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PERSPECTIVES IN ORNITHOLOGY

SIBLING SYMBIOSIS IN NESTLING BIRDS

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Gonzaga: Once more, brothers in arms.

Bertoldo: I'll live and die so.

Philip Massinger, *Maid of Honor* (1632)

IF THE TITLE of this perspective were "Sibling rivalry in nestling birds," readers could hardly be faulted for expecting a traversal of well-trodden ground. We have come to think of conflict among avian nestlings as natural and to some extent inevitable, which is a long way from the traditional view of families as harmonious social units. It is *de rigueur* to state that the theory of kin selection opened our eyes to the once-surprising possibility that the closest of relatives may benefit at one another's expense. The Cain-and-Abel battles of Black Eagles (*Aquila verreauxi*) and other large predatory birds, which had been described as "an inexplicable example of apparent biological waste" (Brown et al. 1977), became potentially explicable as extreme forms of sibling competition in cases where close relatives were also close rivals for limited food and tight space. We learned that nestling egrets, boobies, and ospreys fight to secure food, with sometimes fatal consequences; that nestling bee-eaters can use a modified egg-tooth to slash nestmates; and that kestrels and owls sometimes cannibalize kin. These and many more spectacular examples of sibling rivalry were chronicled in

Mock and Parker's (1997) masterful *Evolution of Sibling Rivalry*, which provided a comprehensive overview of theory and data bearing on conflict within families, especially conflict among siblings. Birds were featured prominently in the book, and dramas within the nest captured widespread interest both within and outside ornithology. Mock and Parker left little doubt that siblings within a nest are often important, and sometimes lethal, competitors for food and space. This focus on conflict is an understandable reflection of changing notions of the family and, in particular, revision of the earlier, somewhat romantic notion that close kin must live harmoniously because of their shared genetic interests. But have we gone too far?

If one uses the scientific literature to gauge relative interest in sibling relations, it is clear that the pendulum has swung sharply to the side of conflict, competition, and rivalry. A recent (November 2006) search of the Web of Science revealed 334 citations for the keywords "nestling conflict" or "nestling competition," and only 11 for "nestling cooperation" or "nestling mutualism." Though I doubt that any serious worker has forgotten that cooperation is also expected among close kin, I suspect that many find conflict a more compelling topic of study than cooperation. Here, to help pull the pendulum back from the pole of conflict among siblings, I will focus on the social benefits that accrue to nestlings during life within a brood.

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SIBLING SYMBIOSIS

In fact, the conflict-cooperation duality is a bit too narrow for my present purposes, and in its place I will borrow from the language of population ecology to refer to symbiosis (Wilson 1975), not among different species, but among siblings. There is a trio of potential symbiotic interactions (Table 1): parasitism, where one benefits and another suffers (as in siblicide); mutualism, where both parties benefit (as when two individuals cooperate to resist a predator); and commensalism, where one benefits and the other neither gains nor loses (as when one individual sits in the shade of another).

BROTHERS IN ARMS: THE BENEFITS OF BROODMATES

The term “brothers in arms” made its first appearance in English literature in Philip Massinger’s 17th-century play *Maid of Honor*. Though it refers to the camaraderie of two Knights of Malta taking up arms in military service, “brothers in arms” seems appropriate for describing alliances that form among siblings during life in the nest. Though propinquity can make siblings rivals for food or space, it can also make them (1) close allies in battles with parents over the level of parental investment and (2) partners in producing and distributing thermal resources within the nest. It is these symbiotic interactions that I will focus on below.

I will mention only briefly the now-familiar benefits of indirect fitness derived from the success of siblings (i.e., if siblings survive and thrive, which results in more descendents, because of an individual’s actions, an inclusive fitness benefit accrues to the latter; Hamilton 1964), because these are well studied and widely understood. And I will not directly address the intriguing issue of multilevel selection within

families, whereby broods potentially become targets of selection, because that topic has been ably addressed by Wilson and Clark (2002).

THE CONCEPT OF THE STRUCTURED FAMILY

My purpose is to examine the forces that push siblings toward increased generosity as opposed to selfishness, and much of what follows, curiously, revolves around parentally imposed competitive asymmetries among contemporary offspring. These occur when parents impose phenotypic handicaps on certain of their progeny and not on others; resulting differences in egg size, hormonal titre, immune-system complement, or birth-hatching asynchrony render some offspring “more equal” than others (Lack 1947, Magrath 1990, Williams 1994, Schwabl et al. 1997, Forbes and Glassey 2000, Royle et al. 2003, Groothuis et al. 2005).

Proximity is a key feature of family living from which opportunities for social symbiosis arise. But not all individuals are equally capable of deriving benefits, and some are more likely to pay costs. Asymmetries of power exist among family members, most obviously between parents and offspring but also among contemporary siblings, where age, developmental, physiological, and size differences place individuals on unequal footing.

