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Male house sparrows deliver more food to experimentally subsidized offspring

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We explored behavioural adjustments made by parent house sparrows, *Passer domesticus*, when the nutritional condition of their dependent nestlings was improved experimentally. Male parents responded to artificially supplemented broods by increasing food deliveries, whereas female parents continued matching the already high rate of control females. Thus, parental care was not truncated in the face of fortified offspring, but actually escalated (ca. 17% more adult food deliveries overall). Supplemented nestlings showed a nonsignificant tendency to recruit into the adult breeding population more than controls. We propose that one important reason why male parents responded more strongly than their female partners centres on the lower marginal costs for additional male posthatching investment, specifically by demonstrating that increasing paternal investment is likely to confer higher fitness than alternative male activities.

In species with expensive parental care, the quantity and quality of nutrients supplied to dependent offspring frequently are major determinants of reproductive success (e.g. Lack 1966; Clutton-Brock 1991) and can affect multiple dimensions of intrafamily social dynamics (O'Connor 1978; Mock & Parker 1997). From an individual parent's perspective, the optimal level of investment in a current brood is likely to hinge on such factors as numbers and growth stages of the young, contributions from other adults (its mated partner, plus any alloparental 'helpers'), prevailing ecological conditions (especially availability of food), and all costs associated with parental activities (Winkler & Wallin 1987). Various features of offspring, including general appearance and various conspicuous signals (collectively referred to as 'begging'), can also affect level of parental care (Winkler 1987; Hussell 1988).

The interplay between prevailing food supply and the relative contributions of monogamous avian partners has been a focus of much empirical research on parental care, mainly explored through two dissimilar but parallel experimental approaches. In the first, one parent's performance is impaired, by being either physically removed

(thus depriving the brood of all its food deliveries: reviewed in Gowaty 1996) or partially handicapped (e.g. with weights or feather-removals intended to retard its investment contributions: Wright & Cuthill 1989, 1990; Sanz et al. 2000; Schwagmeyer et al. 2002). The effects of reduced food deliveries on brood members, and especially on the care responses of the unburdened partner, are then assessed. The opposite approach, artificially increasing food availability, has been used also, usually by creating an additional external source of provisions that the adults can transport to the nest (e.g. Wiebe & Bortolotti 1995; Wright & Dingemanse 1999), less commonly by placing such supplements inside the nest for offspring to consume (e.g. Verhulst 1994).

Experimental protocols involving nutrient supplements that go directly to offspring differ in two key respects from those in which they are routed through adult delivery. First, the nutrients are much more likely to reach the intended targets if there is no intermediary that could opt not to pass them along. Some studies employing feeding stations outside the nest include specific confirmation that at least some of the food is actually transported to nestlings (e.g. Soler & Soler 1996; Boland et al. 1997; Lozano & Lemon 1998), but other workers simply assume that any provisions consumed by caregiving adults free other foodstuffs that would not have been delivered otherwise (e.g. Verhulst 1994). Second, if

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adults never handle the food supplements, subsequent changes in parental care cannot be ascribed on the proximate level to the adults' exposure to the food per se, but only indirectly (through the nutrients' effects on offspring condition and/or behaviour). However one makes additional food available, a common objective of provisioning experiments is to reduce the fitness costs of parenting.

There are opposing theoretical predictions for how care-giving adults ought to respond when investment costs are trimmed (Lessells 2002). The prevailing view is that a parent detecting that progeny are faring unusually well should abridge its current efforts on behalf of future reproductive success. With the overall care burden lightened by extrinsic factors, the resulting parental emancipation might conceivably fall to both adults equally or to one parent disproportionately. Under the assumptions typically made for avian parental care, the male partner usually is regarded as better suited to capitalize on such windfall opportunities (specifically because he may be able to seek additional matings as part of a mixed reproductive strategy: Trivers 1972), though special conditions can randomize (Beissinger & Snyder 1987) or even reverse (Emlen & Oring 1977) which sex should benefit.

Under different assumptions, though, parents should respond to reduced costs of care by increasing current investment. A positive parental response to good offspring condition might be expected if the marginal value of additional investment were exceptionally steep. Such an opportunity might arise if offspring fitness were a nonlinear function of cumulative parental investment, such that escalated effort could bring disproportionate returns in offspring reproductive value (Lessells 2002). Furthermore, any ecological circumstances that devalue a parent's alternative uses for its time and effort should affect the decision about devoting more to a brood already on hand. For example, a dearth of potential replacement mates might erode the incentive for deserting the primary brood to seek other sexual partners (Maynard Smith 1977). And on the simplest proximate level, especially robust offspring may find stronger begging signals to be cost-effective, if parental fitness is not tuned to ignore such inflated demands, a positive feedback loop could emerge for that reason alone (see Discussion).

With theoretical justifications at hand for predicting diametrically opposite parental responses to offspring supplementation, further empirical work is indicated. As part of a larger exploration into the evolutionary stability of avian monogamy, which also included experimental handicapping of individual parents and scrutiny of the unhindered partner's behaviour (Schwagmeyer et al. 2002), we conducted a field study of how providing supplemental food to house sparrow, *Passer domesticus*, nestlings affected the delivery behaviour of (unhandicapped) parents. Specifically, we tested the prediction that parents, especially males, whose offspring were artificially provisioned would reduce their levels of effort. For these supplements, we sidestepped the parents and fed the nestlings directly, thereby guaranteeing that targeted nestlings obtained substantial amounts of high-quality

extra nutrition. And we sampled the subsequent deliveries of parents after overnight delays, in order to minimize the likelihood that offspring behaviour was affected merely by temporary satiety. That is, the delay feature was included to avoid the proximate effects of 'hunger' and make it more likely that offspring signals carried information about the senders' true condition (potential fitness).

