenced not only by endogenous reserves prior to incubation but by availability of exogenous resources. For instance, mate provisioning during incubation in the altricial snow bunting *(Plectrophenax nivalis)* (147) and pied flycatcher (141) enhanced the condition of the females, reduced the time the female was off the nest, and decreased the duration of incubation (also see 296). Moreover, young of females with little or no mate provisioning had earlier nestling deaths or reduced fledgling weights. These may occur because females were in poorer condition following incubation and could not devote as much care to offspring or because provisioning reflects male care after incubation.

Besides affecting the duration of incubation, greater nest attentiveness as a function of better body condition can improve nesting success by increasing

hatching success of eggs. Birds that nest in harsh environmental conditions expose their eggs to these conditions every time they leave the nest. Hatching success is influenced by the temperature of eggs during incubation (70). As a result, birds in poorer condition that must leave the nest more often to forage thus increase the probability of temperature variation that may reduce hatching success. Indeed, hatching success increases with increased body weight of precocial turkeys *(Meleagris gallopavo)* (209) and enhanced maternal nutrition of precocial ruffed grouse *(Bonasa umbellus)* (25) and Scottish ptarmigan *(Lagopus mutus)* (163). Moreover, hatching success of some altricial species, such as yellow warbler *(Dendroica petechia)* (92) and savannah sparrow *(Passerculus sandwichensis)* (67), decreases with increasing clutch size. This suggests that increased investment in egg production may reduce reserves available for incubation. Alternatively, reduced hatching success with poorer nutrition and body weight or increased clutch size may occur because of the production of lower quality eggs due to limited reserves. Either way, such results indicate food constraints.

In short, egg production may not be limited simply by the reserves needed to produce eggs, as argued by early investigators (e.g. 136, 297). Rather, production may be limited by the cost of producing the eggs and maintaining sufficient reserves for the period following egg production (Figure 1).

NESTLING PERIOD

The nestling stage is a period of severe time and energy demands. The energy demands by the young are determined by their hatching pattern, growth rate, brood size, and their thermoregulatory costs; each of these can influence food limitation on the young.

Hatching Pattern

Asynchronous hatching is common, and it produces a size hierarchy among the young that is influenced by intranest variation in egg size (54, 269). The selective forces favoring asynchrony have been debated (23, 54, 108, 110, 111, 136, 137, 154, 190, 192, 220, 222, 268, 269). However, whatever the cause of asynchrony, it results in reduced food demands by the young because the peak demands of individuals will be spread out and the mortality of the last hatched young will reduce the number of young demanding food. These two effects clearly can be beneficial when food is limiting.

Growth Rate

Lack (136) argued that growth rate is a compromise between mortality rate and the extent of the food supply. Higher mortality favors faster growth because the length of time the young are exposed to possible mortality is thereby reduced. However, the greater food demands created by faster growth

rates can reduce the number of offspring that parents can rear. Thus, the resulting optimum growth rate is modified by the risk of mortality and availability of food in the environment. Ricklefs (226) developed a model that suggested birds should always grow at the maximum rate that is physiologically possible rather than the reduction in some rate considered optimum because nestling mortality achieved by growing as fast as possible compensates for any reduction in number of young. Ricklefs suggested that differentiation of skeletal muscles for thermogenesis or mobility at an early age causes myoblasts to be removed from the pool of proliferating cells and thus restricts growth rate (232, 233, 242). He pointed out that legs were the primary source of mobility and thermogenesis for young precocial birds and that legs comprised the major portion of muscle tissue for these birds. Consequently, he showed that variation in growth rates among precocial families was correlated with variation in the relative size of legs (see 232, 233). On the other hand, physiological constraints on growth rates may instead be imposed by brain developmental rates rather than muscle maturation (see 183). Either way, considerable evidence exists to suggest physiological constraints on growth rates for precocial birds (236). Yet, precocial chicks, more than altricial birds, may be limited in growth by physiological constraints, because precocial chicks feed themselves and their susceptibility to mortality may select for rapid growth (see 236; but see 76).