Parentally imposed handicaps divide contemporary siblings into castes of privileged “core” offspring that enjoy superior prospects for growth and survival and disadvantaged “marginal” offspring that suffer reduced growth and elevated mortality (Mock and Forbes 1995, Forbes et al. 1997, Mock and Parker 1997, Forbes 2005). This phenotypic division underpins the concept of the “structured family,” which is useful for examining the dynamics of avian families (Fig. 1). Parents with a structured brood face

TABLE 1. Schematic description of different forms of sibling symbioses in structured families of nestling birds. Though it is more likely that core offspring will benefit (as shown here) from sibling parasitism or commensalism, marginal offspring could potentially benefit from these forms of symbiosis.

	Core offspring	Marginal offspring
Sibling parasitism	+	–
Sibling commensalism	+	0
Sibling mutualism	+	+

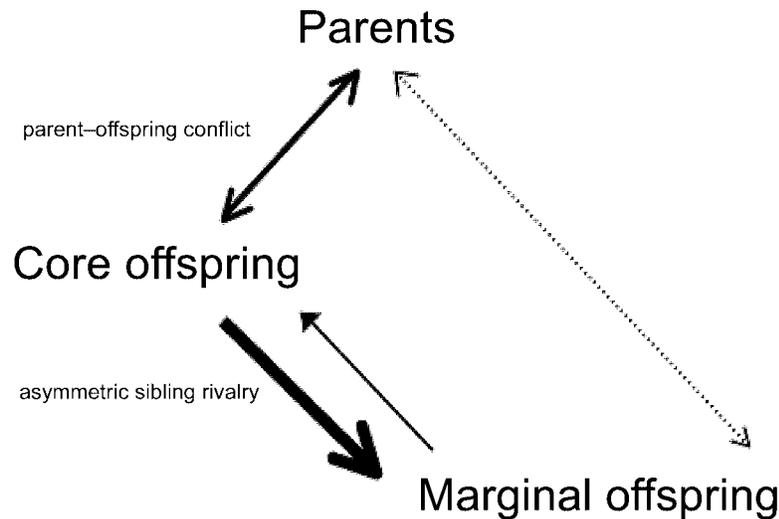


FIG. 1. Schematic view of asymmetric sibling rivalry and parent-offspring conflict in a family with a structured brood. The relative strength of familial interactions is approximated by line width. Both parent-offspring and sibling relations are affected when the brood is structured into stronger core and weaker marginal siblings. Empirical work shows that core siblings have stronger effects on marginal siblings than vice versa. And when core siblings affect how food is allocated within the brood, parents must work through the core brood to affect food allocation to marginal offspring.

a more complex parental investment decision, particularly where older, stronger core offspring have partial or complete control over allocation of resources (Parker et al. 1989, Forbes 1993). In such cases, parents must work through core siblings to influence resource-allocation among their progeny, particularly allocation to junior marginal siblings (Fig. 1). By diverting a smaller or greater share of parentally delivered resources to marginal offspring, core offspring can potentially manage their "investment" in siblings to their own benefit, by mechanisms I will explore below.

SIBLING MUTUALISMS IN BATTLES WITH PARENTS

In altricial birds, nestlings rely on their parents to provide critical resources such as food and warmth. Theory predicts that parents and offspring should disagree over the preferred level of parental investment (Trivers 1974, Mock and Parker 1997; but see Evans et al. 1995 for an exemplary empirical demonstration of parent-offspring cooperation). Offspring demands are generally expected to exceed the parental optima, and communication between parents and offspring plays a key role in setting the level of investment for which nestling

begging has proved to be a model (review in Wright and Leonard 2002).

Contemporary theory views nestling begging as an evolutionary game among parents and offspring, with two key parental decisions, which the offspring can influence: how much to invest in current as compared with future broods, and how to allocate this investment among contemporary progeny (e.g., Parker et al. 1989, Godfray 1991, Rodríguez-Gironés et al. 2001, Royle et al. 2004). Offspring begging potentially affects both these parental decisions.

Begging involves a dual system of vocal and visual cues, and the emerging view is that there is at least a partial functional separation of the vocal and visual elements of begging. Conspicuous visual displays—neck-stretching, gaping, wing-flapping, jostling—appear to be more important to within-brood allocation of parentally delivered food, and vocal cues more important in determining the overall level of brood provisioning (Muller and Smith 1978, Bengtsson and Ryden 1983, Leonard and Horn 2001, Glassey and Forbes 2002, Leonard et al. 2003), though vocal cues can also affect within-brood allocations (Price and Ydenberg 1995, Kilner et al. 1999, Leonard and Horn

2001, Sacchi et al. 2002). Wilson and Clark (2002) made the intriguing suggestion that selection for the design of signals for use within parent–offspring cooperation may simultaneously reflect individual competition and group-level cooperation.