METHODS

House sparrows were studied at two sites (North Base and South Base) in Norman, Oklahoma, U.S.A. These are university-owned tracts of 360 and 770 ha, respectively, once used as military bases in the 1940s. A sparse mix of deteriorating former Navy buildings and newer structures dot both areas and we have maintained approximately 100 nestboxes since 1994 to attract the local (nonmigratory) sparrow population. Boxes are mounted on utility poles, chain-link fences, and exteriors of old buildings.

Experimental Procedure

During April–July, 1995–1999, nests where laying had begun were matched as closely as possible by laying date and clutch size (using only those with four or five eggs), then assigned in sequence to one of four treatments (two of which involved the handicapping of parents: see Schwagmeyer et al. 2002). This protocol resulted in good balance for mitigating possible season effect problems (mean $\pm$ SD Julian date: $165.98 + 28.80$ for control versus $164.77 + 23.80$ for supplemented broods; $t_{48} = 0.16$, $P = 0.87$). At hatching, brood size of the families that were to be experimentally supplemented (median $= 4.0$, 95% confidence interval, $CI = 3.7$–4.2) was virtually identical (Mann–Whitney U test: $U = 385$, $N_1 = 27$, $N_2 = 31$, $P = 0.56$) to that of unmanipulated control families (median $= 4.0$, 95% CI $= 3.8$–4.3). Experimental broods were fed a suspension of commercial nestling growth compound (Exact hand-feeding formula for baby birds: Kaytee Products, Inc., Chilton, Wisconsin, U.S.A.), composed mainly of grains, whole eggs, vitamins and digestion facilitators. Beginning with a single meal on the afternoon of day 3 (day 0 being defined as when hatching began) and continuing with twice-daily meals, chicks received food according to the manufacturer's specifications (diluted 3:1 in warm water until day 5 and 2:1 thereafter) through day 10. On day 11, all chicks were weighed on an electronic balance accurate to 0.1 g and banded (USGS aluminium leg bands plus unique colour combinations of three plastic leg bands). In addition, each nestling was weighed in 14 of the supplemented and 13 of the control broods on days 5, 7 and 9. After day 11, broods were checked for fledging (by observing whether parental feeding visits had ceased) but not disturbed further. Age at fledging was estimated as the midpoint between the last nest check with chicks present and the first with chicks

absent (if a brood was not checked within 2 days of its disappearance, no estimate of fledging age was made).

At each meal, the entire brood was removed from its box and placed on the ground in nearby shade. Individuals were hand-fed the mixture, administered from a 3-cc syringe through a modified hypodermic needle-guard (a rigid plastic tube ca. 6 mm in external diameter whose tip had been removed and the edges filed smooth). This 24-mm tube was inserted into the left corner of a chick's gape and angled left to right past the epiglottis and into the oesophagus before the plunger was depressed slowly to expel the food. We could easily see the crop filling through transparent ventral skin, and thus could terminate pressure on the plunger when the crop was well rounded. When a chick had become temporarily full, we repeated the process with the next sibling and so on until all had been fed once. By that time, the crop of the first chick had drained and the process was repeated for all young, usually two to three rounds, until each had ingested 1–2 ml of the mixture (0.3–0.6 g of dry formula). A typical meal lasted 5–10 min. Extrapolating from manufacturer documentation, the 2–4 ml total of daily supplement received by each nestling in its two hand-fed meals contained roughly 8–16 J, 0.5–1 g crude protein, 0.15–0.30 g crude fat, and 1–2 g crude fibre. Using the estimated daily energy budget (DEB) of 3–10-day-old nestling house sparrows (Blem 1975; Kendeigh et al. 1977) as 25–67 J, the supplements averaged roughly an extra 25–30% DEB.

Control broods were handled at least once a day (brood size was checked after each observation session), as well as during scheduled weighing events and censusing visits. Nevertheless, they were disturbed less often than broods receiving food supplements. Because passerine parents have been shown to reduce food deliveries in the immediate aftermath of human visits (e.g. Burtt 1977), our control broods may have received somewhat more food from their parents both during and following the experimental meals at supplemented nests. Because our intention was to inflate the nutritional state of experimental nestlings, any such parental contributions should have made our manipulation more conservative.

We planned the timing of our twice-daily provisioning to minimize possible proximate effects of the experimental manipulation on behaviour. Broods were fed once at midday and once at approximately 1600 hours, long before parental care would be sampled the following morning (see below). Thus, nestlings went roughly 16 h without supplementation prior to the recording of parental effort (i.e. parental behaviour was assessed when chicks were not satiated artificially).

Offspring Survival

We determined recruitment into the adult breeding population from identifying resident breeders in subsequent years and/or from netting or trapping adults during one or more seasons after they had fledged. We compared whole broods as successful (i.e. producing at least one breeding-age survivor) versus unsuccessful (producing no such adults) via a contingency test. We also analysed survival data using the 'events/trials' syntax for logistic regression, with number of recruits in each brood weighted by brood size at fledging.

