Behavioral Ecology Advance Access published July 16, 2011

Behavioral Ecology
doi:10.1093/beheco/arr091

Forum: Invited Review

Honest begging: expanding from Signal of Need

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Overt soliciting for parental resources, primarily food, is often explained as having evolved to express the fitness gain a signaling offspring would derive from a favorable parental response. This Signal of Need model makes 4 unheralded assumptions: 1) that parents' life-history objective is egalitarian; 2) that contemporaneous siblings participate nepotistically; 3) that dependent young can assess their own reproductive value from internal sources; and 4) that the morphological and behavioral signals we call "begging" are essential for transferring such cryptic information reliably. We review 2 parsimonious alternative types of honest begging. First, if the life-history assumption is relaxed, solicitation signals may be positively correlated with reproductive value, obviating the nepotism assumption. According to this Signal of Quality logic, solicitation signals can be seen as typical handicap-type advertisements of personal merit. Second, by relaxing the assumptions concerning cryptic fitness information entirely, solicitation signals might be purely proximate Signals of Hunger, with parents basing their overriding life-history decisions on nonsignal information streams (ecological costs of foraging plus offspring cues already in the public domain). These 3 hypotheses are easily testable, along with existing models that do not require parents to have complete control over resources.
Key words: honest begging, life history, parental care, signaling theory. *[Behav Ecol]*

INTRODUCTION

After getting the worm and returning to its nest, the proverbial early bird is greeted with cacophonous squawks, colorful open mouths, and jostling nestlings. This scene invites questions about whether such offspring behavior is energetically excessive, perhaps dangerously conspicuous. Ubiquitous and taxonomically diverse—solicitation analogs can be found in birds, mammals, insects, plants, and even leeches, pretty much wherever care-giving adults make recurring deliveries to dependent young—exuberant begging seems to demand a functional explanation. The offspring traits that influence parental investment range from very subtle (e.g., chemical compounds from fruits that are developing properly) to extreme (e.g., siblicidal aggression), combining numerous behavioral, physiological, and morphological phenotypes (reviewed in Mock and Parker 1997; Budden and Wright 2001; Wright and Leonard 2002; Wells 2003; Kilner and Hinde 2008). Although such traits are also used to solicit a few commodities other than nutrition (e.g., parental warmth, see Evans 1994; Weary and Fraser 1995), most studies focus on food because offspring fitness is often limited by rapid growth and development (Lack 1947; Clutton-Brock 1991; Mock and Parker 1997). Parents respond in myriad ways as well, frequently adjusting total food deliveries ("provisioning") or skewing resource distribution among nest mates ("allocating"); alternatively, parents may ignore these traits entirely. And because of the incomplete overlap of evolutionary interests among close kin, the subject of begging has emerged as a crucible for testing theoretical predictions about offspring signals and parental responses. Here, we argue that the scope of inquiry has narrowed prematurely around one signaling model for parent–offspring communication, and we offer an expanded framework with some constructive steps forward.

Young offspring have limited means of influencing the quantity, quality, and distribution of parental care. Their tactical repertoire falls into 3 natural groups. Only one of these, "physical competition," deals directly with nest mates (if such exist) and involves outmaneuvering sibling rivals for limited resources (e.g., taking advantageous position where food transfer is likely, intimidating nest mates, etc.). The other 2 categories hinge on influencing parental behavior, and we follow the communication terminology of Grafen (1990), Maynard Smith and Harper (2003), and others, by distinguishing between true "signals" (behavior and morphology apparently shaped by selection for eliciting desired responses) and "cues" (traits that evolved for other functions but provide information that others find useful). Confusion sometimes arises from a blurring of physical competition and cues (e.g., if parents are influenced by observing which offspring prevail in fights or outhustle siblings for position), but neither of these categories evolved primarily to inform parents, so they can be set aside as we seek to understand the signals that did. By this usage, offspring solicitation signals include all vocalizations, ritualized postures, ornaments, and volitional chemical releases but not the cues of body size, general vigor, and uncontrolled odors. For example, nestling birds must open their mouths before parents can insert food, so that simple act is not specialized for communication, but gaping does qualify as a signal if accompanied by specialized social enhancements (vocalizations, colors, etc.). When we ask why gaping is performed, we are interested in the information borne by this display and how the interests of sender and receiver are affected.

At least 3 distinct theoretical approaches have been applied to how offspring solicitation signals affect parental care. The most popular models rest on the simplifying assumption that

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Received 7 November 2010; revised 16 January 2011; accepted 20 April 2011.

parents enjoy total proximate control over the provisioning and allocating of food, basing their decisions largely on information assimilated from offspring signals. Parents are thus seen as having the power of "active choice" that parallels how females choose sexual partners according to their own aesthetic preferences and life-history circumstances. The 2 other classes of signaling models differ in this key assumption, as both demote the role of parents to making only "passive choices" in the face of offspring control of signal expression. Specifically, in Scramble Begging models, offspring engage in sensory competition for parental notice, signals being the vehicle by which each makes itself conspicuous (Royle et al. 2002; Parker et al. 2002; for an empirical example, see Dugas and Rosenthal 2010). No particular information is postulated as being encoded within them. By contrast, Sibling Negotiation models assume cryptic condition as message content, but nest mates are assumed to play both the roles of signal sender and receiver in deciding among themselves which should receive the next unit of investment before the delivering parent merely complies with that verdict (Roulin 2002).