Experiments such as force-feeding and comparisons among taxa relative to differences in tissue development are less common for altricial birds. However, Reyer & Westerterp (219) used hand-feeding experiments to show that the growth rates of the altricial pied kingfisher *(Ceryle rudis)* were below maximum. Altricial birds may not be as consistently constrained by physiological limits on their growth because most growth occurs while they are relatively immobile in the nest. Moreover, they are dependent on obtaining food from their parents who are concerned not only with feeding the young, but also with protecting them (see 51). Such time demands may commonly lead to growth rates below physiological limits.

One apparent case is tropical birds. Tropical birds grow 23% more slowly than temperate birds (229). Ricklefs (225, 232) pointed out that the slower growth of tropical birds is a counterexample to arguments by Lack (136). Mortality of young is as high or higher in the tropics as in the temperate zones (see 225, 265), and according to Lack's (136) argument, birds should then grow faster in the tropics. However, this example is also counter to the physiological constraint argument by Ricklefs (226, 227, 232, 233, 236); the reduced growth rates of tropical birds cannot be explained by differences in levels of tissue or organ maturity at birth because the temperate and tropical species are ecologically and morphologically similar. This result also does not reflect a diet among tropical birds that is nutritionally poorer, because strictly

insectivorous species show the same or even a higher degree of growth differences (see 223, 229). Moreover, this result cannot reflect differences in thermoregulatory costs because such costs are lower for tropical birds (43). Instead, the reduced growth rates of tropical birds must reflect food limitation via a reduced rate of food delivery by parents.

Growth rates below physiological maximum rates are also demonstrated by aerial insectivores; aerial insectivores grow more slowly than do similar-sized species of perching insectivores in both temperate and tropical regions (223, 229). This difference can be related to the stability of food during the nestling period (190). Food supply of aerial insectivores is variable due to the effects of weather. As a result, the young store lipids as "insurance fat" against temporary food shortages, and the size of these fat stores varies among species, relative to the risk of food shortage (43, 190). The regular starvation of nestling flycatchers, swifts, and swallows documents the need for fat storage (e.g. 43, 59, 137, 169). Thus, slower growth rates of such species can be attributed to food limitation, at least in part due to the need to store fat rather than to convert it to growth.

Similarly, birds in one-egg clutches commonly grow more slowly than birds in larger clutches (36, 224), which may reflect sibling competition (306). However, Bartolotti (36) showed that food delivery times were larger and potentially more variable for birds with broods of one and concluded that the slower growth of offspring in one-egg clutches was due to food limitation (also see 235).

Finally, intraspecific variation in growth rates relative to environmental conditions (e.g. 152, 191, 229, 245, 248) also indicates that temperate altricial birds often are not growing at the physiological maximum, but rather at some rate determined by food delivery relative to demand (238). One of the clearest examples of food constraints on growth rates was provided by Quinney et al (222); nestling tree swallows consistently grew faster in habitats with more food, even when the effects of parents were controlled through transplants. Thus, growth rates of altricial young apparently are commonly limited by food delivery rates.

Brood Size

Food limitation on the number of young that parents can raise is seen by directly examining energy demands and nestling survival rates relative to brood size. The feeding rate of young by parents generally increases with brood size (28, 42, 57, 88, 110, 138, 159, 301). However, the feeding rate does not always increase with brood size (27, 32, 208), nor are increases necessarily proportional to brood size (42, 57, 88, 110, 252). Consequently, nestling mortality often increases and nestling weight often decreases in larger natural broods, but this is not always so (Table 2a). The pattern may not

Table 2 Effects of (*a*) natural and (*b*) experimental variations in brood size and (*c*) loss of male parental help on nestling weight and mortality.

