

A TALE OF TWO STRATEGIES: LIFE-HISTORY ASPECTS OF FAMILY STRIFE¹

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Abstract. Breeding birds can generally be thought of as having evolved life-history traits that tend to maximize lifetime reproductive success. Within this broad pattern, many variations are possible because all traits are co-evolved with numerous others in complex ways. Clutch-size, for example, has long been understood to be frequently lower than the number of young parents are capable of supporting by working at their top capacity, especially in long-lived species. Nevertheless, studies of species with fatal competition among nestmates have shown that parents routinely create one offspring more than they normally will raise, as if counting on brood-reduction to trim family size after hatching. Three general and mutually compatible parental incentives for initial over-production have been identified, with David Lack's *resource-tracking hypothesis* having received the most attention. Extra sibs can also assist each other in some circumstances, but a third explanation for over-production that has been around for nearly four decades, the *insurance hypothesis*, has been surprisingly overlooked and, in some cases, actively challenged. It simply posits that parents create extra offspring as back-ups for members of the core brood that chance to die very early. We propose that the skepticism over the role of insurance is misdirected, that having a back-up is virtually automatic as a contributing incentive to parents and, in some taxa, that it provides a necessary and totally sufficient explanation for over-production. Some empirical approaches to the study of the insurance hypothesis are reviewed, in hopes of encouraging further field study of over-production in general, because that process underlies much of the internal conflict observed in avian families.

Key words: brood reduction, insurance, over-production, siblicide.

INTRODUCTION

"It was the best of times, it was the worst of times . . . it was the spring of hope, it was the winter of despair." So begins Dickens' classic tale. The same powerful words that captured the stark contrasts in society ultimately leading to the French Revolution can also serve as a useful metaphor for one of the great paradoxes in avian ecology: parent birds seemingly lay too many eggs to produce what appear to be too few fledglings. And this provocative contrast of life-history strategies foment its own revolution, which takes the form of sib-sib conflicts that are not only very widespread, but often fatal and sometimes even brutal.

A BROOD TOO SMALL

It has long been appreciated that parent birds (and other taxa) lay more eggs than they will succeed in raising to independence. Indeed, the idea can be traced back to the precursors of *The Origin of Species*.

Two centuries ago Thomas Malthus (1798) anticipated the heart of Darwin's argument by observing that "Throughout the animal and vegetable kingdoms, Nature has scattered the seeds of life abroad with the most profuse and liberal hand; but has been comparatively sparing in the room and nourishment necessary to rear them." Thus, in one modest understatement, he showed clearly that the struggle for survival—and hence for reproductive success—could be cast neatly in terms of how supply is routinely overrun by demand. From this, Darwin painted his fuller picture of Evolution as a process of change that rests fundamentally on natural selection: in

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short, there is a reproductive race going on within each taxon wherein the bearers of more advantageous traits (with emphasis on morphology in Darwin's day) tend to pass those traits along, while the bearers of less favorable traits tend not to spread them.

Half a century ago, when the idea that natural selection acts on life-history traits was first coming into focus, David Lack (1947, 1948) published his keystone papers on clutch-size in birds. Recognizing a tradeoff between offspring quantity and quality, he showed that parental success is often maximized by investing heavily in relatively few offspring. It must be remembered that most biologists of Lack's day did not think clearly about the level(s) at which natural selection is most potent, vaguely imagining that traits arise for benefit of whole populations, species, and even communities.

Accordingly, it seemed to many that the reason parents could be selected to invest heavily in just a few offspring must be because such "reproductive restraint" would be for the greater good (Wynne-Edwards 1962). Lack (1966) argued persuasively against such group-selection, insisting that selection operates far more forcefully at the level of individuals. If individual (or genic) selection reigns, as now seems obviously true, then traits tending to enhance each parent's reproductive success ought to spread. In the sense of promoting self, then, phenotypes are said to be "selfish."

Lack's quality-quantity tradeoff exposed how doing less (raising fewer progeny) can be the better way to run a Darwinian race, because of the enhanced competitive vigor of the offspring reared [see Slagsvold (1986) and Amundsen and Slagsvold (1996) for recent discussions of this quality-quantity tradeoff directly relevant to avian brood reduction]. In tight ecological situations, parents that generate a modest number of *winner*s may often outperform those producing veritable armies of losers. This argument leads to the prediction that animals and plants ought to create the largest number of *high-quality* offspring that they can afford: this tempered value for how many eggs to lay came to be known simply as the "Lack clutch-size." In our analogy of the reproductive race, it can be seen that there are different kinds of races across taxa. Some species are sprinters (short-lived, fast-breeding, etc.); others, marathon runners (long-lived, slow-breeding, etc.). It does not pay a

marathon runner to turn the first of 26-plus miles in less than four minutes; although such a start would provide a massive early lead, the rest of the pack would smile in glee, confident that the leader would be "reeled in" and then left far behind. Thus, a mutant albatross that laid, say, three eggs in its nest might raise fewer to fledging than wild-type conspecifics laying just the one egg.