Here, we recognize 3 active parental-choice hypotheses, which differ primarily in the nature of the information conveyed by offspring signals and secondarily in terms of what parents and nest mates are striving to accomplish. In principle, controlling parents might base investment decisions on solicitation signals that express: 1) the degree to which a given contribution can improve the sender's fitness (i.e., the signal expresses an offspring's need, Godfray 1991, 1995); 2) the fact that the sender is an especially promising vehicle for the production of grand-offspring (advertising an offspring's worthiness, Grafen 1990); or 3) nothing whatever about the sender's reproductive value but merely something of a more proximate nature (Grodzinski and Lotem 2007).

SIGNALS OF NEED

Godfray (1991) brought the active-choice approach to begging in an elegant mathematical model showing how a single offspring might use signals to provide parents with cryptic information about its state/condition and thereby influence investment. This was followed with a fuller treatment accommodating 2 (or more) contemporaneous siblings (Godfray 1995). From the starting premise of total parental control, Godfray's model demonstrates that begging can be stable if 1) an offspring chooses a strength of signal revealing its personal condition (specifically its level of need, the marginal fitness benefit it can gain from receiving more resource); 2) its parent responds positively to the signal's strength (e.g., brings more food when signal intensity is escalated); and 3) signal performance is so costly as to reflect the sender's condition reliably (any marginal value of further resources that might be extracted through deceitful exaggeration being nullified by this extra expenditure). In short, the Signal of Need (SoN) model posits that an offspring expresses its level of need "honestly" and is rewarded by parental solicitude that improves its condition (lowers its need), profiting both offspring and parent.

Although not the first theoretical treatment of begging, Godfray's SoN model quickly stimulated substantial empirical and theoretical research (Figure 1), such that a book-length review of this formerly dormant topic was merited within a decade (Wright and Leonard 2002). As a theoretical model, SoN performed its primary function admirably, sketching a plausible explanation for begging signals. Specifically, it demonstrated the logic by which begging might work if its components all work as postulated ("the level of offspring solicitation can be a true reflection of offspring need as long as solicitation is costly and the benefits of extra resources increase with need," Godfray 1991), leaving open the rather important matter of whether begging does, in fact, function in this manner. Thus, the matter rests, as usual, on whether the assumptions are realistic.

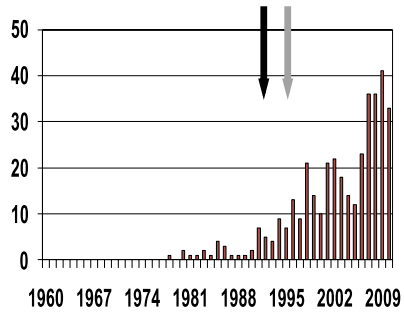

Figure 1
Histogram of publications found in a Web of Science search for keywords "offspring" and "begging" over the past half-century. Arrows indicate the appearance of Godfray's influential signaling models (1991 = black arrow, 1995 = gray arrow).

A SHORT HISTORY OF BEGGING AND PARENTAL CHOICE

Current interest in offspring solicitation is easily traced to a few theoretical roots, and the historical progression is instructive for understanding the current scene. The first flush of theoretical interest emerged from Trivers's (1974) verbal and graphical presentation of parent–offspring conflict, which asserted forcefully that offspring of sexual species must not be "implicitly assumed to be passive vessels into which parents pour the appropriate care." His unexpected notion of offspring empowerment through psychological manipulation was carried to its logical extreme by first assuming total offspring control of begging signal strength in the Scramble Begging models (reviewed in Mock and Parker 1997; Parker et al. 2002). In the process, Trivers introduced the issue of signal honesty: Noting that a nursing calf "cannot fling its mother to the ground and suckle at will," he proposed "deceit" (exaggerating the degree to which investment is truly required) as a psychological weapon for extracting more than is in parental interests to supply. It follows that the first wave of signaling models explored what an offspring should do if running the whole show (reviewed in Parker et al. 1989, 2002).

It is natural that a second generation of parental-choice models would eventually explore the reverse assumption (parents wielding all decision-making power over who gets fed), essentially returning the pendulum to its pre-Trivers position. Meanwhile, a parallel discussion of exaggerated versus deceptive signaling loomed in sexual selection. Darwin's argument that extreme courtship ornaments and displays are limited by countervailing natural selection offered an early explanation for how further signal exaggeration is held in check. Zahavi's handicap principle extended this point considerably, contending that the existence of a balancing point between these opposing selection processes means that signals, however hypertrophied, must necessarily demonstrate the signaler's true quality. As Zahavi (1975, p. 209) put it, "the value of many characters may reside in their action as testing devices." However, because this argument was also expressed only in verbal and graphical forms (with associated lack of precision), it met with extended skepticism, especially when efforts to test it mathematically failed to generate support (e.g., Maynard Smith 1976; Kirkpatrick 1986). Largely neglected for more than a decade, handicap logic was eventually

revived within a broader mathematical treatment of biological signals (Grafen 1990). Grafen's landmark paper built interest in applying handicaps not only to sexual traits in animals and plants but also to other signaling contexts. In a largely overlooked Other Interpretations section, Grafen (1990, p. 527) directly addressed offspring begging as follows: "We apply the model by supposing that the parent wishes to feed the best growing chicks so as not to waste food on the sick." Thus, the very first honest begging model assumed that parents prefer promising offspring over inferior nest mates: Here, an offspring performs Signals of Quality (SoQ) to advertise its good condition.