Quantification of Parental Effort

On the morning of day 3, we recorded parental behaviour during three noncontiguous 60-min samples to establish a baseline for early-phase food deliveries before experimental supplementations began that afternoon. The following morning (day 4), we collected three more behavioural samples, followed by two each on days 5–8 (unless one of the parents had been injected with doubly-labelled water for a related energetics study, in which case a third sample was added on those days), and one each on days 9 and 10. The hours chosen for parental sampling were based on results from a pilot study that determined which morning hours best predicted the parents' whole-day variations (Schwagmeyer & Mock 1997). Overall, each supplemented nest was observed a mean $\pm$ SD of 15.04 $\pm$ 1.64 h; each control nest, 14.44 $\pm$ 2.21 h ($t_{48} = 1.07$, $P = 0.28$).

Observations were made from cars parked 20–80 m from each focal nestbox, using binoculars and/or 20–60$\times$ spotting scopes. We recorded the times of arrival (landing on roof or entry hall) and departure to the nearest second. We also recorded the identity of the parent making each delivery, plus size and type (within the broad categories of insect, seed, or bread) of each food item. Delivered food items were categorized by size as: (1) tiny (<6 mm, barely detectable); (2) medium (typically extending slightly beyond both sides of the parent's bill, roughly 10 mm long); and (3) enormous (20+ mm total length). Because we used seed and bread as baits for walk-in traps at various sites, we always knew the current source locations for those items: if a parent was seen flying from the nest to such a site and returning with only tiny items (typically many such trips in a row), it was assumed to be carrying seeds. Bread pieces were easily identified. Visits for which the observer did not get a sufficient look at the parent's bill (e.g. because of angle, lighting, or speed of entry) were scored as items of unknown size and type. We calculated interobserver agreement from six hour-long samples where two workers collected data on the same focal nests. These paired counts of total parental visits per sample showed 94.6% agreement (range 88.2–100%); assignment of the visiting adult's sex, 97.9% (range 92.9–100%).

Sample Sizes and Statistical Testing

Of the 50 broods for which we collected behavioural data (23 supplemented and 27 controls), two supplemented and one control were depredated (i.e. all nestlings vanished overnight) prior to day 11, and thus had to be excluded from analyses of how parental deliveries affected fledging weight and recruitment. On the other hand, an additional seven broods (four supplemented and three controls) were added in 1997 from a parallel study: these

bolstered the growth and survival analyses, but did not contribute to the study of parental behaviour, which was not quantified at those nests. Ninety-three of the 100 observed parents were banded uniquely (aluminium and coloured plastic leg bands), so we are confident that no individual was used twice.

We standardized prey delivery rates according to current brood size for each day of observations (i.e. on a per-capita basis). Examining the interaction on main effects of sex∗group (i.e. male supplemented versus female supplemented versus male control versus female control) required that we used a mixed model for repeated measures (across the sampled days within each nesting cycle), with one random effect (nest identity) and one covariate (date within the season). Preliminary analysis showed that male deliveries were not linear when individual days were used as the repeated time measure, so the 8-day records were split into time blocks that met the requirement of linearity and allowed scrutiny of the experimental manipulation per se. The main analysis used two such periods: (1) block 1 consisted of days 3 and 4, essentially capturing the pretreatment delivery rates of parents in both groups (only one artificial meal had been administered by the morning sampling period on day 4), and (2) block 2 covered the remaining six days (5–10), during which parents could show the effects of chick supplementations.

The statistical results reported for parental food deliveries (SAS Proc Mixed with compound symmetry covariance structure) are from type III tests for fixed effects once the random effect of nest identity and the season effects (mean Julian date for each brood) were removed. Pairwise comparisons (group∗sex∗block) are from t tests of delivery rate (per chick per hour) least-squares means.

Analyses were performed using SAS Version 8.01 (Cary, North Carolina, U.S.A.) and SPSS Version 11 (Chicago, Illinois, U.S.A.) software. Samples were tested for homogeneity of variances and approximation to normal distributions, with nonparametric tests employed when appropriate. Means are reported ±1 SD, unless stated otherwise.

RESULTS

Parental Visits

Parental food deliveries varied both within season (as a function of Julian date: $F_{1,142} = 14.86$, $P = 0.001$) and in association with experimental group across the nesting cycles (group∗sex∗block interaction: $F_{7,142} = 6.87$, $P = 0.002$), once the seasonal effects were managed. Control females showed increasing food deliveries from block 1 to block 2 ($t_{142} = -3.67$, $P = 0.003$), but their partners did not ($t_{142} = -1.45$, $P = 0.1492$) (Fig. 1). As a result, the sexes of control pairs were virtually identical to one another at first (block 1: $t_{142} = 0.11$, $P = 0.9133$), but then females delivered 20% more food than their partners in block 2 ($t_{142} = 2.31$, $P = 0.0225$).