Lack's message was subsequently expanded to consider the impact on the parents' own reproductive futures, a present/future tradeoff being especially likely in long-lived taxa (Williams 1966, Charnov and Krebs 1974, Smith and Fretwell 1974). From this vantage, it became evident that parents sometimes should be "prudent" (Drent and Daan 1980), in the sense that natural selection may be shaping a general tendency for parents to give rather less than their best effort toward a given brood. Such parental "laziness" can be evolutionarily stable without having to invoke any group-selectionist assumptions of reproductive restraint.

And there are other reasons for why parents in many species appear to "aim low" when setting an integer value on initial family size. American Coots (*Fulica americana*) have recently been shown to curtail their own clutch size in order to stash eggs into the nests of conspecific hosts. Interestingly, these females lay their parasitic eggs first, then create their own clutches that they incubate (Lyon 1998). So there may be various sneaky games going on across species that make clutch-size decisions even more tantalizing.

Most recently, it appears that the construction of even one additional egg may turn out to be far more expensive than we used to think (reviewed below). If egg production and perhaps incubation costs prove generally to be more substantial than currently appreciated, then of course the view that parents often aim too low, a conclusion frequently reached when parents demonstrate the ability to raise eggs or chicks that have been artificially added to their nests (Ydenberg and Bertram 1989), will have to be re-evaluated. Larger families surely require higher expenditures at various points in the cycle, any one of which could tip the balance toward selection favoring a smaller clutch optimum.

A CLUTCH TOO LARGE

In other birds, though, the optimal clutch size may actually be greater than the Lack clutch-size (or the revised-and-prudent Lack clutch-size), at least initially. In many long-lived birds, for which the importance of parents setting a modest upper limit for how much *effort* they will expend is likely to be great, there is good reason to believe that parents routinely *over-produce* at the beginning of a breeding cycle, creating one or a few supernumerary zygotes above their optimum (Kozlowski and Stearns 1987, Mock and Forbes 1995). This is easy to see with many predatory birds, where clutch sizes tend to be low, but the fact that many parents produce one or two eggs more than they will raise to fledging is widespread. Over two millennia ago, Aristotle wrote about the habit of the female eagle "... that lays three, hatches two, and cares for one." And it is even easier to see with plants, where over-production is utterly profligate: a typical fruit tree (the maternal sporophyte) may grow many thousands of incipient offspring (flowers with ovules) before undertaking successive waves of "spontaneous-abortion" events, wherein she first abscises all unpollinated flowers, then those tiny fruits that are poorly located with respect to key nutrients and/or are damaged by pests, before finally dropping almost all the others just prior to the costly deposition of sugars at ripening (Stephenson 1981, Mock and Parker 1997). In short, there is an extremely common pattern across sexual life forms for parents to have a somewhat inflated initial clutch that contains both a *core* family (the number of offspring that the parents are actually trying to raise) plus some *marginal* offspring that are decidedly expendable (*core* and *marginal* defined formally in Mock and Forbes 1995). The variations on how this duality is expressed are endless: in some taxa the core and marginal brood members are easily recognized, their roles rigidly established from the outset (e.g., asynchronously hatching eagles), whereas in others the matter of who will receive full investment and who will be jettisoned along the way cannot be predetermined (e.g., orange blossoms).

INCENTIVES FOR OVER-PRODUCTION

There are three general incentives for parents to over-produce initially, before trimming family size secondarily, either by acts of direct filial

infanticide (such as spontaneous abortion and parental cannibalism) or by allowing acute sibling competition to reach fatal severity. First, initial over-production allows parents to capitalize when unpredictable upswings in environmental conditions happen to increase the number of high-quality young that can be brought to independence at affordable levels of effort—the Resource-tracking Hypothesis (*sensu* Temme and Charnov 1987). This was the pay-off that Lack emphasized and much attention has been given to how frequently those special conditions (the so-called "Good Years") would have to come along to make over-production cost-effective (Pijanowski 1992, Lamey and Lamey 1994). Second, initial over-production may allow parents to rear the full complement of young when various accidents befall a member of the core brood—the Replacement Offspring Hypothesis. And finally, in many taxa the marginal offspring may be able to provide various services to members of the core brood, perhaps as a helper, a meal, or simply as a blanket—the Sib Facilitation Hypothesis. In fact, these three categories of potential value for marginal offspring can be mutually compatible: by creating an extra egg, parents may simultaneously improve the thermal environment for small nestlings (each having a better surface-to-volume ratio in cool conditions), obtain a handy insurance policy against early loss of a core chick, and be prepared for the occasional good-food year.

