Not the Nice Sparrow

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NOT THE NICE SPARROW
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ABSTRACT.—We began our studies of House Sparrow (*Passer domesticus*) biparental care in the mid-1990s by applying the classic Margaret Morse Nice field technique of color-banding individuals. Over the ensuing summers, we slowly accumulated quantitative provisioning records for 100 broods, even as we commenced a series of experimental manipulations. Provisioning data showed parental fitness, as expressed by offspring recruitment into the local breeding population, to be shaped mainly by the adults' ability to deliver enormous insect prey items. It also turned out that production of robust and competitive fledglings routinely involves losing one or more nestlings (brood reduction in 42% of 1,000 multi-chick families). Recruitment success was compensated for the death of an offspring if the subsequent reallocation of food enables surviving nest-mates to gain at least 2 g more before fledging. Video samples showed that parents of day 3 broods favored larger siblings, even though brood reduction typically occurs on ~day 4, suggesting that adults participate actively in promoting some offspring over others. The social dynamic affecting how parents work as a team during provisioning does not fit the pattern expected if partners negotiate actively with one another, but points more toward the likelihood of ''sealed bids.'' Specifically, experimental handicapping of individual parents (tail-weights and hormone implants) indicates partners operate quite independently during brood-rearing. We are now extending our experiments into the incubation phase, where parents are probably better-informed about partner activities, thus potentially able to adjust to fluctuating contributions. Finally, behavioral rules affecting food deliveries seem to differ for females and males. Females normally increase provisioning as the brood ages, but males do not. However, when broods received supplemental nutrients, males matched the female upsurge, accelerating their deliveries by 25%, showing they usually work well below capacity. *Received 31 December 2009. Accepted 28 February 2010.*

Among the many contributions for which bird behaviorists are grateful to Margaret Morse Nice, her pioneering use of color bands is probably the most universal. Color-banding seems utterly fundamental to behavioral ornithologists today— a trifle really—but on 26 March 1928, one pink celluloid ring provided Mrs. Nice with a means of recognizing a particular male Song Sparrow (*Melospiza melodia*) near her Columbus, Ohio home. Soon she banded a second male with a green ring, thereby exposing consistent differences between the two in song, aggressiveness, etc. It is hard to overstate what a difference this innovation has made to behavioral field studies.

Pausing to think about it, much that we take for granted today was not available to Margaret Nice. For example, well before today's ornithological neophyte affixes any color bands, the step of identifying the local avifauna, or even finding out which birds live nearby, promotes a trip to the

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bookshelf for a field guide where the only dilemma is which one to choose. When Margaret Morse Nice arrived in Oklahoma in 1913 (her husband Blaine had been hired in what is now the Zoology Department where we both work), no bird guides or even checklists existed. Although she had strong academic credentials (including a Master's degree from Clark University), she never held a position at the University of Oklahoma. Instead, she stayed physically busy with the traditional duties of wife and mother, while fighting boredom and intellectual frustration by reviving her ornithological interests. Eventually she wrote Oklahoma's first state bird book but, by the time it was published, the family had moved (with Blaine's career) to Ohio State, where she began to focus on avian behavior.

The Oklahoma house that Blaine Nice built (literally!) at 445 College Avenue is just a block from where we now live, but nearly everything else has changed. The streets have been paved, more than one faculty member owns an automobile (indeed, it seems as if most OU students have more than one!), and women now comprise a third of our department's faculty. Meanwhile, Margaret Nice's fields of natural history and ethology have been infused with theoretical and mathematical fibers to form modern behavioral ecology (Parker 2006). We all inhabit this new world, but should pause from time to time and acknowledge the extraordinary spadework that made our studies possible.

That said, many Nice-era roots remain clearly visible, despite being taken for granted. House Sparrows (*Passer domesticus*) were already abundant in Norman when she arrived in 1913, but we have now color-banded several thousand since 1994. Otherwise, we spend much of our field time sitting quietly and, hopefully, recording what the birds would have done in our absence.

The overarching goal of our collaborative research program is to understand what makes biparental care evolutionarily stable. Because cooperation in parenting makes a major contribution to social monogamy, which predominates in Class Aves, we see it as central to understanding that mating system. House Sparrows are abundant and willing to use nest boxes, so we study House Sparrows. This also is consistent with the Margaret Morse Nice tradition of studying ''… what appeared common to so many'' (Nice 1979:263).