Experimental parents matched the scores for control parents closely at first (block 1 pairwise comparisons:
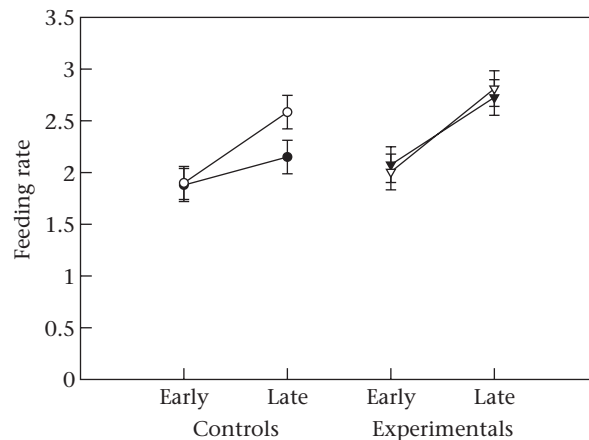

Figure 1. Hourly food delivery rates per chick (least-squares means ± SE) during the early (days 3–4 posthatching) and late phases (days 5–10) of the nestling period for female (open symbols) and male (filled symbols) parents.

supplemented males versus control males: $t_{142} = -0.84$, $P = 0.4031$; supplemented males versus control females: $t_{142} = -0.75$, $P = 0.4527$; supplemented males versus supplemented females: $t_{142} = -0.35$, $P = 0.7236$; control males versus control females: $t_{142} = 0.11$, $P = 0.9133$; control males versus supplemented females: $t_{142} = -0.54$, $P = 0.5920$; supplemented females versus control females: $t_{142} = 0.45$, $P = 0.652$). But after provisioning commenced, parents of both sexes escalated their food deliveries (block 1 versus block 2 comparisons: supplemental females: $t_{142} = -4.03$, $P < 0.0001$; supplemental males: $t_{142} = -3.25$, $P = 0.0014$). Males at supplemented nests outperformed their control male counterparts by more than 25% in block 2 ($t_{142} = 2.43$, $P = 0.0162$), and matched the escalated rates of supplemental and control females closely (block 2 pairwise comparisons: supplemented males versus supplemented females: $t_{142} = 0.43$, $P = 0.6694$; supplemented females versus control females: $t_{142} = -0.96$, $P = 0.3382$; supplemented males versus control females: $t_{142} = -0.60$, $P = 0.5499$).

Out of concern that the observed increase in male visits at supplemented nests might have been accompanied by shifts in diet composition, we examined whether the two opposite extreme food categories (insects classified as 'enormous' and the artificial seed/bread items used as bait) differed dramatically between supplemental and control males. Both of these food categories were uncommon and similar at experimental and control nests. Specifically, the largest prey were not reduced sharply in the supplemented males' deliveries (8.1% of the adjusted total deliveries in block 1, 7.7% in block 2), and matched male deliveries at control nests closely (8.4% and 8.7%, respectively). Seed/bread contributions paralleled this pattern (supplemented: 5.0%, 9.8%; control: 6.3%, 5.1%). When the mixed model analyses were run separately with either the largest insects or seed/bread categories deleted, the patterns reported above for all-deliveries were unchanged.

Offspring Survival and Condition

Nestlings in the two treatments developed in outwardly similar ways, but probably differed in their long-term fitness prospects. Early partial-brood mortality occurred in roughly half of all nests in each treatment (14 of 30 controls; 13 of 25 supplemented nests). In all 13 of the affected supplemented broods, prefledgling deaths involved only one chick and roughly half occurred very late in the nesting cycle (after banding on day 11). In the control broods that experienced nestling loss, 10 lost a single chick, the other four lost two, and most mortality (11 of the broods) occurred before the young reached banding age. Brood size at fledging was equivalent for the two treatment groups (3.3 ± 1.0 for 31 control broods; 3.1 ± 1.2 for 27 supplemental broods) (Mann–Whitney U test: $Z = -0.92$, $P = 0.36$). Individual nestlings gained body mass at similar rates in the two treatments, not differing in weight at any of the three prebanding ages or when banded on day 11. In addition, no treatment differences were apparent in intrabrood mass variation at banding age (see relative difference in nestling mass, RDNM, Table 1).

Despite these similarities in early growth patterns, treatment may have affected the likelihood of surviving to breeding age. Eight of 25 supplemented broods (32.0%) produced recruits to the breeding population, compared with only four of 30 control broods (13.3%) (Fisher's exact test: $P = 0.09$). Across both treatments and all five seasons, a total of 15 fledglings (6.9% of 188 nestlings that reached banding age and were not subsequently found dead in their nests) were resighted as yearlings. These included 10 of the 85 supplemented individuals (11.8%), but only five of 103 controls (4.9%). Logistic regression revealed a marginal effect of treatment on the proportion of fledglings recruited from supplemental and control broods ($\chi^2_1 = 3.13$, $P = 0.077$).

There was no obvious difference in the sex ratios of recruits from supplemented and control broods: seven of the 10 supplemented survivors were males, as were all five control survivors (Fisher's exact test: $P = 0.50$).

Broods fledged at progressively younger ages as the season advanced in both control ($F_{1,24} = 6.73$, $P = 0.016$) and supplemented samples ($F_{1,18} = 6.13$, $P = 0.024$), but there was no difference in how season affected fledging age between the two treatments ($F_{1,40} = 0.12$, $P = 0.73$). Overall, supplemented broods showed a nonsignificant tendency to fledge slightly earlier than control broods (least-squares means = 15.0 versus 15.7 days: $F_{1,41} = 3.23$, $P = 0.0799$).

DISCUSSION

The usual pattern for division of nestling care by house sparrow pairs is for food deliveries by the female parent to increase steadily (as the brood ages) and for the contributions of her male partner to remain unchanged. In our control treatment, female feeding thus rose by one-third but male feeding was statistically flat. By contrast, males tending supplemented broods increased their deliveries by about one-third, while their partners provided their normal increment. Experimental broods thus received extra food from two sources (one artificial and one paternal).