Given Grafen's precedent, it is somewhat surprising that the SoN argument—currently recognized by most authors as the only "honest begging" model—took precisely the opposite tack. After crediting Zahavi (and Grafen) for the signal-cost assumption, Godfray (1991, p. 328) made the crucial assumption "that a parent is selected to give more resources to young in poor condition," thereby neatly inverting the focal message conveyed in offspring signals, positing that offspring escalate their signals when needy, and deescalate when strong. Thus, SoN contravened the routine assumption for sexually selected traits (that they demonstrate a performer's positive features). In brief, the handicap logic of SoQ rests on signals being positively condition dependent; that of SoN makes them negatively condition dependent. Both types of condition dependence can be evolutionarily stable and honest (Lotem 1998), but SoN requires that additional assumptions be met (typically that the signal receivers and rivals have appropriate fitness stakes in the welfare of the signaler). This inversion of message was derived from Maynard Smith's (1991) Sir Philip Sidney game, a model spotlighting how asymmetries in benefits can drive kin-selected altruism (Godfray and Johnstone 2000). The colorful back-story featured the severely wounded Sir Philip Sidney after the Battle of Zutphen in 1586, directing that his water bottle be passed to a more severely wounded (i.e., needier) soldier with the words "Thy necessity is yet greater than mine" (Maynard Smith 1991). If one overlooks the slightly awkward fact that these 2 soldiers were not genetic kin (Maynard Smith and Harper 2003), the model's lesson is merely that differences in the potential benefits (expressed as degree of need) from a social act can easily determine whether $br > c$. Thus, Hamilton's rule remains firmly in charge: When its inequality is satisfied, altruism between kin, including that predicated on asymmetrical neediness, is favored. This was not the first time this fundamental relationship between need and Hamilton's b had been made (see Hamilton 1964, p. 16; Dawkins 1975, p. 128; Parker et al. 1989, p. 847), but it proved extraordinarily influential. Applied to offspring signals, the infectious idea of begging based on need quickly generated widespread enthusiasm.

PROBLEMS SURROUNDING "CRYPTIC NEED"

Godfray (1991) stipulated that begging signals express the offspring's cryptic condition. He made it abundantly clear that "condition" was a synonym for reproductive value ("offspring in poorer condition have lower fitness," p. 328) and used "need" as its antonym. Furthermore, the expressed condition/need of the signaler was required to be cryptic (see also Grafen 1990), ostensibly because the fitness information conveyed to the parent would diminish sharply in value if leaked simultaneously via cues (Krebs 2002), which are noncryptic, by definition. After all, a hypothesis intending to explain how selection produced costly signals would be greatly compromised if parents already had access to such predictors. By signaling its cryptic need, the offspring informs parents about the contribution a food delivery would make to the signaler's marginal fitness (Royle et al. 2002). Thus, a nestling in high condition has low need and displays with reduced vigor; one in maximal condition should not beg at all (Godfray 1991, Figure 1).

Measuring an offspring's potential fitness is extremely difficult in the first place and requiring that such be revealed importantly through signals per se adds to the empiricist's challenge when testing SoN. Conceding that point ("by its very nature, cryptic need is difficult to measure"), Godfray (1995, p. 20) suggested that "it may be possible to identify correlates of hidden condition." So far, this has proven elusive, and most researchers have turned to 2 proxies. Some have related solicitation signals to a plausible fitness proxy like body size or physical development (e.g., avian plumage), citing various studies that link these traits to viability (for references relating fledging mass to recruitment in 22 bird species, see Schwagmeyer and Mock 2008). Unfortunately, as highly accessible cues, these features are not cryptic, thus undermine the postulated value of the begging signal. A greater number of workers have relied instead on the proxy of hunger (operationally defined as time since last feeding), attractively cryptic but not linked convincingly to viability. As various authors have noted (e.g., Price et al. 1996; Saino et al. 2000), a fatally diseased nestling is easily surfeited without improving its chance of breeding, whereas a nest mate enjoying "maximum condition" can be made hungry in short order without jeopardizing its reproductive future. In its essence, the gulf between what an organism wants and what it truly needs is that between proximate and ultimate levels of explanation (see Wells 2003), an as-yet unresolved matter for begging (see Appendix).

Regrettably, the backbone of empirical support for SoN is comprised of numerous variations on one theme that can be labeled collectively as the "hunger experiment." A common protocol involves depriving young subjects of food before quantifying signal intensity (e.g., calling rate, postures, latency to gape, etc.) as a function of time without food. In field versions of this, subjects are manipulated so as to be unable to ingest food (e.g., via neck ligature) and videotaped during delivery visits by their parents; in the more common laboratory version, deprived subjects are tested at regular intervals (e.g., every 10 min) with artificial stimuli (e.g., taped sounds of an arriving parent and/or physical tapping on nestling bills). To date, deprivation experiments have been performed on dozens of species (insects, mammals, and birds) and virtually always produce the expected positive result. In short, it seems as if the hunger effect is solid and unlikely to benefit much from further documentation: The physiological complex that we call hunger inspires escalated solicitations across a wide array of taxa. However, as noted above, hunger is not clearly related to fitness, hence to Godfray's meaning of need (e.g., Price et al. 1996, reviewed in Clark 2002). It is unfortunate, therefore, that some authors use hunger and need as synonyms (e.g., Leonard and Horn 1996; Weary et al. 1996; Kilner and Johnstone 1997; Bell 2008; Manser et al. 2008), occasionally even mixing the terms within a single sentence (e.g., "...in canaries, nestling mouth colour functions to signal need by becoming more intensely coloured with increasing food deprivation," Kilner 1997, p. 966–967). In this context, a new experimental approach, whereby an orally administered appetite stimulant can be used to decouple hunger and condition experimentally, may prove especially useful for future work (Martín-Galvéz et al. forthcoming).

To summarize thus far, SoN is currently the only widely recognized hypothesis for active parental choice (Wright and Leonard 2002). One of its 3 basic components has been consistently supported (in nearly all cases, parents do respond positively to stronger signals), although that feature is equally predicted by passive-choice models (Royle et al. 2002).