We thank the Wilson Ornithological Society for honoring us with the 2007 Margaret Morse Nice Medal and offer the following sketch of some things we have learned about these quintessentially ordinary birds through a series of shared projects. Our goal is not any sort of autobiographical detail, except as it relates to the evolution of our sparrow research program, but to provide an overview of several related studies that have led us to our current work. We do not presume to offer this account as a model of how anyone else should proceed, but students of bird research need not regard the whole field process as mysterious. To reduce that mystery, we explain how we try to extract our guiding questions from the general picture, use them to design empirical exercises, and then seek to re-apply the analyzed results back to the bigger issue from whence we start. Along the way, it must be confessed, we often stumble. Space limitation and reader interest preclude a full chronicling of all our mistakes (trap designs that were prone to equipment malfunctions, an attempt to supplement breeding parents with live mealworms that escaped, occasional duplications of color band combinations, etc.), but we hope students will forgive themselves for similar false starts as they press forward.

We both came of age as scientists more or less as Darwin's theory of sexual selection was being revived after a century of neglect (Campbell 1972) and as several other major pieces of the evolutionary puzzle, especially inclusive fitness theory (Hamilton 1964a, b) and optimality modeling (reviewed in Parker and Maynard Smith 1990), were coming into focus as the foundations of behavioral ecology. Unlike some previous awardees of the Margaret Morse Nice Medal, we had not grown up as bird-watchers per se, but more generally as animal enthusiasts. Knowing from childhood that we wanted to have ''animals'' in our lives, we had gravitated naturally toward animal behavior research while in school. Arriving independently 2 years apart and meeting for the first time as University of Oklahoma faculty members, we continued with our separate lines of study for quite a few years focusing on scramble-competition polygyny and sperm competition in local ground squirrels (e.g., Schwagmeyer 1988, Foltz and Schwagmeyer 1989, Schwagmeyer and Foltz 1990), and fatal sibling rivalry and parent-offspring conflict in egrets (e.g., Mock 1984, 1985; Mock et al. 1987). Realizing that we needed to learn more about mathematical modeling, we visited several British universities over the 1983

Christmas break, pausing to get married in Edinburgh. It was easy to agree on Geoffrey Parker as our theoretical mentor and collaborator, as he had discovered sperm competition (e.g., Parker 1970) was having a major role in the development of Evolutionary Game Theory (e.g., Maynard Smith and Parker 1976, Parker and Stuart 1976, Parker 1978, Parker 1983, Parker and Maynard Smith 1990), and was already deeply involved in modeling both of our research topics (e.g., Parker and Macnair 1978; Parker 1982, 1985). We spent fall semester 1984 with him at the University of Liverpool, taking turns working on models with Geoff and spending the rest of our time either pulling numbers out of squirrel and egret data sets or desperately salvaging our neglected mathematical training. Over the ensuing years, we produced two separate series of publications with Geoff (e.g., Schwagmeyer and Parker 1987, 1990; Parker et al. 1989; Mock and Parker 1986, 1997), then began searching for a field system to explore together. That led first to two field seasons working on Glaucous-winged Gulls (*Larus glaucescens*) in Puget Sound, specifically on their pre-hatching acoustic communications (Schwagmeyer et al. 1991), before we decided to focus on biparental care in House Sparrows.

CHOICE OF PROBLEM

Biparental care and monogamy are not superficially sexy topics, at least on the surface. Except for feathered vertebrates, both traits are exceedingly rare in nature. Thus, the question naturally arises: what ecological and evolutionary forces generally promote the evolutionary stability of reproductive cooperation between two adults? Why have birds, in particular, adopted these as the norm, when other taxa have not? Finally, although many human cultures (including our own) claim both as societal goals, why are they so elusive? It seems logical to explore the underlying problems of shared parental care (seeking what may be broadly general causes) by analyzing the behavioral dynamics with birds. Furthermore, it makes sense to choose a bird that is common and amenable to (non-destructive) experimental manipulation of the targeted behavioral components.