Without saying so explicitly, this argument clearly concerns taxa like birds that invest relatively heavily in offspring beyond the zygote stage. Such taxa typically keep their current clutch or brood in some type of spatial confinement, a *nursery*. The avian nest is a quintessential nursery. But that spatial boundary, when combined with the policy of parental over-production, sets the stage for a Malthusian squeeze on a small scale. In a nest full of newly hatched birds, for example, we have the spectacle of several very close genetic relatives—usually full siblings—that are in the midst of an extraordinarily rapid growth process. A passerine nestling must transform from a tiny, naked, blind, and sessile poikilotherm to a many-times-larger, fully feathered, sharp-eyed, and volant homeotherm in 1.5 to 4 weeks. To achieve all that, it must consume and convert fantastic amounts of high-protein food, every scrap of which must be collected and delivered by one or two adults (ex-

cluding communal/cooperative species). And its predicament can only be exacerbated if its parents over-produced initially and set a prudent limit for how hard they wish to work.

THE PARADOX DEFINED

Thus we reach our paradox: parent birds seem to produce too many incipient offspring (parental optimism) to yield a brood that often appears too small for current ecological conditions (parental conservatism). Under Williams' (1966) view, parents aim for a family size that maximizes the number of high-quality offspring at independence, without unduly sacrificing their own residual reproductive value. Under-appreciated is the fact that one does not get the family size one wants by laying that precise number of eggs. One must thus draw the distinction between the number of young one eventually wants at the *end* of parental investment and the number of eggs one must produce to achieve that desired family size.

Of course, in a perfect world, parent birds would face no uncertainty about the ideal size and composition of their family—forthcoming resources would be wholly predictable, the sex of their progeny would be known in advance, and the health and survival of all offspring would be assured. But in an imperfect world, parents face the challenge of rearing a family in the face of ecological and developmental uncertainties, and the prudent parent may establish contingencies for possible failure.

Parental over-production thus is a multi-purpose solution to many of the uncertainties surrounding family planning (Mock and Forbes 1995). The alternative of enlarging brood size retroactively is less feasible for obvious reasons. The general problem centers on incomplete information, because parents might make quite different choices if they could foretell the future. By analogy, the owner of a hockey club would not pay the salary of a backup goalie if assured that the starting goalie would never be injured. Similarly, a parent bird might choose to lay a smaller clutch if it could know in advance that all eggs would definitely hatch and thrive. The specific question we wish to address here concerns incomplete information and the developmental prospects of offspring: when should parent birds invest in insurance coverage?

Here we focus on an oddly neglected and surprisingly controversial dimension of the clutch-

size literature: when should parent birds invest in Replacement Offspring? There are two related ideas embedded in the logic of replacement, *progeny choice* (sensu Kozlowski and Stearns 1989) and *insurance*. Under progeny choice, parents create surplus offspring so as to have an array from which to select a subset for full investment, possibly gaining a future upgrade in mean offspring *quality*. This idea was developed first to explain seed over-production in plants (Buchholz 1922). Here parents can use the crucible of sibling competition itself to identify the best offspring (Kozlowski and Stearns 1989, Forbes and Mock 1998), rather in the way females visiting a lek may let male-male competition sort out mate quality.

Under insurance, the surplus progeny serve as a hedge against sub-optimal offspring numbers that may arise from early, unpredictable developmental failure or other forms of loss. In short, brood size is a random variable. Insurance is, in fact, the logical complement to Lack's brood reduction hypothesis, where resource level is a random variable and parents must base their clutch size decision on insufficient information about the match between supply and demand. Over-production thus provides contingency options for coping with both ecological and developmental uncertainty. In this paper we wish to focus on insurance *per se*, but refer the reader to Kozlowski and Stearns (1989), Lyon et al. (1994), and Forbes and Mock (1998) for discussions of progeny choice.

The insurance argument is simple and straightforward. Parents add marginal offspring to their clutch/brood as a hedge against early failure of core brood members. Marginal offspring are sometimes competitively handicapped (e.g., by asynchronous hatching) and thus readily identifiable, but insurance logic does not mandate any such handicaps and some parents hedge against offspring failure simply by clutch expansion without adding any phenotypic distinctions between core and marginal brood members.

The reasons why parents often do manipulate offspring phenotypes are varied, but generally serve as a means of moderating the costs of subsequent brood reduction. In obligate brood-reducing species, hatching asynchrony is typically highly exaggerated, such that first-hatched nestlings enjoy an almost insuperable competitive edge. In siblicidal birds (where brood reduction

is substantially caused by sibling aggression, Mock 1984), including various pelicans, eagles, boobies, egrets, and cranes, the marginal nestling is typically bludgeoned to death at an early age whenever the full brood hatches (Gargett 1978, Cash and Evans 1986, Anderson 1989). Where nest-mate asymmetries are less extreme, the executions tend to be more protracted and less certain. In many facultatively siblicidal birds such as Blue-footed Boobies (*Sula nebouxi*) and Cattle Egrets (*Bubulcus ibis*), the extra nestling is often maintained for days or even weeks, during which it simultaneously embodies insurance value (enjoying enhanced survival if eventually predeceased by a senior nestmate) and the Lack potential of adding to the larger absolute number of independent offspring if ecological conditions prove generous (Mock and Parker 1986). The parentally determined initial competitive asymmetries thus modulate the costs and likelihood of brood reduction and the duration of insurance coverage.

