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Point-of-View

Brood reduction: narrow sense, broad sense

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In population biology, *brood reduction* is a familiar and quintessentially ornithological concept, among the most visible of David Lack's many compelling insights. Its meaning seems straightforward enough: the two words surely connote numerically decreasing a sibship during the post-hatching period, while the offspring continue to rely on parental care. Unfortunately, the usage of brood reduction has become more complicated and ambiguous in recent years. In this essay I attempt to make three points: (1) I suggest that the term brood reduction may be most useful if restricted to its original (and explicitly narrower) meaning; (2) I propose some operational criteria by which such brood reduction can be recognized in the field; and (3) I call the ornithological community's attention to parallel phenomena found in other taxa. In this way, I hope to ease some growing confusion, while also showing that even a restricted definition of brood reduction is much more global and intriguing than is generally appreciated. Although I advocate narrower use of the term brood reduction, I hope to promote a broader view of the phenomenon.

Though linked inexorably to David Lack's name, the term brood reduction was first coined by the then-undergraduate Bob Ricklefs, who was testing Lack's unnamed idea that parents create expendable, marginal offspring as a contingency against variable food conditions (Ricklefs 1965). In a nutshell, the hypothesis hinged on the assumption that fatal levels of sibling competition would trim brood size to an appropriate level if food turns out to be low. It was assumed that this destructive process would not kick in if food proves plentiful (but see Pijanski 1992), so the overall effect would be to maximize brood size in the face of stochastic conditions (i.e., it serves in "resource-tracking": Temme and Charnov 1987).

The problem of ambiguity arose later, plausibly from two sources. First, as field observations accumulated showing that families sometimes do lose one or two young offspring for a variety of reasons (that include, but are not limited to, fatal sibling competition), the natural tendency to couple observations with an established phe-

nomenon may have led many workers to the same label. This pigeon-holing inadvertently stretched its meaning. Second, Lack's hypothesis stood virtually alone for decades as the only really attractive functional explanation for the early mortalities (others existed, but were strangely ignored). Conceivably, the temptation to couple one's data with a prominent concept distracted many workers from the implicit assumptions underlying Lack's argument. Whatever the reason behind the emerging ambiguity, the term "brood reduction" now means different things to different workers. To some it is merely a broad *descriptive* phenomenon; to others, a particular *mechanism*. In any case, Lack's hypothesis clearly needed a handle and Ricklefs certainly provided a successful one.

Hatching asynchrony in birds

It is also worth remembering that the phenomenon Lack was originally trying to explain was *hatching asynchrony*, not the fatal consequences thereof. He interpreted asynchrony in Swifts *Apus apus* and other birds as a means by which parents adaptively create relatively disadvantaged (i.e., handicapped) offspring that can be more easily dispatched if and when ecological conditions turn sour. Nowadays, one might restate this parental manipulation of hatching spread as a means by which parents minimize the future costs of sibling competition (see Hamilton 1964, Alexander 1974, Stinson 1979, Hahn 1981, Mock and Ploger 1987).

A recent renewal of interest in these topics has spawned a burgeoning array of alternative explanations for hatching asynchrony (see reviews by Magrath 1990, Amundsen and Slagsvold 1991), many having nothing whatever to do with beneficial pruning of family size via sibling rivalry. Just to name a few quickly, asynchrony has been proposed as a way of: (1) cutting the *peak load* of parental effort (roughly equivalent to making serial payments on an expensive purchase: Hussell 1972, Mock and Schwagmeyer 1990); (2) coercing a philandering

husband into greater investment in the current brood (Slagsvold and Lifjeld 1989); and (3) getting some babies through the most perilous period of predation risk, albeit at an increased cost to the others (Clark and Wilson 1981). It seems clear that the parental phenotype – i.e., the behavior(s) that generate asynchronous hatching patterns – must have evolved many times under different mosaics of selective pressures (a point made compellingly by Clark and Wilson 1981). Whereas the classic Lack competitive dynamic likely played an important role in asynchrony's evolution for some taxa, that process may have been of secondary (or no) consequence in others.

A proposed lexicon

To cover the cases in which an offspring dies from unspecified, unknown, or noncompetitive causes, a neutral umbrella label is still needed. One could argue, as suggested in the opening paragraph, that *brood reduction* really ought to mean just this, that the old term simply ought to be used in its literal and broadest sense. After some personal experimentation, however, I am of the opinion that clear communication is ill-served by trying to redefine and expand a term after several decades of historical usage have led many or most readers to infer something else from it. (A rough parallel exists in the attempt by some to resurrect the term “group selection” and retrofit it with new definitions, apparently hoping that nobody will remember the term's discredited but very common former usage.) For reasons of clarity, then, I suggest that a distinction be made between the very widespread phenomenon of “*partial-brood loss*” (which may be defined simply as **some, but not all, members of a sibship dying from any and all causes**) and the subset of *brood reduction* (**abridgement of family size due to sibling rivalry per se**). Within this narrow-sense *brood reduction* one may find convenient sub-categories, such as *siblicide* for brood reduction that involves substantial overt sibling aggression (Mock et al. 1990, Mock and Parker in press). I heard recently on the radio that “*siblicide*” has now been admitted into the Oxford English Dictionary, so we can presumably use it now without fear of offending the jargon-police.