Biparental investment is most simply explained as the pattern that emerges when neither of the sexual partners has anything better to do with its time. Specifically, if either parent has the realistic option of alternative pursuits that deliver higher average fitness returns, those distractions would likely undermine the joint endeavor (Maynard Smith 1977). Understanding the fitness payoffs available to each ''player'' for its various alternatives lies at the heart of the matter. In many taxa (e.g., mammals and plants), dependent offspring remain physically anchored to the female, extracting nutrients from her for extended periods. This arrangement ''emancipates'' the other parent to explore additional potential reproductive opportunities. Similarly, when offspring are not physically attached, and especially when their basic requirements are lessened (e.g., by precocial development), it is easy to see how uniparental care may suffice across a broader array of taxa. If low-cost offspring are shed soon after fertilization, the uniparent is less rigidly pre-ordained and ''sex-role reversal'' is more easily evolved (males serving as solo care-givers in many fishes and shorebirds, for example). In most birds, combining of egg-laying with altricial development seems to have created a middle zone in which more than one adult can make valuable contributions to offspring welfare. In short, when each embryo is placed in a neutral arena (nest) soon after it has been fertilized—and especially if a hasty departure by the first male reduces the chance that his sperm will fertilize the next ovum—the male has inducements for sticking around at least through the laying period. Thereafter, if he can further his own selfish interests better by providing additional services to his offspring (directly to the eggs and/or by proxy to his partner), than by seeking additional mating opportunities, he may remain. Once hatching begins, the need for provisioning with vast quantities of exogenous food can extend male participation on the home front (along with the continuing parental tasks of defense against weather and enemies, etc.).

Following this argument, ecological and phylogenetic circumstances may provide plausible reasons why biparental care is evolutionarily stable across ~90% of feathered vertebrates (Lack 1968, Clutton-Brock 1991), yet rare in all other life forms. Parental duties seem sufficiently extensive to require a team of care-givers and, perhaps equally important, to preclude either the option of dumping the whole brood-rearing exercise on the other (i.e., the ''cruel bind'' of Trivers 1972), lest the abandoned parent simply follow suit and allow the brood to fail.

To put a face on the overall dynamic, consider House Sparrow reproduction. After ~11 days of incubation (some by the male), four or five hatchlings emerge that will develop from tiny (1–2 g) naked ectotherms into fully feathered, warm-blooded, adult-sized (20–25 g) flying machines within just 2 weeks. During the nestling period, the two adults must find, capture, and deliver (typically one per trip) 3,000 to 4,000 unwilling insects to fuel this growth. At the same time, the parents also provide brooding warmth (at night and on chilly days), resist certain predators (and various other intruders, including hostile conspecifics), and maintain a modicum of nest sanitation by removing fecal sacs. Although most House Sparrows are socially monogamous, some males acquire two partners simultaneously and many females accept gametes from extra-pair males: in our Oklahoma population, ~17–20% of young are sired by other males (and 41–45% of broods contain one or more such extra-pair offspring) (Whitekiller et al. 2000, Edly-Wright et al. 2007). Overall, these are pretty ordinary passerines and, thus, a useful model system.

CHOICE OF SUBJECTS

According to W. L. Dawson (1903:40), ''Without question the most deplorable event in the history of American ornithology was the introduction of the English Sparrow.'' We may wince over that sweeping indictment, hastily noting that the arrival of European hominids was surely more ''deplorable'' for native bird species by virtue of myriad associated ecological nightmares (e.g., novel pathogens, deforestation, pollution, and introductions of numerous destructive exotics, especially pets, livestock, and all the birds mentioned in Shakespeare, etc.), but we get Dawson's point: this is not the most glamorous and beloved bird in the New World. We did not pick it for glamour. As behavioral ecologists, we chose our topic first and then sought the best local bird with which to pursue it. Had bluebirds, chickadees, or wrens piled into our nest boxes, we might well have studied them. But we were expecting sparrows and chose two sparsely occupied (by humans), university-owned tracts near campus for our study areas, partly because many House Sparrows were already nesting in the porous old buildings left from a World War II naval air station. One of these decaying structures is still dignified as the university's Animal Behavior Laboratory. Our goal was to lure sparrows from those decrepit buildings to fine, new nest boxes mounted where we could reach them conveniently. Surveying possible box designs, we learned that standard bluebird houses are annoyingly popular with House Sparrows and explicit warnings advised us that House Sparrows like having a perch, prefer being near human-occupied buildings, etc. We actively catered to sparrow tastes. In the early seasons, we had problems with a few avian predators, particularly Loggerhead Shrikes (*Lanius ludovicianus*) that trap-lined our boxes, harvesting sparrow nestlings simply by sticking their heads through the hole and seizing the tallest beggars. To thwart this, we attached a simple 10-cm long corridor of galvanized hardware cloth to every box. The sparrows did not mind entering through these hall-like structures and mass-predation losses dropped.