Species	Nestling Weight	Nestling Mortality	Sources
a) Natural variation in brood size			
Tyrannus tyrannus	−	+	169
Delichon urbica	−	+	39, 42
Parus major	−	+	200
Erithacus rubecula	0	0	138
Turdus pilaris	−	+	266
Ficedula hypoleuca	0	0	17
Sturnus vulgaris	−[a]	0	133
Sturnus vulgaris	−		58
Denaroica petechia		+	92
Passerculus sandwichensis	−		248
b) Brood size manipulations			
Columba livia	−	+	47
Apus apus		+	199
Tachycineta bicolor	−[c]	0	63
Tachycineta bicolor		+	140
Delichon urbica	−	+	46
Pica pica	0	+	103
Pica pica	0	+[d]	109
Corvus corone	0	+	142
Parus major	−	+	200
Parus major	−	+	203
Parus major	−	+	267
Parus caeruleus	−	0	288
Turdus pilaris	0	+	266
Ficedula hypoleuca	−[b]	+	18
Sturnus vulgaris	−		58
Sturnus vulgaris	−	+	307
Agelaius phoeniceus	−	+	57
Agelaius phoeniceus		+	197
Passer domesticus	−	+	257
Quelea quelea		+	300
Plectrophenax nivalis	−	+	110
Passerculus sandwichensis	−	+	304
c) Loss of male help			
Cirus cyaneus		+	263
Columba livia	−	+	47
Tachycineta bicolor		+	139
Parus major	−	+	34
Parus major		+	254
Parus caeruleus		+	254
Sialia sialis	0	0	93
Ficedula hypoleuca	−	+	3
Prunella modularis	−[e]	+[e]	60
Agelaius phoeniceus	−	+	197
Agelaius phoeniceus		+	165
Dolichonyx oryzivorus		+	316
Melospiza melodia	−	+	277
Zonotrichia leucophrys	−	+	154

[a] A "+" indicates a positive association, a "−" an inverse association, a "0" indicates no effect, and a blank means the response was not reported.

[b] Nestling weight decreased with increased brood size in one of two years.

[c] Nestling weight decreased with increased brood size for yearling adults, but was not significant for older adults.

[d] Mortality occurred after fledging.

[e] Increases in number of adults.

always hold among broods occurring naturally because individual differences in clutch size and reproductive success may result from differences in either ability or experience to forage and care for the young (38, 41, 44–47, 79, 105, 119, 151, 157, 203). Differences in reproductive success have been associated with individual differences in both foraging efficiency (44) and territory quality (see Table 1b). Indeed, experiments (47, 237, 239, 240) clearly show that parents can differ in the number and quality of young they can raise. Thus, observed differences in brood sizes may often reflect individual optima (103, 105, 108, 258).

Experimental manipulations provide a much clearer test of the ability of parents to meet the food demands of their young. A consistent increase in nestling mortality and decrease in nestling weight with artificially enlarged broods (Table 2b) indicates that parents have increasing difficulty meeting food demands of increasing numbers of young. However, the existence of food limitation when energy demands are increased does not necessarily indicate that food was limiting at observed levels. Decreased mortality and increased nestling weight with artificial reductions in brood size (e.g. 109, 188, 197, 267, 307) provide convincing evidence that the young commonly receive less food than the amount that will maximize their size and survival prospects. Increased mortality and decreased weight of nestlings when male parental help is lost (Table 2c) also indicate that the ability of parents to deliver sufficient food is a limit on the number of young that can be raised successfully. Furthermore, these results hold for open-nesting and cavity-nesting species for a wide range of areas (Table 2), indicating that the results are not indicative of a select subgroup of birds.

The reduced weight of nestlings resulting from brood enlargements or removal of parents provides clear evidence that parents are limited in the amount of food they can supply to the young. Four pieces of evidence confirm that the decrease in nestling weight can be due only to the decreased amount of food delivered per nestling rather than to an inflexibility of parents in responding to manipulations (cf 110). First, birds are known to modify their rate of food delivery with changes in brood size (see above). Second, females respond to the removal of male parents by increasing their feeding rates (see studies listed in Table 2c). Third, natural or artificial increases in food can cause increased nestling weight and survival (Table 1), indicating that additional food allows parents to deliver more to their young. The final and most convincing evidence comes from a study by Crossner (58). He increased brood sizes of European starlings through manipulations and provided supplemental food in the territories of some of these broods. He found that the weight of nestlings declined markedly with increased brood size when food was not added (results also found in the experimental manipulation studies listed in Table 2b). However, nestlings of broods that were enlarged and also

provided with supplemental food did not differ in weight from nestlings of reduced or unmanipulated broods that were not provided with additional food. Thus, parents can compensate for extra energy demands of enlarged broods (probably to some upper limit) when additional food is supplied. In short, the experimental evidence on a number of altricial passerines clearly demonstrates that the young are food-limited because parents are limited in the quantity of food that they can supply relative to the energy demands of nestlings.