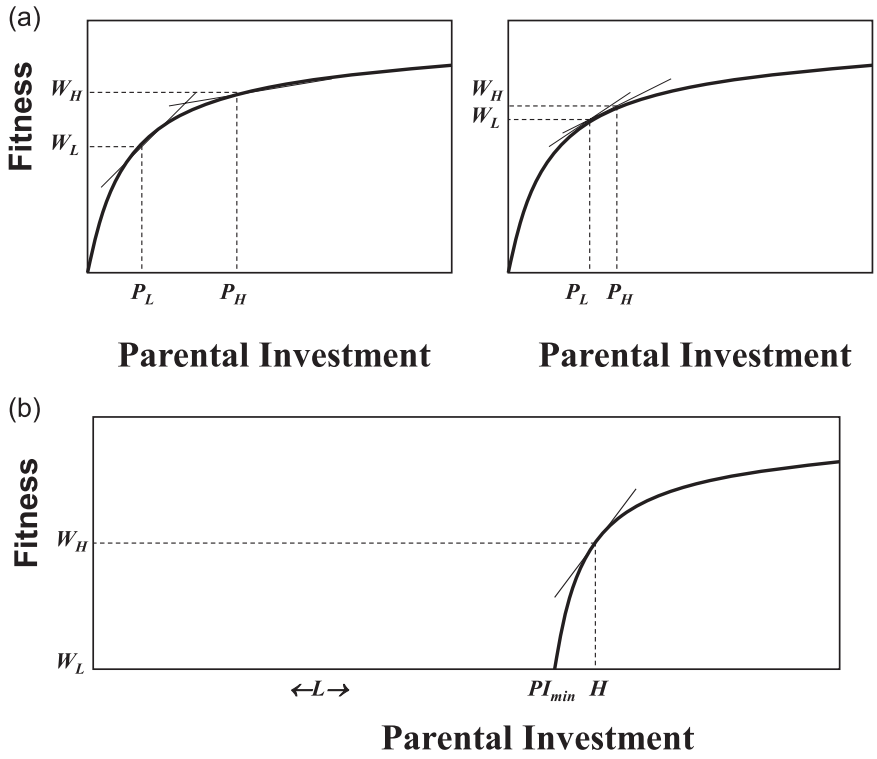

Figure 2
(a) Standard decelerating cumulative gain curve (thick lines) for offspring fitness as a function of parental investment. Two siblings are illustrated, one currently in higher condition (fitness = W_H) by virtue of having received more parental investment (P_H) to that point than its lower condition nest mate. At the moment depicted on the left panel, the marginal gain rates (shown as thin tangents) are such that $L' > 2H'$, so the high- condition sibling benefits more if the next unit of parental investment goes to its low-condition full sibling. Under these circumstances, H should demur from begging and SoN can operate. In the right panel, by contrast, $L' < 2H'$, so the high-condition sibling adds more to its inclusive fitness by trying to obtain the next unit of investment. Here, H is better off begging or using physical competition on behalf of its personal well being. (b) If the fitness curve does not rise immediately with the start of parental investment but rests at zero until some threshold amount has been received, the dynamic between these same hypothetical siblings can differ dramatically from the above diagram. Let PI_{min} represent the down payment that parents must pour into an offspring before any fitness return can be realized. Here, it is apparent that a high-condition sibling may be paired with a nest mate that may not have reached the PI_{min} threshold, in which case its marginal gain rate cannot be twice as steep ($L' = 0$). By the time that both siblings are showing enough promise to make SoN operate properly, the active-choice system may or may not still be in effect and any sibling nepotism shown after that is unlikely to be signal based.

A second premise, that signals express cryptic need, currently stands on shakier ground because hunger is a dubious proxy for fitness. And the third requirement, that signals are sufficiently costly, has been reviewed many times (e.g., Godfray and Johnstone 2000; Chappell and Bachman 2002; Haskell 2002; Wells 2003; Moreno-Rueda 2007; Számadó 2011) without much consensus (e.g., Godfray and Johnstone 2000). The central issue there is not whether signals have any detectable cost whatever, which has been demonstrated repeatedly in terms of energetics (Chappell and Bachman 2002) and risk from predators (Haskell 2002), but "whether the costs are sufficient to enforce signal reliability" (Searcy and Nowicki 2005, p. 132). That is, there are always efficacy costs (for transmission), so the key matter of strategic costs (sensu Maynard Smith and Harper 2003) for maintaining honesty must be isolated. As well, some question remains as to whether any strategic costs are essential for maintaining signal honesty (reviewed in Godfray and Johnstone 2000; Wells 2003; Searcy and Nowicki 2005). Finally, because active parental choice seems to be intrinsically appealing (especially, when offspring are very young, hence too small and feeble to challenge parental control), we suspect that the popularity of SoN derives in part from the dearth of recognized active-choice alternatives.

Finally, the SoN model contains a frequently overlooked module of sibling altruism (explicitly noted by Godfray 1991) that merits closer attention. Accepting for sake of argument that signaling is costly and that 2 concurrent nest mates vary in condition, it follows that the one in better condition is better able to afford escalated signals (or is indifferent to the food). If this stronger/high-condition sibling (represented in Figure 2 by H) opts not to exercise its physical advantages, thereby allowing its more limited/low-condition nest mate (represented by L) to express its greater need effectively, the incentive for such self-restraint presumably derives from the indirect fitness reward. It is easy to show (Figure 2a) that such reticence profits the senior sibling whenever its marginal personal gain from the next unit of parental investment is less than half that available to its full sibling (e.g., Hamilton 1964; Parker et al. 1989). Conversely, we see 2 general contexts in which nepotistic self-restraint is not predicted. First, if the 2 siblings are so evenly matched in condition that Hamilton's rule is not satisfied (i.e., if $2H' < L'$), then the senior sib gains more from self-promotion and should use its superior capacity to out-signal a lesser rival (Figure 2a). Second, if a minimum amount of parental investment must be received before either offspring achieves any viability (PI_{min} in Figure 2b), the magnitude of that start-up investment materializes as a threat to nepotism. A senior sibling may have no indirect fitness incentives until its nest mate reaches PI_{min}, which is likely to take several days (e.g., passerines) or weeks (e.g., eagles and seabirds), during which delay hegemonic parental control of allocation may have