TRAPPING, MARKING, AND CENSUSING

We used the usual trapping methods for building a color-banded population, including walk-in traps baited with seed and bread, mist nets, and even sneaking up on brooding males to catch them in nest boxes. We learned the hard way not to touch desertion-prone females during incubation. We applied three color bands (slitting toy Perler Beads as an inexpensive supply; Hill 1992) and one aluminum band in unique combinations for each bird. After much trial-and-error with a variety of in-box trap designs, we developed a Rube Goldberg contraption involving a modified wire corridor (sporting a drop-down door to prevent exit), some monofilament fishing line, a rat-trap, and remote-control toy car electronics that empowered us to catch uncooperative individual adults during their brief visits to provision chicks (Mock et al. 1997). The general problem was that House Sparrows are smart and wary: catching one member of a pair without disturbing its mate required a trap that was simultaneously invisible, under our instantaneous control from considerable distances, and impervious to strong prairie winds. Once captured, we carried subjects inside an opaque bag to a car, processed it there (weighing, banding, etc.), and then carried it to some stranger's vehicle for release: simply releasing it from one's own car was found to lead to scolding of that vehicle during subsequent attempts to observe behavior.

BEHAVIORAL SAMPLING

Reliable quantification of male and female parental care took advance preparation to opti-

mize the later research effort. A chief goal was to ascertain food provisioning rates by each parent (Frontispiece) across the 2-week nestling period. We needed a sampling regime that would generate representative estimates. Average figures in quite a few published field studies of avian parental care are based on rather scant samples (at times just 15–30 min observations taken on 1–2 days convenient to the researchers) without any attention given to whether these capture the essence of the parents' activities across daylight hours, age of the nestlings, shifts in food availability within and between seasons, etc. Because we were going to do a lot of monitoring over several summers, we wanted to know how much sampling was needed and when this should be done. For this purpose, we conducted a preliminary study in which we recorded parental delivery rates intensively at five nests (covering all daylight hours and brood ages), then performed regressions on these over-sized samples to see if some times of day (and/or combinations thereof) captured most of the variation. We learned that a single hour-long sample taken mid-day yielded a good picture of the whole day's provisioning (between-nest comparison), but one taken in mid-morning did the worst (see Schwagmeyer and Mock 1997 for details). Combining samples delivered 91–99.7% (depending on which hours) of the variation between nests and nearly 80% of within-nest variation. In the seasons that followed, we used these findings to guide our deployments, eventually amassing parenting records for more than 100 broods based on >13 of these selected hours per brood. During these observations, we recorded parents' arrivals and departures, size of prey being carried (three categories, scaled against adult beak), and other activities performed near the nest (e.g., foraging, singing, defending, etc.) These data provided a good picture of parental care in regular sparrow nesting cycles and in those subjected to experimental manipulations.

BUILDING SUCCESSFUL OFFSPRING

At the heart of any parental care problem lies the question of what is needed to produce valuable offspring. There are many components, including protection from the elements and predators, but finding and delivering sufficient food to the brood (provisioning) and then distributing it optimally once home (allocating) are generally assumed to supersede most other concerns, because of the phenomenal growth challenge of offspring. Once eggs have hatched, parentally delivered food is the chief factor limiting growth, survival to fledging, and recruitment to breeding age of House Sparrow offspring; hence it is a major determinant of parental fitness. Provisioning, as the central task shared between the parents, was the initial focus of our exploration into the stability of biparental care.