Competitive handicaps are expected to affect the outcome of begging games, and a robust theoretical prediction is that competitively inferior marginal siblings will need to beg harder to gain what is ultimately a lesser reward (Parker et al. 1989, 2002; Rodríguez-Gironés et al. 2001). This prediction has been empirically confirmed (Lotem 1998a, Cotton et al. 1999, Rodríguez-Gironés et al. 2002, Smiseth and Amundsen 2002). Moreover, if begging is subdivided into functionally separate components—one that influences provisioning and one that affects within-brood allocation—then theory further predicts that core siblings should allow their

marginal nestmates to shoulder the burden of soliciting food from parents and exploit the efforts of their juniors (Rodríguez-Gironés et al. 2002). Effectively, core siblings parasitize the effort of marginal siblings.

SIBLING EXPLOITATION OR MUTUALISM?

An interesting possibility arises. If vocal begging intensity governs parental delivery rate, then older, stronger siblings may benefit from the continued presence of hungry, loud runts. These marginal nestlings may, in fact, be ideal companions for larger core siblings, inducing parents to bring more food though unable to compete for it effectively. Such a mechanism could hold, even if the share of food that core siblings receive were to decline. A simple example based on the despotic allocation model of Forbes (1993) illustrates the logic of this (Fig. 2).

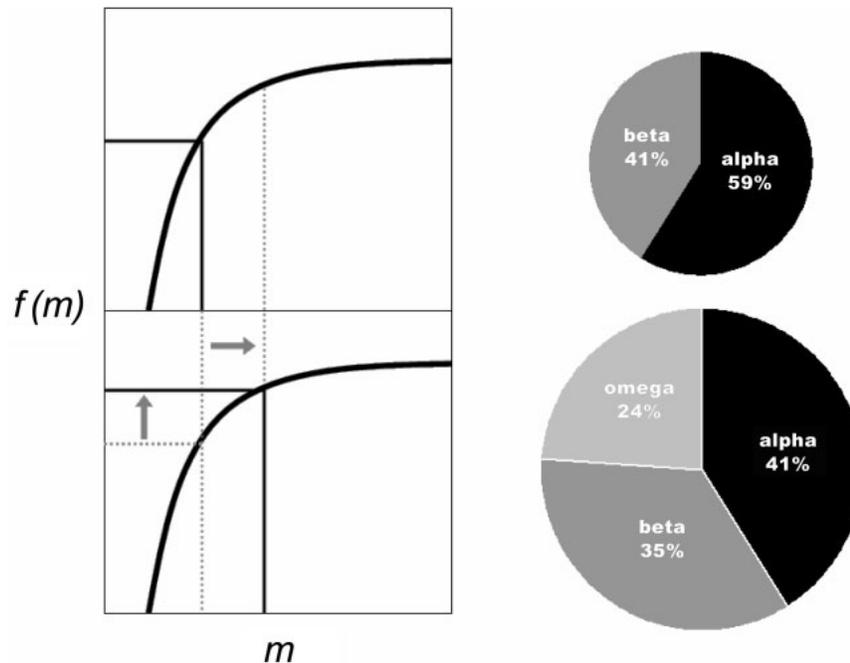


FIG. 2. Schematic overview of the relationship between brood size, food share, provisioning, and fitness in nestling birds. The uppermost panels represent a two-chick brood, with a senior sibling (alpha) and a junior sibling (beta). Food is shared according to a dominance hierarchy. The total food offered to the brood and shares to alpha and beta are represented by the pie chart. The direct fitness ($f[m]$) of alpha in relation to its per-capita food share (m) is shown in the upper left panel. The bottom panels represent a three-chick brood, with alpha, beta, and omega; total provisioning is split three ways, and the share of the pie to alpha now falls from 59% (upper pie chart) to 41% (lower pie chart). But because the overall size of the pie is larger, alpha's m value increases in the larger brood, and alpha's $f(m)$ value rises (bottom left panel).

The model assumes (1) that food is distributed according to an absolute and linear dominance hierarchy that resembles the food-allocation system of some siblicidal birds and (2) that food is shared in accordance with Hamilton's Rule. Moreover, Parker et al. (2002) noted that begging scrambles among chicks of unequal competitive ability generate predictions similar to those of hierarchy models when the handicap is large. Here the most senior member of the brood hierarchy controls how much food to take for itself and how much to leave for its junior siblings. Although I do not expect the quantitative mathematics of this stylized system to apply closely to any empirical system, it illustrates the underlying logic. Given the explicit mathematical function used in the original model for the relationship between provisioning (m) and fitness ($f[m]$), the senior sibling (alpha) should take 59% of all parental provisioning in a brood of two, leaving the remaining 41% for beta. But in a brood of three, the share to alpha falls to 41%, the share to beta is 35%, and the share to the most junior nestling (omega) is 24% (Fig. 2). Does this falling food share mean that alpha is necessarily worse off in a brood of three? Not at all. The direct fitness of alpha need not decline at all if parents simply bring more food to the larger brood, as illustrated in Figure 2. If the pie gets larger, it may not matter that alpha's share of the pie is smaller.