Lack (134–136) argued that birds should raise the largest number of young that they can successfully feed and that the most common brood size should be the most productive, where productivity is measured as the number of young that survive to fledge. Some studies have supported this tenet (67, 108, 125, 200, 307), but many others show that the most common clutch size is smaller than the most productive (33, 38, 58, 142, 164, 166, 169, 188, 203, 221, 258, 266, 273, 275, 278, 290). Although such effects could arise from limitations earlier in the cycle (e.g. limits on egg production—see earlier), they probably occur in most cases because of an inaccurate definition of productivity. Instead of productivity being defined as the number of young that fledge, it should be defined both by the number that survive after fledging to breed successfully, and by the negative effects of the breeding effort on the future potential of the parents.

POSTFLEDGING STAGE

Energy demands of the young are commonly assumed to reach a maximum during the nestling stage (e.g. 24, 28, 125, 134, 225, 261). Indeed, for some species, the most demanding period may occur early in the nestling stage (e.g. 47). However, this assumption may not be generally true. While the number of feeding trips to the nest increases with the age of nestlings (27, 32, 118, 184, 208, 252, 301, 304), the young of many passerines are fed by their parents for twice as long outside the nest as in it (99, 159, 162, 179, 207, 272). Parental effort increases with the age of altricial young (11, 24, 31, 45, 46, 72, 95, 97, 198, 303) and may continue to increase after the young leave the nest. Smith (272) found that feeding rates of fledglings are higher than for old nestlings; this suggests that the energy demands of the young are maximal after they leave the nest but before they become independent (also see 160, 252).

Parents of some species divide their broods (73, 99, 100, 153, 160, 184, 272, 274). This brood division may be necessary in the face of the energy demands of the young relative to the dispersion of food. These may be such that one parent cannot efficiently feed all the young unless they are dispersed. Indeed, Harper (100) showed through experimental manipulation of the food

supply of European robins *(Erithacus rubecula)* that brood division is reduced when food is readily available. Price & Gibbs (210) similarly showed that brood division in Darwin's ground finches broke down in years of abundant food. Also, Nolan (184) and Edwards (73) have shown for prairie warblers *(Dendroica discolor)* and blackbirds *(Turdus merula),* respectively, that parents are limited in the number of fledglings they can bring to independence. In short, the food demands of fledglings continue to limit the number of young that parents can sustain.

The poorer survival rate of young that fledge at lighter weights (see earlier) may reflect not only the poorer condition of the fledging young but also poorer parental care after fledging. Assuming that size at fledging is an indicator of post-fledging care and survival prospects, then based on data from Nur (188), survival appears to increase as a logistic function of size; post-fledging survival increases with nestling weight up to some upper weight limit and then differs little above that limit. As a result, parents can face a trade-off between the number and quality of young that they produce, similar to the number/size trade-off in eggs (see earlier); brood sizes that cause fledgling weights and post-fledging care/survival to fall below maximum are favored because the increase in brood size can offset the increase in fledging mortality, to some limit (Figure 2b). However, continued increases in brood size above this optimum may allow production of more fledglings, but their condition and prospects of survival are sufficiently reduced that fewer young actually survive to the following breeding season. In short, it is not the number of young fledged, but rather the number surviving to breed in the following year that is the true measure of productivity. Under this definition, the average clutch size may be the most productive. Unfortunately, most studies do not report data on which we can judge.

In short, experimental studies consistently show that young are food-limited because parents are limited in the number of young that they can supply with adequate food. The results do not always show how food limitation occurs, nor do they indicate the same degree for all years, species, or even individuals. They do show that the amount of food brought to a brood of young commonly limits the number and quality of young produced per brood.