Supplemented nestlings recruited into the adult breeding population at a marginally higher (but not statistically significant) rate than control broods, suggesting that quantity and/or quality of nutrition normally limits fledgling survival. Interestingly, the three most commonly reported short-term surrogates for nestling fitness (faster growth, greater asymptotic mass, and lower prefledging mortality) were not observed, although there was a marginal tendency for supplemented broods to fledge slightly earlier. In a field provisioning experiment with pied flycatchers, *Ficedula hypoleuca*, Verhulst (1994) showed that enhanced recruitment was similarly not accompanied by elevated mass at fledging. He suggested that such an effect might reflect differences in developmental allocations (e.g. superior plumage) and/or in parental condition that may support greater postfledging investment. Numerous other food-supplementation studies have produced mixed results with respect to fledging mass, with some workers finding young at experimental nests to be heavier (e.g. Arcese & Smith 1988; Richner 1992; Wiebe & Bortolotti 1994), but others not (e.g. Wiehn & Korpimäki 1997; see review by Magrath 1991). We know of no previous studies demonstrating even marginal effects of food supplementation on both parental deliveries and offspring recruitment.

Focusing on the treatment differences in parental care, we offer two simple proximate interpretations for our behavioural results: (1) that parents respond positively to supplemented broods because artificially fortified young

Table 1. Nestling masses (least-square means $\pm$ SD corrected for season) for supplemented and control broods at four ages

Measurement age	Supplemented broods (N)	Control broods (N)	t	P
5 days	15.78 ± 2.78 (13)	15.40 ± 2.78 (14)	-0.35	0.73
7 days	20.80 ± 2.86 (17)	19.49 ± 2.86 (16)	-1.31	0.20
9 days	22.20 ± 2.58 (16)	23.08 ± 2.58 (16)	0.97	0.34
11 days	22.18 ± 2.98 (21)	22.77 ± 2.92 (26)	0.69	0.49
RDNM (day 11)	0.158 (19)	0.210 (26)	1.15	0.26*

RDNM, the relative difference in nestling mass ((heaviest nestling's weight − lightest nestling's weight)/brood mean: Bryant 1978), was calculated for each brood on day 11.
*Degrees of freedom = 40.7 correcting for unequal variances.

may produce stronger signals of solicitation; and (2) that the male in such circumstance may be more free to respond than his partner because of lower prehatching male expenditures. Consistent with the first of these, a preliminary study of nestling begging in our population in 1997 showed that supplemented broods begged more loudly than controls at prefledging ages (G. Wang, unpublished data). Further research is now under way to explore the effects of nestling condition on begging signal strength in this population.

We next develop ultimate explanations that are linked to these proximate possibilities. These are explicitly offered for heuristic purposes that may prove useful in future work. Because the optimal amount of parental investment for an offspring to receive will not equal the optimal amount for a parent to supply (Trivers 1974), our ultimate explanations will consider this disparity (the 'battleground' component of parent–offspring conflict theory: sensu Godfray 1995a, b; Mock & Parker 1997). First, considering that parents supplied more food to offspring in extra-high condition, we propose two mutually compatible ultimate interpretations:

(1) Parents perceive supplemented chicks as being high-quality offspring (because these nestlings have prospered better than expected from the food input parents supplied). It may be in the parents' best interests to provide more food to offspring of higher-than-average quality. A similar effect is expected from the offspring perspective (i.e. offspring of higher quality may optimally take more food from their parents), but in our case only the parents (not the offspring) should be 'deceived' by food supplementation about true offspring quality. This explanation predicts changes in the parents' foraging behaviour.

(2) Food supplementation causes offspring to perceive foraging as less expensive to parents. Enhanced condition may affect how nestlings evaluate the local environmental circumstances, since such improved development may ordinarily mean that parents are highly skilled and/or have easy access to food (i.e. have lower foraging costs). If parental foraging costs are lowered, both the optimal food input for parents to supply and the optimal amount for the offspring to demand (and consume) from their parents increases. In our case, food supplementation should 'deceive' only the offspring about the true foraging costs, not the parents. Thus, this explanation predicts changes in offspring begging.

For the second behavioural result (that the increased food came mainly through escalation in the male parent's food input), we suggest the following.

(1) A substantial increase in foraging may be more cost-effective for the male because of his lesser prehatching expenditure, thus he may optimally augment his food input more than the female. A predominantly male-related increase would also be optimal from the offspring's perspective, for the same reason.

(2) Because the male parent's genetic relatedness to the focal brood averages lower than that of his partner, nestlings may beg more vigorously to him (i.e. his future reproductive success is of less importance to them than their mother's). However, that result should be opposed, and perhaps nullified, by the fact that his provisioning becomes relatively more expensive to him as the proportion of the brood sired by other males (extrapair fertilizations, hereafter EPFs) increases.

The Model

To explore these points more rigorously, we present a form of model used by Houston & Davies (1985), and more recently investigated by Lessells (2002), that follows 'sealed bid' assumptions. By this we mean that parents commit themselves to provide a particular amount of food for a given level of offspring begging and vice versa, with the interactive function between parties changing only in evolutionary time. There is evidence that parental deliveries follow this general pattern in the Oklahoma house sparrow population studied here (see Schwagmeyer et al. 2002). Furthermore, increased food input from each caregiving adult is assumed to raise the success of current offspring and to reduce the prospects for the parent's future offspring.