lapsed. This delay problem is also exacerbated if the function is sigmoidal (slow to accelerate) rather than steeply decelerating (Cotton et al. 1999). Such reduced incentives for nepotism have long been cited for understanding early obligate siblicide in raptors (Stinson 1979; reviewed in Mock and Parker 1997).

DYNAMIC PROBLEM, STATIC MODEL

Although it has been noted repeatedly that a dynamic games modeling approach is needed to add realism to iterative parental care (Godfray 1991, 1995; Johnstone 1996; Bonabeau et al. 1998; Godfray and Johnstone 2000; Budden and Wright 2001; Searcy and Nowicki 2005; Jeon 2008; Kilner and Hinde 2008; Dobler and Kölliker 2009), this point is frequently missed. As a result, SoN is often viewed as a general rule-of-thumb that parents apply steadily throughout the period of offspring dependence rather than shifting continually. The resulting logic trap is easily exposed: If parents of multi-offspring broods were to allocate food consistently to whichever offspring is currently most needy, then even accidental intrabrood variation in nest mate condition would be "repaired" quickly. From there, it follows that parents would hardly trouble themselves to create sibling disparities intentionally. Instead, all siblings would reach independence together as a closely matched set and density-dependent mortality, that is, brood reduction, would be rare (allowing for individual instances where the SoN system faltered). Parents with inadequate resources would methodically underfeed all their young, producing runt fledglings with dim future prospects, if not whole-brood starvation (Davis et al. 1999). Clearly, this is not what happens in nature, where numerous field studies show parents overtly favoring core offspring (e.g., Forbes et al. 1997; Mock and Parker 1997) whose initial size advantages are often engineered by parents themselves. Certainly, brood reduction befalls a substantial proportion of avian families (Lack 1947; O'Connor 1978; Mock and Parker 1997). And the widespread preference of avian parents for larger nestlings is presumably a principal behavioral rule used by Old World cuckoos exploiting host parents.

We know of no immediate prospects for a truly dynamic game model of begging but suggest that interim progress can be made on the general problem by contemplating in a less formal way how the various players (parents plus offspring in different levels of condition) are most likely to maximize fitness. Specifically, begging is overdue for an infusion of life-history thinking, and several excellent models already exist as guides (Haig 1990; Bonabeau et al. 1998; Jeon 2008).

The first step is to shed any assumptions that parents necessarily have the goal of raising all their young. It has been known for many decades (Lack 1947) that brood reduction can be so valuable to parents that they often create sibling disparities to facilitate its implementation. Efficient brood reduction is the abettor of another widespread life-history trait, parental overproduction (Kozlowski and Stearns 1989; Mock and Forbes 1995). Parents gain several fitness advantages by initially creating an optimistic family size (hedging against various uncertainties) that routinely proves too large while also structuring the brood in advance of any adaptive pruning. Because of overproduction, resources are habitually stretched thin and local resource (i.e., sibling) competition overrules relatedness (Mock and Parker 1997). Such contexts are inimical to the SoN views that parents automatically favor the neediest offspring or that stronger nest mates should submerge their personal interests. In fairness, Godfray (1991) explicitly restricted SoN to "a narrow range" of offspring condition (above the parent's abandonment threshold) for addressing how solicitation signals operate and mentioned the mathematical caveat of local (not global) stability. When the SoN approach was later expanded to accommodate broods of 2 (Godfray 1995), the intermediate option of terminating one offspring and diverting the emancipated parental investment to the other was not addressed fully, and later workers have seemed to assume whole-brood survival as the parents' life-history objective.

ACTIVE-CHOICE ALTERNATIVES TO SoN

For starters, Grafen's Signal of Quality (SoQ) hypothesis must be revived, applying the original handicap logic that signalers advertise merit rather than expressing need. It is unclear why this simple and attractive alternative to SoN has been almost totally neglected (for rare exceptions, see Weary and Fraser 1995; Saino et al. 2000); perhaps the word "begging" connoted impressions of pleading rather than boasting. The SoQ interpretation has high-condition offspring emitting stronger signals (which they can better afford), and the positive parental response (more food to stronger signalers) skews investment toward progeny with the greatest reproductive value. If the family budget is tight, this places limited resources where they will bring the richest fitness returns (e.g., numbers of grand offspring). Worded differently, SoQ minimizes the parents' wasting investment on lost causes. Positively condition-dependent signals inspire parental favoritism through a positive feedback loop. Here, brood reduction may be routine, or junior siblings may receive enough to thrive when seniors approach satiety (nature's version of "trickle-down economics"). One common observation that seems curiously at odds with SoQ is the much-documented hunger effect on solicitation strength. Because the beneficiaries of a positive feedback loop are least likely to be hungry, the fact that food deprivation really does inspire escalated signaling does not fit in an obvious way to the SoQ argument. (As noted earlier, the hunger effect does not fit especially well with SoN either but blurring the distinction between offspring proximate-level wants and ultimate-level needs has obfuscated that.).