PREDICTIONS OF INSURANCE THEORY

The fundamental prediction of insurance theory is that the fitness prospects of marginal offspring vary in a density-dependent manner, rising when predeceased by a core sibling (Lundberg 1985, Forbes 1990, 1991, Forbes and Lamey 1996). This can be evaluated non-experimentally simply by monitoring the fates of marginal offspring in relation to that of core offspring (when these subsets are phenotypically recognizable). Examining the success of marginal offspring in unmanipulated nests that do and do not experience losses of core chicks can yield useful insights, although such data must be interpreted cautiously for the usual reason of potential covariation. For example, there may be differences in the quality of parents across pairs, the possibility of terminal egg neglect (Evans and Lee 1991), and so forth. Stronger tests of insurance theory, therefore, are based upon experimentation.

Experimental tests. Insurance was first suggested as a resolution to the puzzle of species characteristically laying two eggs but rearing only a single chick to fledging. Dorward (1962), Kepler (1969), Cooper (1977), and Nelson (1978) all suggested that the surplus egg could serve as a back-up against hatching failure. In such obligate taxa, measuring insurance value is straightforward: any and all surviving marginal

offspring can only represent insurance value. As a semantic aside, it is interesting that the phenomenon we label as "obligate brood reduction" (defined by convention as referring to species in which 90%+ of broods lose a nestling to sib-competition; Simmons 1988, Mock and Parker 1997) is probably not as rigid as our usage implies. Whether increased survivorship in such taxa represents maladaptive failures in the brood-pruning system (perhaps the normally prolonged hatching span was accidentally compressed), or are adaptive responses that are simply sporadic (such as taking advantage of rare ecological bonanzas) is unclear (Simmons 1997).

Insurance value was experimentally confirmed in the elegant experiment of Cash and Evans (1986). Their protocol was simple: one set of randomly selected parents was deprived of their insurance coverage by the removal of the marginal egg from each nest, then their success was evaluated relative to a matched sample of parents that had been allowed to keep their backup offspring. Their subject was a typical obligate species, the American White Pelican (*Pelecanus erythrorhynchos*), which typically lays two eggs, but almost never fledges both chicks (≤ 1.1 percent of broods in the population studied by Evans 1996). Most marginal sibs perish in their first week of life from nestmate harassment and food deprivation (Cash and Evans 1986, Evans and McMahon 1987). The experiment produced two salient results—parents with no marginal chicks experienced the normal rates of hatching failure in their lone remaining egg (20 percent of nests), but had no back-up ready; in consequence they fared worse than control parents. A third group of parents that had started with three eggs (the ones relocated from the trimmed clutches) fared no better than parents with two. Thus, one extra egg yielded valuable insurance coverage, but a second insurance egg yielded no additional benefit (see Appendix 1).

Forbes et al. (1997) performed a similar experiment in facultatively brood-reducing Red-winged Blackbirds (*Agelaius phoeniceus*), adding and removing core or marginal eggs to clutches. The survival of marginal offspring hinged upon the fate of core offspring, falling in nests with core eggs added, and rising in nests where core eggs were removed. However, a parallel result was not observed among core offspring themselves. Indeed, adding or removing

marginal offspring had no discernible effect on the fate of core offspring, demonstrating the cosetted position of core members. A similar experiment performed on Yellow-headed Blackbirds (*Xanthocephalus xanthocephalus*) yielded identical results (unpubl. data). In these studies, the same underlying pattern was observed in unmanipulated broods as a function of whether they experienced any natural hatching failure. The survival of marginal offspring rose sharply in broods where at least one egg had failed to hatch. Comparable effects have been observed in facultatively brood-reducing Dark-eyed Juncos (*Junco hyemalis*), European Starlings (*Sturnus vulgaris*), and Yellow-headed Blackbirds (Smith 1988, Stouffer and Power 1990, Barber and Evans 1995).

Here we see clearly the effects of asymmetric sibling rivalry: within-brood phenotypic handicaps (in this case, hatching asynchrony) buffer a portion of the brood from developmental uncertainty (Mock and Forbes 1995). As a consequence, parents are left with one caste of low-variance progeny (the core brood) whose prospects for growth and survival are relatively secure, and a second caste of high-variance progeny (the marginal offspring), whose fitness prospects rest upon ecological, social, and developmental contingencies (Mock and Forbes 1995, Forbes et al. 1997). As their presence or absence has little if any effect upon the fate of core offspring, marginal offspring represent, in effect, a stock of cheap, disposable offspring.