REPRODUCTIVE COSTS ON PARENTS

Timing And Cause Of Energy Stress For Adults

Food limitation on adults appears to be due primarily to time limitation; time spent caring for young competes with time for caring for themselves. This time limitation is what makes the energy reserves of parents important to reproductive success; increased reserves mean less time required to feed themselves and more time for young. Such effects clearly occur during

incubation (see earlier). Time limitation also appears to occur during the nestling and fledgling stages. For example, Nur (187) showed that increased brood size caused increased weight loss and decreased survival of female but not of male parents. He concluded that this result documented that feeding activity alone could not account for the weight loss of females because both parents feed the young. However, only females brood their young in blue tits *(Parus caeruleus)*. The time needed for brooding in addition to feeding the young may limit the time that females have available for feeding themselves. Similarly, adults lost weight during the brooding period in the starling (307). Furthermore, both sexes brood their young, and parents of both sexes showed similar weight losses (307). Thus, the period when parents brood and feed the young may limit the time they have available for feeding and maintaining themselves (187).

Parents may also face time limits during the late brooding and postbrooding periods due to the need to guard the young against predation; time spent guarding the young may compete with time available for gathering food (T. Martin, unpublished manuscript). In short, parents can be under time constraints throughout their nesting cycle (including incubation, brooding, postbrooding, and probably fledgling). As a result, increasing reproductive costs with increasing brood sizes are not necessarily due to substantially greater energy costs of foraging for the young (e.g. see 46, 298; but see 219, 285). Rather, the costs may be due to the increasingly restricted time available for caring for themselves and, hence, to a need to use their endogenous reserves.

Effects Of Food Limitation On Parents

Food limitation on parents can affect their reproductive potential in three ways. First, as parents are increasingly food-limited due to lessened endogenous resources, they must spend more time acquiring exogenous resources for maintenance. Consequently, less time can be devoted to nest attentiveness, causing greater food limitation on the young, through greater hatching failure, incubation duration, and nestling mortality (see earlier). Moreover, such parents generally end the reproductive event with lower SE.

MULTIPLE NESTING ATTEMPTS Second, reproductive costs may cause delayed or reduced success of future broods. Indeed, the temporal delay before the onset of a new brood is longer when it follows large broods or when food conditions are poor (127, 195, 275, 280). Moreover, experimental enlargements of broods have caused delayed and less successful future nesting attempts in the same season (267) and the following year (247). Reduced

success of future attempts is a direct cost. However, delayed renesting also exerts costs on reproduction in three ways: (*a*) If delays are long enough, renesting may not be possible, and thus the number of attempts possible in a season is reduced. (*b*) Later broods are generally less successful than earlier broods (see later). (*c*) Survival of fledglings from later broods often is lower (see later).

The importance of multiple breeding attempts has been underemphasized in considerations of food limitation. For many birds, increases in clutch sizes may not be feasible with increases in food (e.g. Table 1c) because clutch size may already be at the physiological limits of a parent's ability to care for young. Instead, increases in food may allow parents to end a breeding attempt in better condition and allow quicker acquisition of the reserves necessary for a second brood. Thus, beyond some level of food abundance, parents increase their reproductive potential by increasing the number of broods rather than individual clutch size. Indeed, supplemental feeding did not increase the clutch size of willow tits *(Parus montanus)* but did increase the frequency of second clutches (37). Similarly, in black-throated blue warblers *(Dendroica caerulescens),* experimental reductions and natural annual variation in food abundance did not affect clutch size but did strongly influence second brood attempts (244). Finally, this strategy was strongly expressed by Darwin's finches; numbers of broods varied from 1 to 10 per year with variation in food abundance (89).