Recent studies offer bird and insect results somewhat easier to reconcile with SoQ than with SoN. For example, total food amounts (provisioning rates) predict fledging size and eventual recruitment as breeders in a house sparrow (*Passer domesticus*) population (Schwagmeyer and Mock 2008), where brood reduction is both common (42% of 1000 broods) and so early (median 4 days posthatching) that parents still have full control and total brood demand is unlikely to have outstripped parental provisioning capacity. At this age, videotaped parents actively skew allocations toward larger siblings (Mock et al. 2009). Furthermore, broods receiving supplemental nutrients solicit more loudly, receive 25% more total food (mainly from the normally slacking male parent), and probably recruit more often into the breeding population (Mock et al. 2005). When nestling mouth flanges were modified with yellow paint to resemble high-condition nestlings, parents preferred feeding them over nest mates wearing "low-condition" paler paint (Dugas 2009). In short, food is often limiting and the high incidence of brood reduction is probably facilitated by active parental discrimination against lesser-but-currently-viable offspring.

Similarly, earwig (*Forficula auricularia*) mothers hatch >90% of their 55 eggs and then supplement larval self-feeding with regurgitation. Roughly half of the larvae die from density-dependent causes, even in safe (lab) conditions, as shown by removing larvae (which reduces mortality) or preventing maternal subsidies (which increases it, Kölliker 2007). Offspring nutritional condition is revealed as a chemical signal through variation in cuticular hydrocarbons (2 alkanes and 1 alkene). If the cuticular hydrocarbons are extracted from larvae that have been either deprived (low food) or well

fed (high food) and transferred to filter paper for blind presentation, mothers respond more strongly to the high-food stimuli (carrying more food and distributing it to a larger proportion of their broods, Mas et al. 2009).

Setting aside feeding history for the moment, several provocative but underexplored directions present themselves. There is no reason to assume a priori that parents must choose either SoN or SoQ: They may be able to use both strategies. In a sequential version, parents might overproduce and aim initially to maintain the whole brood (via the SoN rule) while gathering updated information on foraging costs and other ecological components of the family resource budget (Forbes and Mock 1996). By keeping everyone alive at least temporarily, the mutually compatible incentives for overproduction (resource tracking, insurance, and sib facilitation, Mock and Forbes 1995) are extended. If and when keeping an intact family becomes a luxury parents can no longer afford, a switch to SoQ could restrict investment toward the most promising subset (as proposed by Stamps et al. 1985). Note that such a transition might require nothing more than a facultative change in the parents' priorities (e.g., McNamara and Houston 2009), and these adults are the only family members with direct access to the out-of-nest ecological information for its implementation. Assuming only that the early SoN phase does not erase sib–sib disparities to the point that brood reduction becomes prohibitively expensive, such a facultative switch might work well. (An alternative mechanism driven entirely by facultative offspring positioning [Kölliker and Richner 2004, p. 947] would offer flexibility but is tied only indirectly to external food availability via a trickle-down process.).

A simultaneous version of the SoN/SoQ combination might involve sexual conflict between 2 task-sharing parents (Lessells 1998). A tiny but much-cited literature suggests that females of some avian species deliberately feed their smallest nestlings preferentially (Stamps et al. 1985; Gottlander 1987; Krebs 2002), whereas their mates feed indiscriminately (passively favoring larger nest mates). Further exploration of such systems might consider the possibilities of (and reasons for) differing gender-specific responses (Lessells 1998).

To this point, we have tacitly assumed that the cryptic information expressed in the signal captures an ultimate-level component of fitness (need or "merit"), which is ostensibly what the signal receiver (parent) is most interested in learning (Searcy and Nowicki 2005). How a neonate is imagined to assess its own potential reproductive value in formulating this signal is a physiological matter yet to be addressed. In parallel, the parent is assumed to get that critical information from the signal per se, a component that plausibly affixes value to the signals we seek to understand. However, this whole cluster of assumptions is relaxed in our third active-choice hypothesis, which we label Signal of Hunger (SoH) for parallelism but which resembles another neglected argument called the "fuel–gauge hypothesis" (Grodzinski and Lotem 2007). Though a bit narrower than SoN and SoQ by virtue of being restricted to volitional signals (for their ephemeral properties), the beauty of SoH lies in its relative parsimony. Its basic premise, that the cryptic information expressed in solicitation signal strength is merely a proximate indication of fullness, enjoys an impressive empirical foundation from the hunger experiments. The key for converting this into an adaptive parenting tool lies in recognizing that the essential companion information on which parents evaluate fitness and make their life-history decisions is already available in the form of simple cues (body size, general vigor, development on schedule, etc.). These cues are something of an inconvenience for SoN and SoQ (being noncryptic, they dilute the value of the hypothetical signals' content), but they are integral to SoH. Meanwhile, both generations benefit from an "honest" transmission of information about which offspring are most ready for additional food (Grodzinski and Lotem (2007) added a slightly more complex version of this idea by incorporating digestive rates, which they call their "efficiency-based model," but the central idea remains straightforward).