RELATED ISSUES FOR FACULTATIVE SPECIES

In obligate brood-reducing species, like American White Pelicans, the marginal egg's value can be credited almost entirely to its insurance role, but in facultative brood-reducing taxa, there is the additional chance that a marginal chick can fledge alongside its core siblings, thus deliver extra reproductive value (RV) (*sensu* Mock and Parker 1986) to its parents. The measurement problem is only slightly more complex for such species and a simple method for partitioning RV is described in Appendix 2.

Several workers have rejected the whole notion of insurance value when they find some broods in which marginal offspring survive with their core-brood siblings. If the supposedly redundant marginal offspring does not oblige by dying when its nestmates survive, some would

assert that insurance must not hold (Mead and Morton 1985, Lessells and Avery 1989, Bollinger et al. 1991). From the above, we hope it is clear that insurance does *not* require that redundant marginal offspring be eliminated from the brood, even though this often does occur and is virtually guaranteed in so-called obligate brood reducers.

The error seems to have two components. First, the presence of redundant (unneeded) offspring may represent the cost of the premium for insurance coverage. As long as the total benefits (replacement of failed core offspring) outweigh the total costs, insurance is favored (Forbes 1990, 1991). Moreover, hatching asynchrony serves to diminish the competition costs of extra offspring, even when the marginal chick manages to survive (see below). Second, marginal offspring can serve multiple functions simultaneously. Even though the marginal offspring may not end up substituting for a failed core sib, it may provide a reproductive bonus if resources are sufficiently plentiful.

The view that eliminating marginal offspring is necessary for an insurance system probably arose from the early generation of insurance ideas in the obligate brood-reduction literature (Dorward 1962, Kepler 1969, Woodward 1972). If both the core and marginal offspring survive to hatch, the latter almost always becomes the victim of fatal sibling aggression and/or socially enforced starvation. Because insurance offspring are routinely discarded in such species, the same expectation seems to have been transferred, falsely, over to facultative brood-reducers. In short, the key distinction is that in facultative systems, the marginal offspring may eventually shed its insurance function (as the core brood passes from its period of highest mortality risk), but still retain some other value to the rest of the family. Or the marginal offspring may simply be redundant, adding to the overall cost of an insurance strategy (Forbes 1990, 1991).

To summarize, in facultative systems there are multiple incentives for producing marginal offspring. Aside from insurance benefits, marginal offspring may yield a reproductive bonus when feeding conditions are favorable, which Lamey et al. (1996) referred to as "lottery" offspring, a term that nicely emphasizes the probabilistic nature of life-history decisions for parent birds. Moreover, marginal offspring need not survive to yield benefits to parents or sibs. We note par-

enthetically that the champion multi-purpose marginal offspring to date seem to belong to the American Kestrel (*Falco sparverius*), where extra eggs not only serve insurance and lottery functions, but enable progeny choice by adaptive sex ratio adjustment, and even facilitate the development of other family members by serving as meal for elder siblings and parents during acute food shortfalls (Bortolotti et al. 1991, Wiebe and Bortolotti 1992, 1995, Wiebe 1996).

Finally, we know almost nothing about the possible long-term effects of acute but non-fatal sibling competition. Most studies rely on easily-measured variables (typically survival to fledging and body condition at fledging) as surrogates for parental reproductive success, which is itself a surrogate for direct fitness. The studies of Cattle Egrets, for example, have focused on the one-third of nests in which the victim dies from the combined effects of food deprivation and physical abuse, without anything to say about the two-thirds in which the youngest chick merely goes through several weeks of consuming somewhat less than a full share of the food. Although dead victims can be assigned a lifetime reproductive success of zero with a high degree of confidence, the long-term effects of temporary or partial starvation may be extremely important to the overall fitness payoffs of all family members. There has been much documentation of positive relationships between fledging mass and recruitment into various breeding populations, but few explorations of the relationship between hatching order and survival to adulthood. The strongest case is for Western Gulls, *Larus occidentalis*, on south-east Farallon Island (Spear and Nur 1994). Using 352 3-chick broods and searching diligently for banded survivors over a period of years, they amassed data showing that *A*- and *B*-chicks (the two senior-most hatchlings in each brood) not only have a higher fledging rate than *C*-chicks, which duplicated the usual short-term pattern found in many asynchronously hatching species, but also enjoy higher survival to the age of 12 months. Beyond that point, remaining *C*-chicks survive through the second year at rates comparable to their elders. And the latest hint along this front comes from a long-term study of Little Egrets (*Egretta garzetta*) in southern France, where Thomas et al. (1999) examined whether senior siblings might achieve higher reproductive performance as adults. By individually marking thousands of broods and

searching later when these marked birds were adults (whose ranks within their natal broods were known), they showed that mating pairs in which at least one partner had been an *A*-chick raised larger broods than those containing at least one known *B*-partner, which in turn had larger broods than if the known-rank parent had been *C* or *D* in its nest of origin. If this turns out to be a general pattern (a very big "if"), then parental favoritism toward senior siblings (as better vehicles for the production of grand-offspring) makes even more sense, as does parental indifference to the suffering of marginal chicks.