PARENTAL SURVIVAL Third, reproductive costs can reduce survival of parents. Parents often lose weight when feeding their young (63, 174, 178, 179, 302), and increased weight loss can reflect increased daily energy expenditures (e.g. 219). Weight losses are greater among those parents with larger broods (18, 19, 41, 110, 187, 285, 307), and parents have been observed to gain rather than lose weight when brood sizes are reduced (41, 33). Weight losses provide indirect evidence that rearing broods exerts a cost if such weight losses delay renesting or decrease survival. Freed (82) and Norberg (186) argue that weight losses are adaptive because the reduced weight reduces the energy costs of foraging. While weight losses may allow more efficient foraging, weight losses may still represent a cost; decreased survivorship of parents with increased brood sizes or numbers suggests that increased reproductive effort can exert a cost on survival (19, 41, 68, 126, 187, 286).

Brood sizes or weight losses are difficult to interpret directly in terms of reproductive costs, due to confounding factors. For example, Smith (273) found increased survival among females with naturally occurring larger broods. However, a positive correlation may be expected between brood size

and adult survival due to individual differences in breeding capabilities (105); individuals with greater total energy due to environmental quality or individual efficiency can allocate more parental effort, allowing larger brood size, while still retaining a greater somatic effort, allowing greater potential survival, than parents with a smaller total energy (Figure 1).

To control for effects of differences in total energy among individuals, tests of reproductive costs require experimental manipulations. However, even experimental manipulations need to be carefully interpreted. For instance, DeSteven (63) found no relationship between brood size and adult survivorship after experimental enlargement of broods. However, she increased brood size by only 2 young. Reproductive costs are the result of total PE reducing SE below SE*, and PE is the result of energetic costs during egg production and incubation as well as during nestling care. Given that birds do not incur the extra egg production costs when broods are experimentally enlarged, increasing brood size by 2 may not increase reproductive costs enough to cause reduced survival. Instead, costs may be expressed as reduced future reproductive success (see above). Unfortunately, DeSteven (63) did not examine renesting attempts or reproductive success in the following year. Furthermore, intensity of reproductive costs will vary among years because the intensity of food limitation varies among years (see above). Thus, single-year studies, like that done by DeSteven (63), may occur in a year in which food limitation may be relaxed, exacting lower reproductive costs. Indeed, the return rate of adults was twice that of earlier studies at the same site. This may reflect either increased colony age and more efficient trapping efforts or a year more favorable for adult survival (63).

Askenmo (19) found decreased male survival when broods were enlarged. However, the lowered return rates of males may reflect an increased rate of emigration in response to the manipulations rather than actual mortality (105). Kluyver (126) reduced clutches by one half and found that approximately twice as many adults survived, but the increased survival may simply reflect reduced winter competition between young and adults (265). Tinbergen et al (286) reanalyzed Kluyver's data and concluded that the costs of reproduction, in terms of reduced survival, were expressed in years when winter food abundance was low. Again, these results emphasize the importance of multiple-year studies and consideration of variation in the intensity and expression of reproductive costs.

Nur (187) found in blue tits a consistent decrease in female survival with an increase in brood size, based on a large sample size (n = 215 clutches) and wide differences among brood sizes (range = 3–15 young). Feeding and reproductive effort in the pied kingfisher also have a strong influence on adult weight loss and adult survival (218, 219). Finally, Ekman & Askenmo (74) showed that widowed males with lower reproductive effort had higher sur-

vivorship than males that cared for a brood. Moreover, willow tits invested more energy in reproduction (greater clutch and brood size and weight) than the crested tit *(Parus cristatus)*, and willow tits had greater adult mortality. These results and the consistent patterns of weight loss and gain relative to brood size in other studies provide strong evidence that increases in brood size place an increasing cost on adults.

I have stressed the importance of parental condition and total energy drain during all stages of a nesting event, and this point is particularly important to consideration of reproductive costs as indexed by weight losses. Parents that invest more energy in a larger clutch size during egg production and greater nest attentiveness during incubation may end incubation at relatively low weights. Adults that end incubation at lower weight and have less reserves to lose may show less weight loss than parents that begin and end the nestling period in better condition (i.e. parents with greater TE). This is similar to the result seen during incubation for Canada geese (see earlier). In this case, better parents will actually show greater weight loss; thus, weight loss will not indicate parental condition or survival potential. Instead, absolute weight may be a better indicator of breeding stress. Indeed, examination of data in Nur (187) shows that the percentage of females that survived to the following breeding season was much less for females that weighed the least amount at the beginning of the nestling period (0.071%) than for females that lost the most weight (0.250%). Thus, energy reserves available at the beginning of the nestling stage (as determined by monitoring weight loss during the entire reproductive event) need to be included in future studies. Moreover, manipulative increases in brood size as a test of reproductive costs may need to be larger than in some previous studies to compensate for the lack of energy investment in producing extra eggs.