This basic argument was presented in Forbes (1993) to explain why selfish siblings may not profit from brood reduction if parents diminish parental investment as a consequence (see also Rodríguez-Gironés 1996). Study of nestling begging behavior provides a proximate behavioral mechanism for this limit to selfishness: senior siblings may enjoy an increment to their personal fitness (not to mention inclusive fitness) from being in a larger brood if junior nestmates help to secure more parental investment for the entire brood.

Recently, dramatic evidence of this effect has been found in studies of brood-parasitic cowbirds. Kilner et al. (2004) demonstrated experimentally that Brown-headed Cowbird (*Molothrus ater*) nestlings profited from the presence of host Eastern Phoebe (*Sayornis phoebe*) nestlings. Parent phoebes brought more food to nests with both phoebe and cowbird nestlings than to nests with only solitary cowbirds, and cowbirds grew faster in nests when reared alongside host nestlings. The larger cowbirds can outcompete

host nestlings by virtue of their larger size (Lichtenstein and Sealy 1998) and, as Kilner et al. (2004) showed, exploit the food-solicitation effort of their smaller, unrelated nestmates.

There is no obvious reason why similar dynamics would not hold in normal, structured bird families in which larger, stronger core siblings can outcompete marginal nestmates in within-brood competitions, as Lotem (1998b) and Kilner (2003) have suggested. One could model this formally, but a verbal model is probably sufficient, given that the result is self-evident. If the extra begging effort of a marginal sibling raises the level of parental investment for the current brood, core siblings may benefit directly from the presence of marginal offspring, even though they are competitors for food.

Here, I wish to differentiate between conventional kin-selected altruism (a loss in personal fitness to the senior sibling is more than offset by the gains in indirect fitness, in accordance with Hamilton's Rule) and potentially mutualistic, or at least commensal, symbioses between siblings, where we would expect gains in direct fitness for core offspring.

If both the core and marginal siblings enhance their level of provisioning through the begging effort of the latter, the term "sibling mutualism" applies. If, however, the core sibling benefits and the fitness of the marginal offspring is unchanged, the interaction is a "sibling commensalism," in which the begging costs of the marginal offspring are offset, presumably by an increased food ration. Finally, if the core sibling benefits at the expense of the marginal sibling, "sibling parasitism" is the best description. Presumably stronger core siblings are able to manage the benefits or costs that accrue to their marginal counterparts. Therefore, core siblings ultimately determine whether the sibling relationship amounts to parasitism, commensalism, or mutualism.

Mock and Parker (1986) reported a potential example of sibling mutualism in nestling Great Egrets (*Ardea alba*), where the presence of a younger broodmate was beneficial to a stronger sibling. They found that parents were likely to abandon singleton broods early but not late in a breeding season. They speculated that if enough time remained in the current breeding season, early-nesting parents could opt to re-lay and potentially rear a larger brood; this would favor a policy of abandonment. Later-nesting parents

without the re-nesting option were apparently better off rearing their singleton offspring than not reproducing at all. Thus, in broods of two where core siblings held the power of life or death over marginal nestmates, there was a powerful disincentive for siblicide early in the nesting season: the withdrawal of all parental investment.

THRIFTY-OFFSPRING PHENOTYPES FAVOR SIBLING MUTUALISM

Sibling symbiosis depends on an initial family structure that generates asymmetric sibling rivalry (Forbes and Glassey 2000). The competitive disparity ensures that the core siblings can sequester a greater share of parentally delivered resources without difficulty. Marginal siblings are thus consigned to the role of inferior competitors during their nestling life. Consequently they will, on average, receive less food, grow more slowly, and die more often than core nestmates. But by becoming less expensive to core siblings who can withhold resources, marginal siblings are more likely to avoid death in the nest, and thus make commensalism or mutualism more likely.

Given their role of junior partner in a sibling symbiosis, it seems logical that marginal offspring would adopt strategies that make the best of a bad situation, a possibility that has been little explored. I will call such strategies "thrifty-offspring phenotypes." They are potentially important factors in the social benefits that accrue to broodmates, because they affect the fitness payoffs for selfishness or generosity.

One obvious place for a thrifty-offspring phenotype to be manifest is in digestive physiology, where adaptive changes in gut retention time may reflect feeding conditions (Sibly 1981, Karasov 1996). We might reasonably expect marginal progeny with diminished and more variable access to food to pursue a different digestive strategy than that of core siblings (e.g., by extending the retention time in the gut of the food they receive, thus extracting a greater proportion of the available nutrients). Although this question has not been directly addressed, there is a related finding that is of interest in this context. During periods of privation, nestling House Sparrows (*Passer domesticus*) retained ingested food in the gut for a longer time (Lepczyk et al. 1998), which is consistent with the notion of a thrifty-offspring phenotype.