Though *partial-brood loss* is admittedly a rather bland descriptive term, it has the vital advantages of having a fresh, untainted start and implying nothing about the significance of the observed mortality. Examples initially dubbed *partial-brood loss* can later be re-assigned, when improved evidence so indicates.

Application

The incomplete hierarchy of terms proposed here tracks the amount of information needed for consistent usage.

There is usually little dispute over what constitutes “dead” versus “alive”, so judging a nest to have experienced *partial-brood loss* is a relatively easy call. Identifying *brood reduction* (in the narrow sense) is now a bit trickier, as it requires some operational criteria for how sibling competition is to be detected. This can be as simple or labyrinthine as a given worker chooses, so long as the method used is operational and replicable. For herons, which hatch asynchronously, I use three commonsense elements to decide whether sibships losing members were cases of *partial-brood loss*, *brood reduction*, and/or *siblicide*. (1) Just prior to death, do victim sibs appear to be underfed (or short of some other critically limiting resource)? Are they emaciated? (2) For the population, do victims tend to be the last-hatched members of their broods? And (3) are the victims physically beaten prior to death? If we know only that a given species hatches an average of, say, three eggs per nest but usually fledges only two young – and cannot answer any of these questions in the affirmative – then *partial-brood loss* is probably as far as we should go.

To get the answers, question (1) can be addressed in a variety of ways, including direct observation of meals or repeated census visits that reveal a reliable pattern of weight loss prior to death, etc. Question (2) can also be resolved through censusing. Question (3) is best answered from direct observations (Is the victim socially excluded from food by sibling attacks?), but sometimes physical wounding (severe enough to be detected during censuses) yields equivalent information (e.g., Mock 1985).

I stress that the terminology offered here is one of many possible solutions. The problem is scientific murkiness, not wordsmithing. Others may prefer to stick with a broad definition of *brood reduction* (perhaps akin to the *partial-brood loss* advocated here), so my true hope is that they will simply state their meaning explicitly.

Diverse manifestations

Even in this narrow competitive sense, *brood reduction* is a good deal more widespread than is generally realized, though the systematic search for it is really just beginning. Its essential ingredient is a mismatch between offspring demand and supply (usually parentally delivered food, but sometimes over other stakes – like future reproductive opportunity). In some cases, the resource shortage is never actually reached, either because pre-emptive sib-killing reduces the demand in advance (though such *pending competition* is easier to conceptualize than it is to demonstrate) or because an incipient rival meets its end early from some stochastic agent of death (e.g., accident, exposure, tapeworm, grab-and-run predator, etc.). In this latter scenario, the *raison d'être* for *brood reduction* may vanish, the mismatch between supply and demand having

been already corrected by *partial-brood loss*. But when no such event occurs, the competitively superior siblings do the job, either by nonaggressively outconsuming the victim or through various forms of active sabotage. In numerous (mostly non-avian) taxa, the victim's execution is perpetrated by its own parent. Such filial infanticide may evolve because it obviates more costly resolutions to the pending competition: if so, then it could be viewed fairly as an indirect evolutionary product of sibling rivalry.

Various parallels and extensions of these phenomena have been found in unfeathered animals plus many plants. To make the point that avian brood reduction belongs in a larger context of sibling rivalry phenomena, I briefly describe a few selected examples from other taxa. Two basic features unite all these systems: parents tend to err on the side of offspring overproduction (usually only by a modest one or two progeny in most animal systems) and available resources are accordingly inadequate. Furthermore, most competitive sibships are spatially confined in a physical 'nursery' (Mock and Parker in press), which may take such forms as nest, den, womb, branch, or fruit.

Embryonic siblings of pronghorn *Antilocapra americana* compete fatally for womb space. First, many blastocysts vie for implantation sites, with two winners eventually securing positions and commencing development in each horn of the uterus. Soon the anterior sib grows a long rear-directed process (the 'necrotic tip') that literally skewers its womb-mate lengthwise (O'Gara 1969). As a result, litter size at birth is usually two, one from each uterine horn. Something remarkably similar occurs in seedpods of a tropical tree, *Dalbergia sissoo*, where the most distal individual seed discharges chemicals that effectively inhibit growth of its several pod-mates. Because the whole pod is eventually wind-dispersed, weight minimization is believed to be important (Ganeshaiyah and Uma Shaanker 1988), so this competition is essentially over sole possession of an ultra-light aircraft. For other plant examples, see Stephenson (1981), Haig (1992), and Mock and Parker (in press).