INSURANCE VALUE AND THE FREQUENCY OF REPLACEMENT

Another argument used in opposition to the insurance hypothesis focuses on whether the gambit pays off frequently enough to have favored over-production (Brown et al. 1977, Williams 1980, Simmons 1988). This seems to have begun with an unfortunate calculation decision made in an influential early paper (see Appendix 1), but even setting history aside, this reasoning omits another key consideration: when the policy is cashed, the benefit received can be very large, in some cases salvaging an entire breeding season. It follows that insurance need not be claimed often to be cost-effective. To put this in human terms, one need not have repeated auto crashes to make car insurance worthwhile.

Balanced against a policy's claims, of course, are the premium costs, which appear small at first glance for bird eggs. In obligate brood-reducing birds in particular, eggs are tiny relative to female mass, and have been assumed to represent a negligible energetic investment (but see Anderson 1990 for an alternative view). Recent work with some facultative brood-reducers suggests that the costs of both egg production and maintenance may be decidedly non-trivial.

When the first-laid egg of Lesser Black-backed Gulls (*Larus fuscus*) was removed experimentally, forcing these determinate-layers to create a fourth egg in order to reach their normal clutch of three, the parents raised fewer and lighter fledglings than parents that had not been thus taxed. Furthermore, when laying was completed, the experimentally stressed mothers had substantially diminished pectoral muscles than the control mothers (Monaghan et al. 1998), in-

dicating significant costs to both generations of family members.

The costs of incubating an extra egg may similarly have been underestimated (and often ignored entirely). Twenty-one Common Tern (*Sterna hirundo*) pairs were given a third egg to incubate on the second day after completing their own two-egg clutches (normal range = one to three). That egg was returned to its home nest just before hatching, so the only difference between these experimental nests and 20 untaxed controls occurred during the incubation period. Interestingly, the impact of the manipulation was borne mainly by the second-hatched chick in the experimental broods, which grew more slowly and fledged at lower average mass than its control-nest counterparts. Similar comparisons for the senior nestmate showed weaker (statistically nonsignificant) effects in the same direction. The authors interpreted these results as evidence that taxed parents brought back less food and the intra-brood size hierarchy buffered the elder chick (Heaney and Monaghan 1996).

Such costs would stand as a disincentive for adding marginal eggs to the clutch for whatever reason. In addition, the costs of evicting surplus marginal nestlings may also extract high costs, although such a challenge to the core nestling might simultaneously serve a parental purpose by screening out low-quality core offspring (Simmons 1988). Given the typical 2- to 5-day head-start found in obligate brood reducers, a senior sibling that cannot defeat its newly hatched nestmate is probably not worth rearing anyway (Forbes 1991). In some species, such as Hooded Grebes (*Podiceps gallardoi*) and Harpy Eagles (*Harpia harpyja*), parents pare eviction costs by abandoning or burying marginal eggs once the core egg hatches successfully (Rettig 1978, Nuechterlein and Johnson 1981). Eviction costs may well be more expensive in facultative brood-reducers where the competitive advantage enjoyed by core sibs is less dramatic.

In assessing insurance premiums it is also instructive to examine those cases where parents waive insurance coverage—i.e., uniparous species such as certain large raptors and seabirds. The obvious question is *why not* add a second egg to the clutch? We can only speculate as to the causes of such missing coverage, but two possibilities immediately suggest themselves. First, the production and maintenance costs of supernumerary offspring in some of these spe-

cies are likely to be non-trivial. In many uniparous seabirds, eggs are relatively large (>25 percent of female body mass: Lack 1968), and likely involve a considerable energetic expenditure to produce and incubate (Anderson 1990, Mínguez 1998). Perhaps the premium cost for such insurance is simply unaffordable. Alternatively, uniparous eagles and boobies may forego the potential benefits of insurance because they have very high hatching success (minimizing need for a back-up, Anderson 1990) and/or because circumstances may favor the production of one unusually large egg in place of two smaller ones (Simmons 1997).

Second, the temporal advantage of insurance is diminished in environments with reduced seasonality. If parents can simply begin anew immediately after losing a singleton egg, the penalty for failure is less severe than in cases where parents have to wait until the following year to try again, and the value of insurance wanes. Conversely, in strongly seasonal environments, immediate re-nesting may be possible, but only at a cost of reduced survival prospects for the resultant progeny. Under such circumstances insurance value grows.