The thrifty-offspring phenotype may also extend to begging behavior. That nestlings escalate begging effort when their nestmates beg louder is well established (Price et al. 1996, Leonard and Horn 1998, Leonard et al. 2000, Neuenschwander et al. 2003). That marginal offspring, on average, beg harder for less reward is also well established (see above). Might marginal offspring strategically adjust begging intensity to expected outcome? For example, consider the case of a single marginal sibling sitting alongside two older and stronger core siblings, whose parents allocate food according to success in the begging competition (e.g., the nestling that stretches its neck the highest wins). If both core siblings beg maximally, the marginal sibling is almost certain to lose the begging competition. Why, then, should the marginal sibling expend much effort, particularly on the visual components of begging that influence within-brood allocation? If it is almost certain to lose, why should it squander resources that might be put to better use later or in alternate functions such as growth and maintenance?

This is similar to the problem of how to allocate advertising resources during political campaigns: campaign expenditures are highest when the competition is highest (Coyte and Landon 1989). Parties do not waste resources on constituencies where the outcome is virtually certain. Instead, both parties divert resources to battleground states.

Nestling birds represent an intriguing parallel: as noted above, dominant core siblings spend less on begging, on average, than marginal siblings. But do the latter modulate their spending according to the likelihood of success? When they stand little chance of winning, do they trim begging expenditures? This effect could be manifested as a curtailed begging effort by marginal siblings when core siblings exhibit intense begging, all else being equal (e.g., a shorter duration or lowered intensity of begging), or as a reduced investment in the visual displays that are less likely to secure more food than the vocal components of begging that may induce parents to bring more. These remain open and interesting questions for field workers.

THE PARADOX OF "REFEEDING" NESTLINGS

A paradoxical behavior among begging birds is the phenomenon of "refeeding," where

parents place a food item in a begging nestling's mouth but then remove it when it is not swallowed immediately. The food item is then offered to another nestling. In Red-winged Blackbirds (*Agelaius phoeniceus*), my students and I have observed this behavior routinely, with a single food item sometimes being offered to several nestlings before it is eventually swallowed. Casual conversations with other workers on nestling begging reveal that they have seen the same behavior in other species. Other than Wilson and Clark (2002), who described similar observations in Red-winged Blackbirds, little appears to have been published on this puzzling behavior. The obvious question is why a nestling would not accept an offered food item when begging?

This may represent another form of cooperative behavior that is related to the dual components of nestling begging: vocal cues that induce parents to bring more food, and visual cues that affect within-brood food allocation. Vocal begging requires an open gape, into which parents deposit food. But if vocal begging serves chiefly to induce parents to maintain or elevate rates of provisioning (see above), it may pay sated or partially sated nestlings to engage in vocal begging, to ensure future food, even when they have little interest in the current food item. Moreover, not swallowing an offered food item, allowing parents to retrieve it and offer it to another nestling whose hunger level is greater, may represent sibling generosity, in that it allows parents to divert food to nestlings whose immediate need is greater. This is conceptually similar to, though mechanistically different from, Roulin's "sibling negotiation" hypothesis, whereby nestlings engage in begging between feeding bouts to resolve whose need is greater (Roulin et al. 2000, Roulin 2004). It is possible, however, that this refeeding behavior has a more prosaic origin, a reflection of nestlings being sated and simply unable to swallow another food morsel. But why sated nestlings would still be gaping is unclear.

THERMAL COOPERATION AMONG NESTLING BIRDS

Thermal relations are another potential context for sibling cooperation. Work on mammals shows clear thermal advantages (higher body temperature, digestive efficiency, and survival) to offspring living in litters as opposed to living alone (Alberts 1978, Sokolov and Blumberg

2001, Bautista et al. 2003). Does the same hold true for birds?

Altricial birds reveal their reptilian ancestry in beginning life as passive ectotherms and making the transition to active endothermy during nestling life. Physiological ecologists have long known of the collective benefits of group living for nestlings, perhaps the simplest being that the age of effective endothermy for a brood is earlier than the age of physiological endothermy for individual nestlings (Dunn 1975, 1976). Huddling and bulk inertia allow broods to stabilize temperatures earlier than individuals can. The energy savings of group living that are derived from reduced costs of thermoregulation can potentially be redirected to other functions, such as enhanced growth (Dawson and Evans 1957, 1960; Dunn 1980).

If we superimpose the concept of family structure on this discussion, an intriguing set of questions arise. First, do younger marginal offspring save energy by using the earlier onset of physiological endothermy of older core nestmates? This is perhaps an example of sibling commensalism, if the marginal offspring are merely harvesting surplus heat production from senior core siblings, or sibling parasitism if marginal siblings are draining warmth from core siblings.