Suppose that offspring are produced in broods of size n. Let the personal fitness of an offspring be $f(y)$, where y ($=y_m + y_f$) is the amount of food consumed by that offspring, and y_m and y_f are the complementary inputs from male and female parents, respectively. Parents must forage for the y_m, y_f units of food given to each offspring (i.e. a total of $ny_m = Y_m$, $ny_f = Y_f$ for the brood), and this has a cost to the male of $g(Y_m)$, and to the female of $g(Y_f)$, measured in terms of each parent's lost future reproductive success. We examine the 'battleground' (sensu Godfray 1995b; Mock & Parker 1997) between conflicting parental and offspring interests; that is, what food input would parents ideally give and offspring ideally receive?

Assume that a parent's expected relatedness to offspring in its present brood is the same as to its future broods, and that neither parents nor offspring can recognize whether they are related (specifically that a male parent cannot feed his own offspring preferentially). Selection on parents acts to maximize the present reproductive benefits minus the costs of current investment in terms of future reproductive success of that same parent:

$$W_m = r_m[nf(y) - g_m(Y_m)] \text{ for the male parent;} \qquad (1a)$$

$$W_f = r_f\left[nf(y) - g_f(Y_f)\right] \text{ for the female parent;} \qquad (1b)$$

where r_m is the average coefficient of relatedness between a randomly chosen brood member and the male parent, and r_f is that between a randomly chosen offspring and the female parent. Recall that y is each parent's per-chick delivery score and Y is its per-brood total. Differentiating equation (1a) with respect to y_m, equation (1b) with respect to y_f, and setting each solution equal to zero produces the result that

$$f'(y) = g_m'(Y_m) = g_f'(Y_f), \qquad (2)$$

that is, the biparental care evolutionarily stable strategy (ESS) is such that both parents have the same marginal

costs of foraging, which are equal to the marginal benefits attained by the offspring (Fig. 2; see also Lessells 2002). (For explanation of this procedure, we mention that the technique of taking first derivatives and setting them equal to zero identifies the values of y_m and y_f that maximize parental fitness.) Note that under our assumption of constant relatedness between parents and current versus future offspring, relatedness is not a part of the optimal solution for parental investment.

The interests of the offspring will be different (Trivers 1974). The offspring's fitness is its personal fitness through the food received, discounted by the cost of that food in terms of its siblings. We partition the contributions to offspring fitness stemming from the two parents' efforts, starting with the male. The fitness of a focal offspring that deviates by taking $y_m \neq y_m^*$ from its male parent (all such deviations are assumed to be unilateral, involving no change with the other parent), when the remaining $(n-1)$ brood members each take the offspring ESS, y_m^*, from the same parent is

$$W_{om} = f(y) - r_m g_m \left(y_m + (n-1) y_m^* \right) - r_f g_f \left(n y_f^* \right). \quad (3a)$$

Similarly, the fitness of a focal offspring that deviates by taking $y_f \neq y_f^*$ from its female parent is

$$W_{of} = f(y) - r_f g_f \left(y_f + (n-1) y_f^* \right) - r_m g_m \left(n y_m^* \right). \quad (3b)$$

We can find the offspring's ideal food input from each parent by differentiating equation (3a) with respect to y_m and equation (3b) with respect to y_f, and setting each solution equal to zero. This gives

$$f'(y) = r_m g_m'(Y_m) = r_f g_f'(Y_f), \quad (4)$$

which is clearly different from equation (2) because r_m, r_f are both less than 1.0.

Following previous treatments (e.g. see Mock & Parker 1997), we assume that $f(y)$ rises with decreasing slope. A suitable explicit function is

$$f(y) = V[1 - \exp(-cy)], \quad (5)$$

where c and V are positive constants; c defines the rate at which $f(y)$ rises to its asymptote, and V sets the asymptotic value, which could relate to the intrinsic 'quality' of the chick (Fig. 2a).

Most plausibly, the overall cost function, $g(y)$, rises with increasing slope from $g = 0$ at $y = 0$. A suitable function is

$$g_m(Y_m) = h_m[\exp(aY_m) - 1] \text{ for the male parent;} \quad (6a)$$

$$g_f(Y_f) = h_f \left[\exp(bY_f) - 1 \right] \text{ for the female parent.} \quad (6b)$$

Here, a and b are positive shape constants expressing how a unit of investment in the current brood depresses future parental fitness. The higher a or b, the more quickly the food-provisioning costs escalate for the male (a) or female (b) parent (Fig. 3b): generally, we expect the female's cost curve to be steeper (i.e. $a < b$), because she has already invested more than the male by the time offspring need
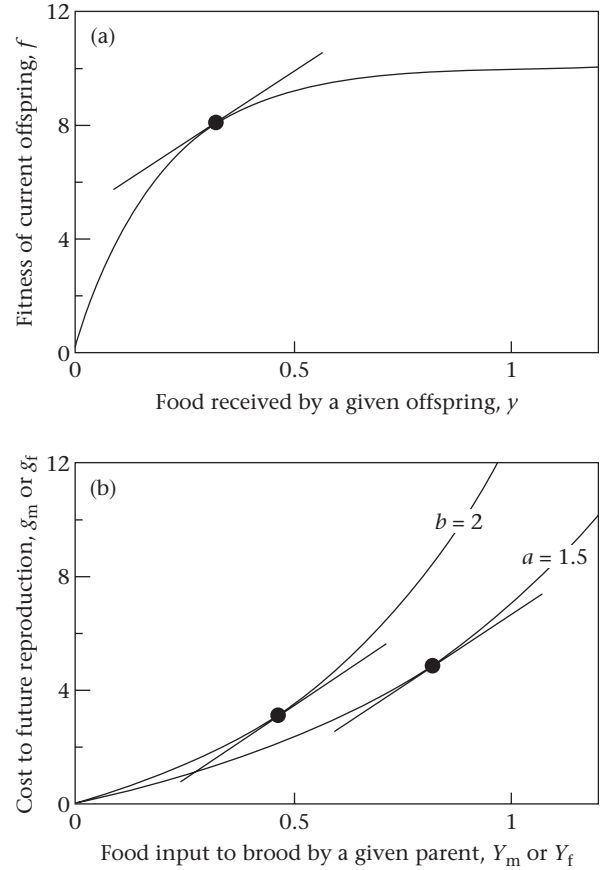