HATCHING ASYNCHRONY AND INSURANCE

Clearly, the role of insurance is central to the issue of avian clutch size. But insurance is also relevant to the matter of why parents confer phenotypic handicaps upon certain of their progeny, and, if only by default, advantages to others. A lively discussion about the adaptive significance, if any, of avian hatching asynchrony has emerged over the last two decades (Magrath 1990, Stoleson and Beissinger 1995, Stenning 1996). It seems odd to us that the value of marginal offspring as a hedge against developmental uncertainty has often escaped the notice of those concerned with the question of avian hatching asynchrony. Because insurance is the only viable explanation for the presence of marginal eggs in obligate brood-reducing species (Dorward 1962, Cash and Evans 1986, Anderson 1990), it is, by extension, the *only* global or automatic component of the fitness payoff for promoting hatch asynchrony. Indeed, recent work on American White Pelicans suggests that hatching asynchrony is optimized to provide insurance coverage for the period when core offspring are at greatest risk (Evans 1996).

We propose that the key question concerning the insurance value of marginal eggs in multiparous species is not whether it exists, but how much of a contribution it makes. We do not suggest, however, that insurance is the only, or necessarily the most important, explanation for the presence and extent of hatching asynchrony in facultative brood-reducers. Nor do we suggest that hatching asynchrony *per se* is always beneficial. Even though an insurance benefit may hold, this may be more than offset by other costs. As Magrath (1990) notes, hatching asynchrony lies amid a series of co-adapted traits, and will reflect a balance among these. We would argue that, excepting only uniparous taxa, insurance will virtually always be at least one component of this evolutionary calculus.

CHANGING PERSPECTIVES ABOUT AVIAN FAMILIES

Once we recognize the parental combination of initial over-production plus reliance on brood-reduction to trim family size as twin components of a comprehensive life-history strategy, several previously confusing things start to make more sense. Two decades ago, R. J. O'Connor (1978) argued that sibling aggression must be a manifestation of parent-offspring conflict and most of us quickly agreed with that assessment. His idea was that siblicidal activities lead to the overt destruction of offspring that are potential vehicles for parental fitness, so the selfish actions of one nestling against another must be at odds with the parents' best interests. This led to the general expectation that parents should interfere, actively or subtly, with sib fights and/or the social starvation process. The literature on siblicide at that time was minuscule and anecdotal, consisting mainly of indirect evidence gathered from highly sporadic visits to eagle and owl nests (Ingram 1959, Steyn 1975, Gargett 1978). But O'Connor's predictions were very much in the minds of several research teams that independently discovered siblicide occurring wholesale in colony-nesting birds (Braun and Hunt 1983, Mock 1985, Drummond et al. 1986), a logistical windfall that made empirical study truly feasible. And one of the most impressive things that this wave of researchers observed was that parents simply were not leaping into the fray to protect victims, nor slipping food to the victims on the sly. Parents were physically present for many of the nasty attacks, but

did virtually nothing to interfere (Mock et al. 1990).

This anomaly forced some re-thinking. Perhaps parents do not interfere because that would merely delay the inevitable (Drummond 1993), in which case siblicide would constitute a true case of parent-offspring conflict (Trivers 1974). Or perhaps parental interference itself might be *facultative*, such that its expression hinges on the parents' assessment of unfolding ecological realities, preserving the victim when they judge food to be abundant, but passively condoning its execution when times are lean. Or are the parents in some kind of collaboration with the killers: having set up the whole brood reduction process, do parents just let the drama play itself out?

Family conspiracy? We do not know the answers to all these questions, but the idea of a parent-bully collaboration no longer seems as fanciful as it once did. Parents do, in fact, behave in ways that *create* competitive asymmetries within a brood of siblings, doling out advantages to some and handicaps to others. Indeed, it is the parental act of commencing effective incubation prior to the completion of laying that provides the embryos within early-laid eggs their head start. Once hatching is completed, that first chick is free to grow larger (and stronger) than the volume limit imposed by the rigid shell and it can use this advantage in competing within the hierarchical sibship. Furthermore, parents may not really be sacrificing much by losing part of the current brood. In long-lived species, a bit of simple quantitative modeling shows that remarkably little improvement in parental survivorship compensates them adequately for the loss of an offspring or two per breeding cycle (Mock and Forbes 1994).

Thus we are left with a radically different interpretation of family structure than existed only a few short years ago. Parents are unlikely to have equal interests in all their progeny (*contra* Trivers 1974); rather, they quite routinely play favorites. The death of one or more progeny follows directly from initial parental over-production. Instead of representing a fitness loss to parents, brood reduction may well serve their interests, restoring the balance to prudent levels of expenditure on current offspring. For older, stronger core siblings, the likely winners in sibling competitions, it represents the best of times.

For marginal offspring with the most to lose, it may well be the worst of times.