A facultative switch in parental responsiveness, this time based on cues, is easy to imagine and has the virtue of not requiring that offspring carry special insights into their own cryptic condition beyond what we recognize in ourselves as hunger. Instead it is the parents, perceiving that continued whole-brood survival is suboptimal (based on multiple information streams, including those deriving from the world beyond the nursery), that SoH proposes as resetting their response rule so as to ignore further solicitation signals from their least valuable offspring. Basically, when ecological cues dictate that parental foraging costs have become too steep to satisfy the growing brood's collective demand (e.g., depressed food availability, predator-inspired caution, elevated thermal costs, parental self-feeding requirements, etc.) and/or that brood-based cues indicate particular offspring as languishing (e.g., from genetic defects, parasites, etc.), parents adopt selective sales resistance. For this to work, parents must be capable of recognizing which individual offspring are no longer worthy of investment (see Godfray 1991). Certainly, a vast literature documents adult ability to adjust foraging strategy to diverse environmental changes (Ydenberg 2007), so the requisite assessment abilities are presumably widespread. Noting that their lab observations of size-dependent feeding and maternal preference for the smallest nestling in budgerigars (*Melopsittacus undulatus*) might be artifacts of captivity and ad libitum food, Stamps et al. (1985, p. 36) clearly anticipated this possibility, suggesting that parental solicitousness "does not preclude a female's shifting her preference to the penultimate nestling and selectively starving her youngest nestling. Hence, complex feeding strategies favoring or maintaining small (young) nestlings are not only consistent with brood reduction but may be required if parents are to retain control over the conditions for brood reduction in asynchronous broods."

To review, the SoH hypothesis provides a proximate-level explanation for functional solicitation signals, without requiring any cryptic information about offspring fitness potential (cf. SoN and SoQ). SoH signals are useful to the individual offspring by attracting the next parental delivery in rough proportion to its hunger. Surfeited nestlings commonly stop begging after a large meal, temporarily disinterested in food (mediated by feedback from crop proprioceptors, circulating blood sugars, hormones, etc.). Such an offspring may even have reached the point where its capacity for digesting food is reduced, further devaluing the signals, and/or the upper limit to begging may be set by parental willingness to respond (including sales resistance) based on assessment of offspring condition from cues. If the signals lose effectiveness on their targets, the incentive to escalate them wanes. No altruistic self–restraint is required, but SoH certainly can accommodate offspring integrating nest mate interests (from cues and/or enthusiasm for food), tuned by Hamilton's rule. Begging may thus be a sloppy expression of desire that nevertheless provides parents with useful information for their bookkeeping. As such, solicitation signals need not be costly but should be adjustable to parental delivery rates (reward schedules), attuned to the signaling milieu of nest mates, and generally truthful.

TESTING THE ARRAY OF ACTIVE-CHOICE HYPOTHESES

Immediately after sketching SoQ within the context of his broader theory of biological signals, Grafen (1990, p. 527)

summoned empiricists to do their part in the broader scientific enterprise: "It is not a point of this section that these are the correct explanations of roaring in red deer, nestling begging, or stotting. Zoology is not an armchair subject in which these matters of fact can be decided in theoretical comfort ... the ideas should therefore be considered along with other candidate explanations when evidence is being interpreted and not be rejected on the grounds that they are simply absurd." If this final clause sounds a bit defensive (as if fearing that his ideas on signal honesty might be dismissed unfairly), Grafen need not have worried. That primary message about handicaps and signals was warmly received, even though his brief mention of SoQ aroused no stir in the begging literature. Instead, empirical work on begging since 1991 has considered SoN almost exclusively (e.g., see Wright and Leonard 2002), with scant mention of "other candidate explanations" for honest soliciting until quite recently. Indeed, a major challenge with rigorous testing of SoN has centered on aforementioned inaccessibility of its key components, especially costliness, crypticity, and a more compelling proxy for need. Alas, we have no magic solution for measuring marginal gain rates of fitness functions, but we believe that a more critical evaluation of model components combined with contrasting predictions from other active-choice hypotheses may help get things moving a bit more. In particular, we suggest 3 constructive steps:

1. We propose a moratorium on further replication of the hunger experiment, at least as an end unto itself. So far as we can tell, nobody doubts that animals intensify food solicitation signals when hungry, so let us move on.
2. We see that the first hurdle to cross concerns whether parents or offspring are primary controllers of provisioning and/or allocation (Royle et al. 2002). If the former, proceed to step 3; if the latter, these are the wrong models. The signaling aspects of offspring-controlled systems are addressed by Scramble-Begging or Sib-Negotiation approaches, whereas physical competition may eclipse signaling altogether in many cases. In some cases, determining which generation controls food may require nothing more than close observation; otherwise, experimental manipulations are often feasible. As a corollary, researchers should pay special attention to how such control often shifts from parents to offspring as the dependent young grow and mature. Many of the studies currently invoking SoN are dealing with nestling birds that had usurped much, if not all, of that control from hard-pressed parents.
3. When active parental choice seems indicated, we offer Table 1 as a point of entry.

Table 1

Five test questions for teasing apart the active-choice hypotheses for offspring solicitation signals

Test questions	SoQ	SoN	SoH
1. Signal is condition dependent?	Yes, positively so ☑	Yes, negatively so ☑	Not predicted
2. Incidence of brood reduction?	Common	Rare ☑	Common
3. Is altruism required?	No	Yes ☑	No
4. Hunger effect predicted?	Not predicted	Plausibly	Yes ☑
5. Food skew goes to whom?	Strongest ☑	Weakest ☑	Hungriest ☑

SoQ = offspring signal expresses the individual's future reproductive value as an advertisement eliciting additional parental investment; SoN = offspring signal expresses the individual's expected fitness gain from additional parental investment; and SoH = offspring signal expresses only the individual's proximate-level interest in receiving food. ☑ indicates the most diagnostic predictions.

In closing, we return to Trivers's point that offspring are not totally passive vessels into which investment is poured. Whereas we argue here that an improved understanding of solicitation signals requires greater consideration of life history than has been the case for active-signaling models to date, the reverse may also be true: Discussions of life history should take into account that dependent offspring are likely to play active, and potentially important, roles in shaping the decisions of care givers. This review has focused on the information content of offspring solicitations to controlling parents, but other modeling approaches (e.g., Scramble-Begging, Sibling Negotiation, etc.) cover other assumptions and the roles played by physical competition add to the complexity, as do the relative contributions from different sensory modalities. For example, the properties of morphological offspring signals differ substantially from those of fast-changing behavioral ones: Morphology is quite possibly better suited for encoding information about long-term condition (SoQ), whereas other components of the signaler's display passes information about more ephemeral aspects of cryptic condition (e.g., hunger). Overall, we may just be scratching the surface on this diverse and provocative topic.