Figure 2. (a) Offspring fitness function (equation 5); that is, the expected fitness of the current offspring in relation to the amount of food it receives (y, the sum of the inputs from the two parents). The curve shown has $V = 10$, $c = 5$. (b) Parental cost functions (equations 6a, 6b); that is, the future costs of providing food for each parent (the total for the brood is Y_m for the male and Y_f for the female). The top curve is for the female, whose foraging costs rise more steeply (here $b = 2$ compared to $a = 1.5$ for the male; $h = 2$ for both sexes). At the evolutionarily stable strategy (ESS) for the parents, the marginal gain rate (=slope, illustrated as tangents to the curves) of the offspring fitness function equals the slope of the cost function for each parent (Lessells 2002). For the parameters used here (with a brood size of $n = 4$ and relatedness $r_m = r_f$) the ESS values can be calculated from equations (7a) and (7b) as $y^* = 0.32$, $Y_m = 0.81$, $Y_f = 0.47$.

feeding. We further partition the short-term costs into two alternative fitness routes through a second pair of constants that scale the relative costs of investing in the focal brood (to which food deliveries are made, etc.) versus pursuing extrapair reproduction. Simply, h_m and h_f affect the magnitude of each sex's cost curve in terms of the extrapair fitness a parent could obtain if he/she did not feed the current brood. For clarity, we refer to a and b as the 'depletion-cost constants' (i.e. how parent's condition causes its foraging costs to escalate), and to h_m and h_f as the 'opportunity-cost constants' (i.e. how foraging time is scaled in terms of time pursuing extrapair reproduction).

The intergenerational battleground can now be defined. Substituting (5) and (6) into (2) for the parents, and calling $Q = (abn + ac + bc)$, we obtain the ideal food levels for
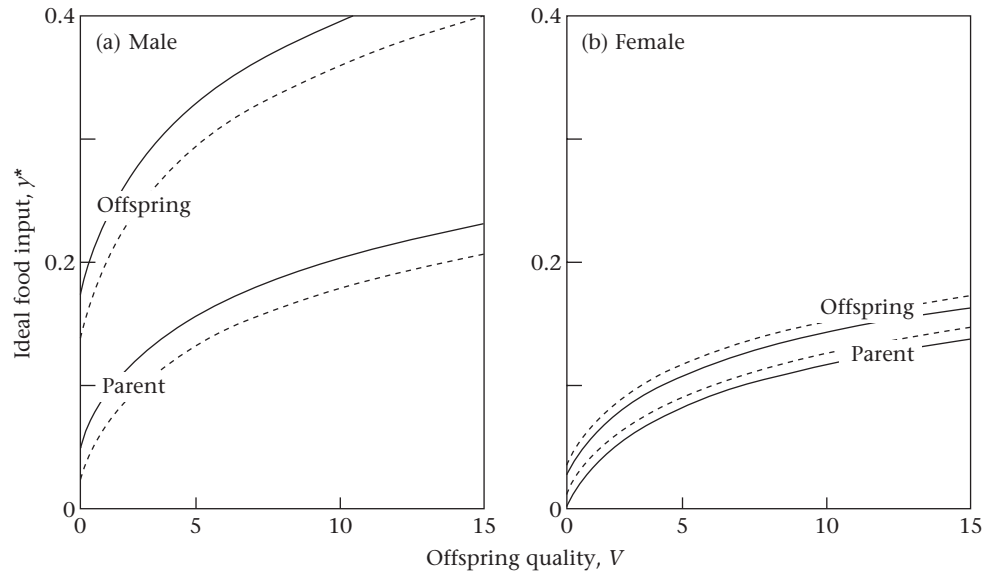
Figure 3. The parent–offspring battleground in relation to offspring quality, V. Broken curves are for $p = 0$ (i.e. the male opportunity-cost scaling h_m is inversely related to r_m) and continuous curves are for $p = 1$ (i.e. $h_m = h_f$). Parameters are $a = 1.5$, $b = 2$, $c = 5$, $r_m = 0.4$, $r_f = 0.5$, $n = 4$, $k = 1$. (a) Ideal evolutionarily stable strategy, ESS, food inputs for the male to supply per chick (lower two curves), and for each chick to demand from him (upper two curves) in relation to increasing quality, V, of the current offspring. (b) Ideal ESS food inputs for the female to supply per chick (lower two curves), and for each chick to demand from her (upper two curves) in relation to increasing quality, V, of the current offspring.