DOMINANCE AND WINTER SURVIVAL

Food limitation during winter can exert detrimental effects on body condition and thereby negatively affect breeding success in the following breeding period (13, 209, 216). One negative effect may be later breeding. Later initiation of nesting can be detrimental because it can cause production of young when food supplies are declining (see earlier). It can also affect dominance interactions, because juveniles from early broods generally contain more dominant individuals than juveniles from later broods (16, 87, 123) and overwinter survival generally is higher for dominant than subordinate birds (16, 21, 84, 90, 123, 279). In short, food can be limiting over winter, but such effects do not necessarily preclude food limitation during breeding and, in fact, may exacerbate it by affecting adult condition negatively.

SUMMARY AND CONCLUSIONS

While food may be superabundant for birds during breeding in some habitats and systems, food is often limiting to reproductive success and survival at the levels of both the young and the parents in many systems. At the level of the young, this assertion is most clearly expressed by the consistent increase in size and survival prospects of the young when brood sizes are artificially reduced or the food supply is increased. A variety of other experimental and correlative evidence also supports this. Future work needs to take a broader approach; the total nesting period needs to be included in studies. In particular, survival of young after they leave the nest has not been examined in most studies reviewed here, and that represents a serious short-coming. If energy demands of young are greatest after leaving the nest, then the consequences of compromises made during previous stages may be most clearly expressed by both adults and young at this stage.

Examinations of reproductive costs on parents have been fewer and less complete in their treatment. One problem that has plagued earlier work is a tendency to focus on energy limits and costs during individual nesting stages (e.g. egg-laying, incubation, nestling, fledgling). Consideration of body condition and total energy drain during all stages of a reproductive event is critical for evaluation of reproductive costs. Reproductive costs can be expressed at subtle levels such as through effects on multiple breeding attempts, and these levels apparently can play an important role in recruitment. There is evidence for delayed or fewer renesting attempts following large breeding efforts or decreased food abundance, and for increased weight losses and reduced future survival or reproductive success with increased brood sizes. All this suggests that parents commonly incur reproductive costs due to food limitation. Thus, future tests of reproductive costs need to be sensitive to costs at more subtle levels and relative to the total energy drain.

Finally, the absence of a correlation between summer diets and feeding morphology, or a tighter correlation in winter, has led to conclusions that populations are not experiencing food limitation and competition in summer, or that such processes are more important in winter (e.g. 83, 85, 211, 312). Yet, the evidence summarized here suggests that food does often limit fitness in summer. This seeming incongruency may reflect a fallacy in the previous arguments; when species feed on widely divergent food types in summer as opposed to winter, morphological adaptations should reflect differences in the *relative* costs of differences in morphology for feeding on the two food types. For example, birds such as those in the studies cited feed on seeds in winter and insects in summer. The relative cost of eating insects in summer when a morphology is adapted for feeding on seeds is probably small. These birds feed on lepidopteran larvae and grasshoppers (Acrididae), and a seed-eating

bill should not hamper such prey acquisition overly much. On the other hand, a slender bill adapted to an insect diet has a large cost on winter feeding; slender bills are not strong enough to crack seeds. Thus, the cost of an insectivorous morphology on seed-eating is relatively much greater than the cost of a granivorous morphology on insect-eating. Consequently, food can actually be more limiting in summer than winter, and selection will still favor a morphology adapted to a winter diet because of these differences in relative costs. Hence, this analysis indicates that food limitation in summer should be examined more carefully. Moreover, food limitation can be expressed in different ways: food limitation in winter may lead to morphological adaptations, whereas food limitation in summer may be met by modifications of reproductive strategies.

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