If food is limiting, the simplest prediction is that offspring growth and survival should be density (brood-size) dependent for a given level of parental effort. This is usually assessed over the short span of the nestling period (volant offspring being necessarily harder to count) as one discrete exercise. In many field studies, brood size at hatching is compared with survival and body mass at fledging (typically defined as banding age, just before first flight). This requires only a brief census visit at hatching and measurement of body size during the banding process. Few field studies calibrate those relationships with intensive sampling of actual food delivered, presumably because this feature is tedious and time-consuming. A separate exercise, seldom performed in tandem with pre-fledging evaluation, extends the matter from that point by comparing how fledging production (e.g., size and numbers of banded chicks) translates into offspring survival to breeding age. This second step has produced far greater documentation (for at least 22 avian species; reviewed by Magrath 1991, Schwagmeyer and Mock 2008) of the commonsense idea that parents producing more and larger fledglings should consequently achieve greater recruitment of breeding offspring.

We were committed to doing the necessary observations of provisioning, as an essential part of analyzing biparental division of labor, and took the opportunity to combine the two steps (pre-fledging and post-fledging) on the marked House Sparrow population. Mean offspring mass on day 11, to our mild initial surprise, was not predicted by total food deliveries, but was strongly predicted by the rate at which the ''enormous'' category of insects (>2 cm total body length, hereafter, ''e-prey'') were provided (Schwagmeyer and Mock 2008). Once a correction is made for the much greater volume and mass of e-prey, it seems likely these grasshoppers, caterpillars, etc. can provide most of the nutrition early in the season, despite being relatively uncommon (~14% of all deliveries). Thus, total amount of

food is important, as expected, but simple counts of parental food trips—as might be recorded by automated devices—would have pointed to the opposite conclusion.

We used reobservations of 100 banded offspring from a sample of 1,028 broods to evaluate how chick numbers and mean mass relate to local recruitment. This measure of parental success was predicted by both size and numbers of offspring at banding (Schwagmeyer and Mock 2008).

We found that our data from 99 broods observed for provisioning rates were sufficient for a direct assessment of how food deliveries affect recruitment. This connection had been established before only once, for Long-tailed Bushtits (*Aegithalos caudatus*), a cooperatively-breeding British bird (MacColl and Hatchwell 2003). Total delivery counts once again failed to predict survival to breeding age in our sparrows, but e-prey deliveries did (Schwagmeyer and Mock 2008). Overall, it seems clear that e-prey availability is a key determinant of parental success and these food items have an especially strong effect on recruiting for earlier broods.

Considering that parents presumably cannot simultaneously maximize both the number and sizes of current brood members, much attention has been given over the years to short-term adjustments they may make during the period of offspring dependency. Early mortality of individual nestlings has the potential to relax competition for insufficient food and the idea that brood reduction might be engineered by parents as part of an adaptive strategy for tracking unpredictable food availability dates to the classic writings of David Lack (1947, 1954). The resolution of acute sibling rivalry in some taxa includes extreme forms of nestling aggressiveness and even specialized weaponry, but in many it results from low-key processes of scramble competition (reviewed in Mock and Parker 1997). Passerine brood reduction falls overwhelmingly into the latter category and it is hard to learn unambiguously whether the loss of any given brood member makes a positive contribution to the inclusive fitness interests of surviving parents and siblings, an overall negative, or a matter of little importance one way or the other (O'Connor 1978).

We found that 42% of 1,000 multi-chick House Sparrow broods experienced partial-brood mortality between hatching and fledging (Mock et al. 2009) with greater frequency in larger broods, as one would expect. Most of these losses occurred early in the nestling period (median day 4), before parental capacities to provision are likely to be overtaxed. We found parental provisioning (in the closely observed sample) increased from broods of three to broods of five, and per-capita food remained relatively even. Family size was a strong predictor of whether brood reduction occurred (provisioning and family size are both good predictors of the proportion of the brood surviving to fledge). Once a single-chick mortality event had occurred, parents did not trim their provisioning rate, as has been documented for siblicidal Cattle Egrets (*Bubulcus ibis*; Mock and Lamey 1991) and Brown Pelicans (*Pelecanus occidentalis*; Ploger 1997); thus, sparrow survivors tended to receive a food bonus in the aftermath of brood reduction.