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APPENDIX 1. SINGLE- VS. DOUBLE-INSURING.

The Cash and Evans (1986) experimental data showed no advantage to having a second insurance egg when the eventual family size will shrink to one nesting. This makes sense from fundamental probability theory. Let q be the proportional probability of a given egg's embryo surviving through the whole period before the siblicidal cancellation of the insurance policy (typically a few days after hatching), with values ranging from 1.0 (chick always hatching and surviving to that age) to 0.0 (always dying). A parental decision to lay only one egg thus faces a failure risk of $1 - q$. We can play with various values of q and plug in estimate costs, but to keep this simple, imagine that success is achieved by four chicks out of five, such that $q = 0.8$ and $1 - q = 0.2$.

An alternative parental decision to produce a second egg can now be examined using this framework and the same values. Whereas the risk of disaster was 0.2 with one egg, that falls sharply to $0.2^2 (= 0.04)$ with a back-up in place. This is because we now seek the combined probability that *both* eggs will result in failure, which requires multiplication. From the binomial expansion, we can show that these same numbers give an overall proportion of 0.64 for the parents whose two eggs will produce two thriving chicks (here is where siblicide will be needed), and 0.16 will have either a healthy *A*-chick or a healthy *B*-chick. Presuming only that *A*- and *B*-chicks are genetically equivalent, such that parents do not care which singleton they raise, the insurance payoff of 16 percent is potentially quite attractive.

Pressing on with the hypothetical laying of a third egg, it is clear that parents gain rather less on margin. From the production of *C*, parental risk of having nobody to rear falls only to $0.2^3 = 0.008$, while the total proportion of broods requiring siblicidal correction climbs sharply to 0.896 (0.384 will have some combination of two chicks to fight it out, while another 0.512 will hatch everyone, thus needing double-siblicide to trim family size down to one).

APPENDIX 2. A SHORT GUIDE TO CALCULATING INSURANCE VALUE.

The necessary data for assessing the "insurance reproductive value" of marginal offspring are seldom collected, which may be largely responsible for the idea having been overlooked generally. On a purely descriptive level, the steps differ according to system. For most asynchronously-hatching birds it is a simple matter of marking eggs by order of laying and recording fates chronologically. One determines who predeceases whom and how often. In most altricial birds, the distinction between core and marginal offspring is straightforward. Under the most common passerine hatching pattern, where a single chick hatches a day or so behind its elder nestmates, the designation is obvious: the runt is likely to be the marginal chick and everyone else constitutes the core brood. At the ex-

treme, however, where the entire brood hatches asynchronously across a considerable span, as in certain parrots, owls, and icterids, the distinction between core and marginal offspring is blurry. Here, following the fate of individual offspring and measuring the frequency with which a later-hatched offspring succeeds *only because it was predeceased by an earlier-hatched sib* become of paramount importance.

Unfortunately, failure to keep individualized records, compounded by the groundless assumption that all observed chick mortality must have involved the junior offspring, led to a dramatic underestimation of the insurance value (at 2.5 percent) for Black Eagle second eggs and hence to the conclusion that obligate siblicide in that high-profile species appears to be "an inexplicable example of biological waste" (Brown et al. 1977). Reanalysis, using only the most detailed subset of the same eagle records, suggests that second eggs provide the eventual survivor much more often: indeed, as in several other obligate brood-reducing birds, the second Black Eagle egg, far from doomed, produces a fledgling about one time in five.

Quantifying the benefits of insurance coverage is a relatively simple matter. Mock and Parker (1986) presented an easy empirical model for measuring insurance (RV_i) and extra reproductive value (RV_e) of marginal offspring, which are calculated as:

$$RV_i = (1 - q)P_i$$

$$RV_e = qP_e$$

where q is the proportion of broods in which all core offspring survive, P_i is the proportion of marginal chicks surviving in broods where a core chick has failed, and P_e is the proportion of marginal chicks surviving in broods where no core chick has failed. Lamey et al. (1996) present an alternative method of calculating insurance value, as they correctly note that the Mock and Parker calculation somewhat inflates the selective advantage of insurance in facultative brood reducers: many of these marginal chicks included under P_i would have survived even if not predeceased by a core chick. The method of Lamey et al. (1996) also incorporates the dynamic component of insurance—a core offspring that fails late in the period of parental care is not the same as one that fails early. Alternatively, we might consider P_i as representing "gross" insurance value and define a new function, the "net" insurance value or RV'_i , as the difference in proportion of marginal chicks surviving in nests with and without the timely failure of core offspring:

$$RV'_i = P_i - P_e$$

This net insurance value is simply the increment in survival that the marginal offspring enjoys when predeceased by a core sib. This formulation serves, of course, only as a first approximation for non-experimental studies, as P_e may not be the same for all parents losing vs. not losing a core chick. For example, low quality parents may be more accident-prone, thus benefit more often from having insurance.