As a corollary, is there within-brood variation in the onset of physiological endothermy? If marginal siblings indeed derive thermal benefits from core siblings, might they defer onset of physiological endothermy because of the exogenous heat production of their nestmates? In other words, why turn on the furnace when it is warm outside? The results of Ovadia et al. (2002) are consistent with the notion of marginal siblings using core siblings as "hot-water bottles": later-hatched nestling House Sparrows maintained a higher temperature than expected for their size.

A later onset of endogenous heat production may represent another manifestation of the thrifty-offspring phenotype. Marginal siblings could shave the costs of endothermy, which may be especially valuable given the likelihood that they will face reduced access to food in the presence of stronger core siblings. This logic was applied by Durant (2002) to examine the thermoregulatory behavior of Barn Owl (*Tyto alba*) nestlings. He found that later-hatched (marginal) owlets were more likely to use mechanisms of

behavioral thermoregulation than their older nestmates—which, he speculated, may be attributable to decreased investment in muscle maturation in favor of enhanced growth.

More generally, heat production is potentially a cooperative venture among broodmates (Wilson and Clark 2002). Instead of siblings acting as consumers of limited resources, as is the case with food, nestmates are now resource (heat) producers. Sharing the burden of heat production reduces the cost to each individual. As with the relationship between begging and parental investment, brood-level processes surrounding thermoregulation affect individual decisions. Selfishness that results in loss of a sibling may secure more access to food for a stronger senior sibling, while simultaneously reducing the collective benefit of heat production. At the extreme, there may even be a minimum brood size that is efficient in environments where cold stress is likely (Yarbrough 1970). Under such circumstances, it may not pay for a core sibling to eliminate a competitor, if the result is a degraded thermal environment with reduced returns on sibling-parental investment for the remaining siblings, or parental abandonment of a now unprofitable brood, or both. This logic is essentially the same as that presented by Mock and Parker (1986) for deterrence of siblicide in nestling egrets.

CONCLUSIONS

Brood living entails both individual and collective costs and benefits. Behavioral ecologists have focused chiefly on the cost of competition and the potential for conflict among nestling birds. But nestlings live in close-knit groups—they are, quite literally, brothers “in arms”—and this creates the potential for selection to mold various brood-level symbioses. Though proximity can often lead to competition and conflict among family members, it also creates the intriguing possibilities of sibling mutualism and commensalism—possibilities that have barely been explored.

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LITERATURE CITED

- ALBERTS, J. R. 1978. Huddling by rat pups: Group behavioral mechanisms of temperature regulation and energy conservation. *Journal of Comparative and Physiological Psychology* 92:897–906.
- BAUTISTA, A., H. DRUMMOND, M. MARTÍNEZ-GÓMEZ, AND R. HUDSON. 2003. Thermal benefit of sibling presence in the newborn rabbit. *Developmental Psychobiology* 43: 208–215.
- BENGTSSON, H., AND O. RYDÉN 1983. Parental feeding rate in relation to begging behavior in asynchronously hatched broods of Great Tit *Parus major*. *Behavioral Ecology and Sociobiology* 12:243–251.
- BROWN, L. H., V. GARGETT, AND P. STEYN. 1977. Breeding success in some African eagles related to theories about sibling aggression and its effects. *Ostrich* 48:65–71.
- COTTON, P. A., J. WRIGHT, AND A. KACELNIK. 1999. Chick begging strategies in relation to brood hierarchies and hatching asynchrony. *American Naturalist* 153:412–420.
- COYTE, P. C., AND S. LANDON. 1989. The impact of competition on advertising: The case of political campaign expenditures. *Canadian Journal of Economics* 22:795–818.
- DAWSON, W. R., AND F. C. EVANS. 1957. Relation of growth and development to temperature regulation in nestling Field and Chipping sparrows. *Physiological Zoology* 30: 315–327.
- DAWSON, W. R., AND F. C. EVANS 1960. Relation of growth and development to temperature regulation in nestling Vesper Sparrows. *Condor* 62:329–340.
- DUNN, E. H. 1975. The timing of endothermy in the development of young altricial birds. *Condor* 77:288–293.
- DUNN, E. H. 1976. The relationship between brood size and age of effective homeothermy in nestling House Wrens. *Wilson Bulletin* 88:478–482.
- DUNN, E. H. 1980. On the variability in energy allocation of nestling birds. *Auk* 97:19–27.
- DURANT, J. M. 2002. The influence of hatching order on the thermoregulatory behaviour of Barn Owl *Tyto alba* nestlings. *Avian Science* 2:167–173.
- EVANS, R. M., M. O. WIEBE, S. C. LEE, AND S. C. BUGDEN. 1995. Embryonic and parental