We took two further steps to explore whether parents might favor or disfavor brood reduction. We affixed tiny video cameras above false ceilings inside 11 nest boxes containing broods of four and recorded how food was distributed when nestlings were sufficiently young (3 days) that allocation could be attributed safely to parental decisions (i.e., not to nest-mates' jockeying effectively for positional advantage). The idea was to see if fully empowered parents show overt favoritism toward the smallest chick(s) in each brood by giving runts more food. These parents skewed allocation more to larger chicks (Mock et al. 2009), a pattern that persists (and often increases) after the stronger chicks usurp increasing control over allocations. Thus, brood reduction victims tend to be those that were smallest initially. Second, we analyzed the trade-off between size and numbers of fledglings on recruitment to estimate how much additional body mass of surviving nest-mates is required to compensate parental fitness for loss of one offspring. This exercise suggested that one chick's death is fully reimbursed if its surviving siblings fledge about 2 g heavier (e.g., by virtue of the food the victim would have consumed). Beneficial reallocation probably occurs often, apparently when parental control is at its peak (Mock et al. 2009).

The foraging task shared between two sparrow parents is something of a malleable abstraction, perhaps roughly estimated (within a range of limits) when clutch size is first known to both partners, but then shifting over the course of events including hatching failure, seasonal ebb and flow of food availability (insect hatches,

periods of inclement weather, etc.), and loss of nestlings.

DO PARENTS NEGOTIATE WITH EACH OTHER?

The most influential hypothesis for biparental cooperation outlines a behavioral dynamic between two monogamous partners as being the fruit of a negotiation (Chase 1980, Houston and Davies 1985, McNamara et al. 1999). This assumes that each parent has a generally self-serving level at which it is willing to work, but must coordinate with a like-minded partner. The ''self-serving'' qualifier reflects that participants are not genetic kin, so their confederation is held together by personal fitness interests (*cf.* inclusive fitness incentives). Each individual seeks the best deal possible, despite needing a sexual partner, within the framework of its joint reproductive enterprise, while prefering that its partner provide somewhat more than half of the work. Both partners cannot realize this preference simultaneously. Just as union representatives and owners engage in a series of offers and counter-offers during a labor dispute (Maynard Smith 1982), male and female parents are envisioned as adjusting and re-adjusting their levels of effort, either in evolutionary time or in real time, until each is satisfied that it cannot get a better deal. This final pair of positions is, in the parlance of evolutionary game theory, the ESS (Evolutionarily Stable Strategy) solution.

One attractive feature of this Negotiation Model for biparental care is its testable prediction of *partial compensation*, the optimal response that a parent should make if its partner seems to do less than its share. For illustration purposes, imagine that an idealized pair has a clean 50-50 split of the family-raising labor, then the male starts gold-bricking by cutting his share down to 30% of the total, leaving a 20% shortfall. The model reasons the female should not compensate fully (by making up the whole difference), but take up only part of the slack. If the system is working properly, the male's interest in offspring welfare should prompt him to increase his contributions (whereupon she decreases, etc.) until equilibrium occurs.

Field tests of the Negotiation Model had begun to appear in print as we were starting our sparrow project. The basic experimental approach involves unilateral handicapping, that is imposing a burden on one partner to reduce its contributions and simulating ''gold-bricking.'' With one parent slowed, the unencumbered partner's behavior is monitored to see if it provides partial compensation (vs. full compensation or even no compensation, etc.). We followed the example of Wright and Cuthill (1989) in crimping four small lead split-shot fishing weights onto the rectrices of the handicapped parent (male or female), loading ~5–7% of total body mass away from its center of gravity. After finding that some birds in the first season had lost these weights, we painted them with red nail polish in later years, enabling us to confirm retention through spotting scopes. Limiting our study pairs to those with clutches of either four or five eggs, we rotated among the experimental and control treatments (minimizing season effects). Our routine was to sample pre-treatment provisioning behavior for a total of ~5 hrs prior to treatment (typically by day 5 post-hatching) and to collect another 9–10 hrs of data after treatment.