As with nestling birds, food shortages have been shown to limit the growth and future success of individual neonates in other animal and plant groups. On Isle Royale, Michigan, mating pairs of chorus frogs *Acris triseriata* amplex in small rocky pools along the Lake Superior shore, such that all the resulting tadpoles in a given pool are usually siblings. Growth speed (which determines both time till metamorphosis and body size at that stage) and survivorship are limited by the supply-demand balance, as demonstrated by food-supplementation experiments (Smith 1983, 1987, 1990). Similarly, male pipefishes and seahorses (Syngnathidae) carry their clutches in special ventral pouches, wherein developing embryos receive protection, diffused oxygen, nutrients, and osmoregulation from the father. A negative relationship between offspring size and numbers at emergence indicates density dependence (resource limitations),

hence a sibling scramble competition (Ahnesjö 1992a,b, Vincent et al. 1992).

The element of overt aggression is added to fatal rivalries in some mammals, just as it is in siblicidal eagles, boobies, egrets, and other birds. Spotted hyaenas *Crocuta crocuta* and barnyard swine even have precocial teeth that serve as anti-sib weapons. Piglets use their projecting incisors with slashing lateral head movements to contend for the sow's more productive anterior teats. In big litters, siblings slightly larger at birth retain their advantages through such bullying and are less likely to die during the early weeks of nursing (Fraser and Thompson 1990, Fraser 1990). Hyaena neonates fight viciously, starting immediately after parturition; if the two are of the same gender, one virtually always dies (Frank et al. 1991). This sex-specific type of siblicide resembles the lethal 'local mate competitions' of fig wasps (Hamilton 1979) and various parasitoid wasps (reviewed in Godfray 1993), where newly hatched brothers fight to the death for the chance to fertilize their own sisters. In honeybees, it is the eldest proto-queen that kills her royal sisters and wins the reproductive throne.

A conspicuous difference between most avian and non-avian siblicides concerns the typical final disposition of the corpse. Though some birds do consume the victim (e.g., Bortolotti et al. 1991), most observers report that the carcass is either discarded by parents or left to decompose in the nest (reviewed by Stanback and Koenig 1992). On balance, this suggests that the primary incentive for avian *brood reduction* is cutting the total brood demands (cf. Ingram 1959), thereby dulling the rivalry. In many other taxa, however, cannibalism appears to be the rule (e.g., Elgar and Crespi 1992) and, in some cases, the act of consumption per se assuredly lies at the heart of the exercise. For example, in sand tiger sharks *Eugomphodus taurus* the largest embryo depletes its yolk reserves quickly and then swims around inside the mother's uterus, killing and eating all its siblings plus whatever additional eggs are supplied later (Gilmore et al. 1983). Equally remarkable collaborations between mothers and favored offspring are evident in various snails and insects, where 'trophic' eggs are steadily supplied for the sustenance of certain offspring (reviewed by Crespi 1992, Baur 1992, Kukuk 1992). Burying beetle *Necrophorus vespilloides* parents often produce more larvae than the food source (typically a dead mouse) can support. When the crunch comes, the parents kill and consume their surplus offspring, regurgitating that material for surviving sibs (Bartlett 1987, C. Creighton pers. comm.).

Finally, no discussion of sibling cannibalism would be complete without acknowledging the extraordinary developmental polymorphisms found in some amphibians. For half a century, it has been known that three spadefoot toad species, *Scaphiopus* spp., can drastically alter their gross morphology and diet in response to worsening environmental conditions. Specifically, in a shrinking desert pool certain members of a larval sibship quickly

grow massive jaws and associated structures as they shift from an omnivorous detritus diet to a highly carnivorous one that includes siblings. These 'carnivore-morph' tadpoles develop much more rapidly and have a much higher probability of metamorphosing before the puddle evaporates completely (Pfennig 1992). Interestingly, when given a choice between sib and non-sib prey, spadefoot cannibals selectively consume the latter, apparently basing their decision on small 'taste' samples taken during preliminary nips (Pfennig et al. 1993). A similar kinship discrimination spares siblings in some cannibalistic populations of tiger salamanders *Ambystoma tigrinum*, which also undergo special morphological modifications when switching to a cannibalistic lifestyle (Pfennig and Collins 1993). Provocatively, the closely related marbled salamander, *A. opacum*, does exactly the opposite, preferring to eat siblings over non-sibs (Walls and Blaustein unpubl.)!

In conclusion, the increasing research activity surrounding the phenomena of avian partial-brood loss, brood reduction, and siblicide seems ready to take its place in a much more broadly comparative behavioral and life-history literature (Mock and Parker in press). It will surely help if we choose our tools of communication carefully.

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