- preferences for incubation temperature in Herring Gulls: Implications for parent-offspring conflict. *Behavioral Ecology and Sociobiology* 36:17–23.
- FORBES, L. S. 1993. Avian brood reduction and parent-offspring “conflict.” *American Naturalist* 142:82–117.
- FORBES, S. 2005. *A Natural History of Families*. Princeton University Press, Princeton, New Jersey.
- FORBES, S., AND B. GLASSEY. 2000. Asymmetric sibling rivalry and nestling growth in Red-winged Blackbirds (*Agelaius phoeniceus*). *Behavioral Ecology and Sociobiology* 48: 413–417.
- FORBES, S., S. THORNTON, B. GLASSEY, M. FORBES, AND N. J. BUCKLEY. 1997. Why parent birds play favourites. *Nature* 390:351–352.
- GLASSEY, B., AND S. FORBES. 2002. Muting individual nestlings reduces parental foraging for the brood. *Animal Behaviour* 63:779–786.
- GODFRAY, H. C. J. 1991. Signalling of need by offspring to their parents. *Nature* 352:328–330.
- GROOTHUIS, T. G. G., W. MULLER, N. VON ENGELHARDT, C. CARERE, AND C. M. EISING. 2005. Maternal hormones as a tool to adjust offspring phenotype in avian species. *Neuroscience and Biobehavioral Reviews* 29:329–352.
- HAMILTON, W. D. 1964. The genetical evolution of social behaviour. *Journal of Theoretical Biology* 7:1–52.
- KARASOV, W. H. 1996. Digestive plasticity in avian energetics and feeding ecology. Pages 61–84 *in* *Avian Energetics and Nutritional Ecology* (C. Carey, Ed.). Chapman and Hall, London.
- KILNER, R. M. 2003. How selfish is a cowbird nestling? *Animal Behaviour* 66:569–576.
- KILNER, R. M., J. R. MADDEN, AND M. E. HAUBER. 2004. Brood parasitic cowbird nestlings use host young to procure resources. *Science* 305:877–879.
- KILNER, R. M., D. G. NOBLE, AND N. B. DAVIES. 1999. Signals of need in parent-offspring communication and their exploitation by the Common Cuckoo. *Nature* 397:667–672.
- LACK, D. 1947. The significance of clutch-size. *Ibis* 89:302–352.
- LEONARD, M. L., AND A. G. HORN. 1998. Need and nestmates affect begging in Tree Swallows. *Behavioral Ecology and Sociobiology* 42: 431–436.
- LEONARD, M. L., AND A. G. HORN. 2001. Begging calls and parental feeding decisions in Tree Swallows (*Tachycineta bicolor*). *Behavioral Ecology and Sociobiology* 49:170–175.
- LEONARD, M. L., A. G. HORN, A. GOZNA, AND S. RAMEN. 2000. Brood size and begging intensity in nestling birds. *Behavioral Ecology* 11:196–201.
- LEONARD, M. L., A. G. HORN, AND E. PARKS. 2003. The role of posturing and calling in the begging display of nestling birds. *Behavioral Ecology and Sociobiology* 54:188–193.
- LEPCZYK, C. A., I. E. CAVIEDES-VIDAL, AND W. H. KARASOV. 1998. Digestive responses during food restriction and realimentation in nestling House Sparrows (*Passer domesticus*). *Physiological Zoology* 71:561–573.
- LICHTENSTEIN, G., AND S. G. SEALY. 1998. Nestling competition, rather than supernormal stimulus, explains the success of parasitic Brown-headed Cowbird chicks in Yellow Warbler nests. *Proceedings of the Royal Society of London, Series B* 265:249–254.
- LOTEM, A. 1998a. Higher levels of begging behavior by small nestlings: A case of a negatively correlated handicap. *Israel Journal of Zoology* 44:29–45.
- LOTEM, A. 1998b. Manipulative begging calls by parasitic cuckoo chicks: Why should true offspring not do the same? *Trends in Ecology and Evolution* 13:342–343.
- MAGRATH, R. D. 1990. Hatching asynchrony in altricial birds. *Biological Reviews* 65: 587–622.
- MOCK, D. W., AND L. S. FORBES. 1995. The evolution of parental optimism. *Trends in Ecology and Evolution* 10:130–134.
- MOCK, D. W., AND G. A. PARKER. 1986. Advantages and disadvantages of egret and heron brood reduction. *Evolution* 40:459–470.
- MOCK, D. W., AND G. A. PARKER. 1997. *The Evolution of Sibling Rivalry*. Oxford University Press, New York.
- MULLER, R. E., AND D. G. SMITH. 1978. Parent-offspring interactions in Zebra Finches. *Auk* 95:485–495.
- NEUENSCHWANDER, S., M. W. G. BRINKHOF, M. KÖLLIKER, AND H. RICHNER. 2003. Brood size, sibling competition, and the cost of begging in Great Tits (*Parus major*). *Behavioral Ecology* 14:457–462.
- OVADIA, O., B. PINSHOW, AND A. LOTEM. 2002. Thermal imaging of House Sparrow