Females in control (unmanipulated) pairs typically increased provisioning throughout the nestling period, while males leveled off after about the fifth day (Mock et al. 2005). Our experimental treatments showed unexpected responses. When males were handicapped, they had only a slight decrease in mean delivery rate, but they reduced their e-prey deliveries significantly; their mates showed a non-significant increase. More unexpectedly, at the nests where females received tail-weights, burdened females showed little reduction in their food deliveries, but their partners substantially increased provisioning anyway. Consequently, the broods received considerably more food than usual. Thus, if the positive male response was to his mate's behavior at all, it could not have been because she was doing less. More generally, we found little evidence that parents are responding to each other's provisioning rate (as required by the Negotiation Model), leading to the conclusion that parental effort is tied more directly to other factors (perhaps brood condition) and is more like a ''sealed bid'' with independent parental decisions (Schwagmeyer et al. 2002).

We also handicapped male provisioning performance with a second experimental manipulation, this time by surgically inserting small tubes containing time-release testosterone beneath the scapular skin, implanting empty tubes for controls. This produced a more dramatic reduction in male provisioning, as well as a reduction in male

incubation time (62% lower than controls for both measures), but a significant female compensatory increase was observed only during incubation. At that stage of the cycle, testosterone-dosed males appeared to reallocate time and effort to non-parental activities, as they did more singing and behaved more aggressively (both to other males and to their own partners) than control males. These hormone results showed that male and female workloads are strongly inter-related when offspring are still inside eggs, but not after hatching (Schwagmeyer et al. 2005). One interpretation of this difference considers that both parents are likely too busy when seeking and delivering prey items to keep track of each other's contributions (their independent visits to the brood typically last only 1–5 sec and encounter each other only by chance). In contrast, most incubation changeovers are face-to-face and the other changeovers are likely to carry information about when the partner departed (from the lingering tell-tale warmth of the eggs). We are currently exploring the behavioral dynamics of shared incubation in a new series of experiments.

WHEN PARENTING COSTS ARE REDUCED

Parents detecting their offspring are developing ahead of schedule might be expected to reduce their costly provisioning activities, either to use the time and effort for immediate reproductive advantage (especially males that can fertilize additional females) or for maintaining higher personal condition to benefit future offspring. The approach typically used for such load-lightening studies is to make food readily available to the experimental pairs (e.g., a feeder near the nest) and simply assume that a nontrivial amount of the extra nutrients is passed along to the offspring. We took a less trusting route by hand-feeding nestlings with commercial baby bird food twice a day. Specifically, we suspended nutrient powder in warm water to form a thin gruel and squirted it directly down the esophagus of each brood member through a modified syringe. Supplemented broods thus received an extra 25–30% of their estimated Daily Energy Budget, over and above whatever their parents supplied. We sampled parental provisioning as before, averaging ∼15 hrs at each of the 23 experimental broods.

Parents did not abridge their food deliveries to these supplemented nests (Mock et al. 2005).

Instead, females showed their usual provisioning increase after day 5, but this time their males escalated in lock step, outperforming control males by 25%. This male rate increase did not come at the expense of food quality (e.g., the proportion of e-prey in the diet remained constant). Subsidized nestlings, despite this extra nutrition, neither gained weight more rapidly nor achieved higher mass by banding age, but they recruited into the local breeding population at a somewhat higher rate (11.8%) than matched controls (4.9%).

Thus, it appears males do not automatically divert their attention away from the current brood when parental burdens are lessened, but may respond positively to stronger offspring. Some data on begging call intensities showed that our supplemented broods begged more loudly, suggesting a possible proximate cue underlying paternal responses, but we found no evidence these broods differed visibly from normal (i.e., no mass effects). The asymmetrical responsiveness of the parents to subsidized broods may stem primarily from females already operating near their maximum (a ceiling effect), while males have extra reserves that normally remain unspent, or are channeled elsewhere.

FULL CIRCLE

We close this discussion of our research program where we started with explicit appreciation of our debt to Margaret Morse Nice for demonstrating the value of color bands. The huge amount of time and effort we have invested over the years in building and maintaining study populations of recognizable individual sparrows is a direct reflection on its central role in our work. Of course, numbered metal bands opened many research areas, but the advantage of being able to identify individuals without re-capture and from a distance truly revolutionized behavioral ornithology. Every project described would have been either totally impossible or substantially weaker without that preliminary step. One cannot even be certain that a given subject has not been used already in either the same study (with loss of statistical independence) or in a previous experimental manipulation (with the risk of introducing bias from that earlier treatment) without known individuals. One small celluloid band placed on one special sparrow in 1928 gave so much to so many.

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