FUNDING

We were indirectly supported while writing this article by the US National Science Foundation (IBN-0843673 and IOS-0909882).

We thank many colleagues for discussions, criticisms, and helpful comments on the ideas presented in this paper, including P. L. Schwagmeyer, L. S. Forbes, A. Lotem, M. Kölliker, S. Nowicki, J. Wright, T. Haff, E. Knowlton, A. Clark, R. Kilner, G. A. Parker, S. West, and the Oxford Social Evolution Journal Club. We would also like to acknowledge the University of Oklahoma Zoology Department's Ecology and Evolutionary Biology Graduate Program for its support for our research.

APPENDIX

THE LIMITED EQUIVALENCY OF HUNGER AND NEED

"Your debutante just knows what you need, but I know what you want." (Bob Dylan, Memphis Blues Again).

Soon after the SoN model was expanded from its single-offspring introduction (Godfray 1991) to accommodate multi-offspring families (Godfray 1995), practical questions arose about how to measure need operationally. This straddling problem between an idealized theoretical variable and some accessible metrics, common in theory-driven disciplines like behavioral ecology, was confronted clearly for begging by Price et al. (1996). As a first step, those authors proposed distinguishing between "short-term need" (i.e., hunger: the amount of food needed to achieve satiety) and "long-term need" (i.e., viability: the total amounts needed through successful fledging) for nestling yellow-headed blackbirds (*Xanthocephalus xanthocephalus*). Relabeling the problem did not solve it, of course (Price et al. used aspects of body size as their operational proxy for long-term need), but the logic obstacle was clearly identified (reviewed in Saino et al. 2000; Clark 2002; Wells 2003). In a similar vein, Wright et al. (2002) adopted an intermediate step (their "medium-term need" called attention to possible cryptic adjustments of digestive efficiency) to add further complexity and realism.

All else being equal, it makes some intuitive sense that offspring in lower condition may also be hungrier, at least on average, than those in higher condition. Variation in condition is surely not independent of past feeding history, including that of the very recent past. We see

no problem with this scenario as one possibility among several for how begging signals might be used by parents engaged in the effort to raise all their progeny: Within the limits of its assumptions, the SoN model seems internally consistent. But how often is "all else equal?" Because offspring fitness is affected by various factors other than recent feeding history, hunger is likely to be a crude barometer at best. Some of these (e.g., brood size, brood composition, parasite loads, ambient temperatures, etc.) have also been shown to affect begging levels, along with other aspects of offspring life (e.g., reinforcement schedules), all of which cloud the information parents might extract from signal variation. As well, offspring of different sizes may have different capacities for storing and digesting food, adding further noise to interpreting their enthusiasm for more (but see Wright et al. 2010). At this point, therefore, it is premature to assume that variation in potential marginal fitness gain is usefully expressed in offspring signal variation.

When a tiny nestling is removed from its nest and deprived of food for 90 min or so in a warm lab without nest mates, all else is probably as close to equal as can be achieved. Within-subject designs are powerful precisely because they minimize contributions from confounding factors (rivals, parasites, temperature, recent feeding history, etc.): The design's statistical virtue thus may unintentionally magnify hunger's impact on begging signals. But the inescapable fact remains that the subject's viability is virtually unchanged, even as it responds with escalated solicitations when stimulated. This exercise, therefore, cannot examine the combined effects of variation in need and variation in desire on fluctuations in signal strength because it addresses only desire and signaling. It has also been shown recently that the typical practice of artificially feeding these subjects to excess before commencing the deprivation period (a step intended to standardize fullness) simultaneously disrupts the normal digestion processes (Wright et al. 2002, 2010; Grodzinski et al. 2009), complicating interpretation of results. In any case, the reverse inference, that indicated hunger level is a key component in parental mechanisms for estimating offspring fitness potential, requires several more assumptions and thus is even more dubious.

Statistically, one would like to know how well the easily measured test factor (deprivation time) and its correlated response (signaling) predict some aspect of the more elusive model component (say offspring probability of recruiting into the breeding population). In practice, the wildly mismatched time-frames (signaling being measured in seconds, hunger in hours, and recruitment after many months) frustrates resolution: slopes and r squares are not realistic goals. So we often end up relying on the intuitive premise with which we started, rather than on a rigorous empirical test. Pseudoprogress can be riskier than ignorance if its lures us into a cul-de-sac of complacency. The best option for now is likely to be deliberate caution. Meanwhile, renewed effort to seek alternative correlates of condition (Godfray 1991) might prove fruitful, perhaps physiological ones that are simultaneously accessible to the signaler alone (hence cryptic) and can be shown to figure prominently in successful development. Immune responses to simulated pathogens (Saino et al. 2000) and inconspicuous ectoparasites (Christe et al. 1996) have been considered in this regard.

Lastly, questions have been raised occasionally about whether it is even possible for parents to rescue lagging offspring with extra food, a matter that seems likely to vary both between species and as a function of the laggard's disadvantage (type and magnitude). Not all problems are soluble through additional food and some nestlings with seemingly simple nutritional deficiencies do not respond with compensatory growth when given more (Lepczyk and Karasov 2000; Brzęk and Konarzewski 2004), whereas some of those that do "catch up" may show an assortment of deferred costs (Metcalfe and Monaghan 2001).

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