- nestlings: The effect of begging behavior and nestling rank. *Condor* 104:837–842.
- PARKER, G. A., D. W. MOCK, AND T. C. LAMEY. 1989. How selfish should stronger sibs be? *American Naturalist* 133:846–868.
- PARKER, G. A., N. J. ROYLE, AND I. R. HARTLEY. 2002. Begging scrambles with unequal chicks: Interactions between need and competitive ability. *Ecology Letters* 5:206–215.
- PRICE, K., H. HARVEY, AND R. YDENBERG. 1996. Begging tactics of nestling Yellow-headed Blackbirds, *Xanthocephalus xanthocephalus*, in relation to need. *Animal Behaviour* 51:421–435.
- PRICE, K., AND R. YDENBERG. 1995. Begging and provisioning in broods of asynchronously-hatched Yellow-headed Blackbird nestlings. *Behavioral Ecology and Sociobiology* 37:201–208.
- RODRÍGUEZ-GIRONÉS, M. A. 1996. Siblicide: The evolutionary blackmail. *American Naturalist* 148:101–122.
- RODRÍGUEZ-GIRONÉS, M. A., M. ENQUIST, AND M. LACHMANN. 2001. Role of begging and sibling competition in foraging strategies of nestlings. *Animal Behaviour* 61:733–745.
- RODRÍGUEZ-GIRONÉS, M. A., J. M. ZÚÑIGA, AND T. REDONDO. 2002. Feeding experience and relative size modify the begging strategies of nestlings. *Behavioral Ecology* 13:782–785.
- ROULIN, A. 2004. Effects of hatching asynchrony on sibling negotiation, begging, jostling for position and within-brood food allocation in the Barn Owl, *Tyto alba*. *Evolutionary Ecology Research* 6:1083–1098.
- ROULIN, A., M. KÖLLIKER, AND H. RICHNER. 2000. Barn Owl (*Tyto alba*) siblings vocally negotiate resources. *Proceedings of the Royal Society of London, Series B* 267:459–463.
- ROYLE, N. J., I. R. HARTLEY, AND G. A. PARKER. 2004. Parental investment and family dynamics: Interactions between theory and empirical tests. *Population Ecology* 46:231–241.
- ROYLE, N. J., P. F. SURAI, AND I. R. HARTLEY. 2003. The effect of variation in dietary intake on maternal deposition of antioxidants in Zebra Finch eggs. *Functional Ecology* 17:472–481.
- SACCHI, R., N. SAINO, AND P. GALEOTTI. 2002. Features of begging calls reveal general condition and need of food of Barn Swallow (*Hirundo rustica*) nestlings. *Behavioral Ecology* 13:268–273.
- SCHWABL, H., D. W. MOCK, AND J. A. GIEG. 1997. A hormonal mechanism for parental favouritism. *Nature* 386:231.
- SIBLY, R. M. 1981. Strategies of digestion and defecation. Pages 109–139 in *Physiological Ecology: An Evolutionary Approach to Resource Use* (C. R. Townsend and P. Calow, Eds.). Blackwell, Oxford, United Kingdom.
- SMISETH, P. T., AND T. AMUNDSEN. 2002. Senior and junior nestlings in asynchronous Bluethroat broods differ in their effectiveness of begging. *Evolutionary Ecology Research* 4:1177–1189.
- SOKOLOV, G., AND M. S. BLUMBERG. 2001. Competition and cooperation among huddling infant rats. *Developmental Psychobiology* 39:65–75.
- TRIVERS, R. L. 1974. Parent–offspring conflict. *American Zoologist* 14:249–264.
- WILLIAMS, T. D. 1994. Intraspecific variation in egg size and egg composition in birds: Effects on offspring fitness. *Biological Reviews* 69:35–59.
- WILSON, D. S., AND A. B. CLARK. 2002. Begging and cooperation: An exploratory flight. Pages 43–64 in *The Evolution of Begging: Competition, Cooperation and Communication* (J. Wright and M. L. Leonard, Eds.). Kluwer Academic Press, Dordrecht, The Netherlands.
- WILSON, E. O. 1975. *Sociobiology: The New Synthesis*. Belknap Press of Harvard University Press, Cambridge, Massachusetts.
- WRIGHT, J., AND M. L. LEONARD. 2002. *The Evolution of Nestling Begging: Competition, Cooperation and Communication*. Kluwer Academic Press, Dordrecht, The Netherlands.
- YARBROUGH, C. G. 1970. The development of endothermy in nestling Gray-crowned Rosy Finches (*Leucosticte tephrocotis griseonucha*). *Comparative Biochemistry and Physiology A* 34:917–925.

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