each parent as

$$y_m^* = \frac{1}{Q}\left[b\ln\left(\frac{Vc}{h_m a}\right) - \frac{c}{n}\ln\left(\frac{h_m a}{h_f b}\right) \right] \text{ for the male;} \quad (7a)$$

$$y_f^* = \frac{1}{Q}\left[a\ln\left(\frac{Vc}{h_f b}\right) - \frac{c}{n}\ln\left(\frac{h_f b}{h_m a}\right) \right] \text{ for the female;} \quad (7b)$$

and substituting (5) and (6) into (4) gives the ideal food levels for the offspring

$$y_m^* = \frac{1}{Q}\left[b\ln\left(\frac{Vc}{r_m h_m a}\right) - \frac{c}{n}\ln\left(\frac{r_m h_m a}{r_f h_f b}\right) \right] \text{ from its father;}$$
$$(8a)$$

$$y_f^* = \frac{1}{Q}\left[a\ln\left(\frac{Vc}{r_f h_f b}\right) - \frac{c}{n}\ln\left(\frac{r_f h_f b}{r_m h_m a}\right) \right] \text{ from its mother.} \quad (8b)$$

Consider again the cost function, $g(y)$ for parents (equations 6a, 6b). Recall that depletion-cost constants a and b change the relative shape of each parent's cost curve (and that the female's is steeper: Fig. 2a), whereas the opportunity-cost constants h_m and h_f scale the overall cost's magnitude. For a female, if egg dumping is negligible, all provisioning effort goes to her own offspring. For a male, however, there is likely to be a negative relationship between r_m and EPF availability. The lower the average r_m of males to offspring in the broods they provision, the more EPF opportunities exist in the population. If provisioning offspring and searching for extrapair matings are mutually exclusive

activities, the male's opportunity-cost scaling constant (h_m) will be inversely associated with average local male relatedness to current broods. For example, if $r_m = 0.25$, this implies that males have equal prospects of gaining offspring in nests other than their own, and hence the value of time spent seeking such matings (i.e. the opportunity costs of provisioning) would be double that applying if $r_m = 0.5$.

A rigorous approach to the relation between the parameters h_m and r_m is complex, and for simplicity we assume an inverse relation between h and r so that

$$h_m r_m \phi = h_f r_f = k, \quad (9)$$

in which $\phi = (r_f/r_m)^p$, where p $(1 \geq p \geq 0)$ defines the strength of the male's opportunity costs of provisioning the present brood, in terms of missed EPFs. Note that k is a baseline measure of how time-consuming it is for parents to obtain food: as such it can be thought of as an index of habitat quality (see below).

The sex differences in opportunity-cost constants (h_m and h_f) are greatest at the limit where $p = 0$, representing the case where male provisioning of the present brood and searching for EPFs are mutually exclusive activities. When $p = 0$, $\phi = 1$, and so $h_m r_m = h_f r_f = k$ in equations (8a) and (8b), and thus the effect of asymmetric relatedness between offspring and the two provisioning parents effectively cancels out from the offspring's ideal strategies. From equation (9), the parents have equal scaling factors ($h_m = h_f$) only when the male is the father of the entire brood ($r_m = r_f = 0.5$). As shown above, when the male is the father of less than that, his time spent provisioning is proportionately more expensive (because of potential EPFs he forfeits) than that of the female. Thus, benefits to offspring of extracting more from the male (because

$r_m < r_f$) are counterbalanced by the fact that they lose extrapair paternal half-siblings.

Opportunity costs are lowest at the opposite limit ($p = 1$), where provisioning the current brood does not interfere at all with a male's ability to seek EPFs. Equation (9) then generates equal opportunity-cost scaling for each parent ($h_m = h_f$), whatever the level of EPFs (i.e. for all $r_m \leq r_f$).

Applying (9) gives the optima for the parents as

$$y_m^* = \frac{1}{Q}\left[b\ln\left(\frac{Vcr_m\phi}{ka}\right) - \frac{c}{n}\ln\left(\frac{r_f a}{r_m \phi b}\right)\right] \quad \text{for the male,} \quad (10a)$$

$$y_f^* = \frac{1}{Q}\left[a\ln\left(\frac{Vcr_f}{kb}\right) - \frac{c}{n}\ln\left(\frac{r_m \phi b}{r_f a}\right)\right] \quad \text{for the female,} \quad (10b)$$

and for the offspring as

$$y_m^* = \frac{1}{Q}\left[b\ln\left(\frac{Vc\phi}{ka}\right) - \frac{c}{n}\ln\left(\frac{a}{\phi b}\right)\right] \quad \text{from its father,} \quad (11a)$$

$$y_f^* = \frac{1}{Q}\left[a\ln\left(\frac{Vc}{kb}\right) - \frac{c}{n}\ln\left(\frac{\phi b}{a}\right)\right] \quad \text{from its mother.} \quad (11b)$$

The above four equations (10–11) are used to define the parent–offspring battleground (see Figs 3, 4). In our house sparrow population the average relatedness between the female provider and the offspring, r_f, can be approximated

to 0.5 since there is a very low incidence of egg dumping (less than 2%). Modal brood size, n, is 4. The probability of extrapair fertilizations, however, is not trivial (Whitekiller et al. 2000), and we estimate the average relatedness between the male provider and offspring in his nest, r_m, as ≈ 0.40.

Figure 3 shows how sexual conflict and parent–offspring conflict relate to the quality, V, of offspring in the current brood. The male's depletion-cost constant for provisioning (a) is fixed, so that changing V in equation 5 affects the value of the current brood in relation to the expected value of future broods. The ideal parental allocations increase for both male and female parent with rising V (comparison of parental curves in Fig. 3a and 3b), but because the depletion costs escalate more steeply for the female ($b > a$), the male ideally supplies more food to each offspring than the female, a difference that enlarges with V. The difference in optimal allocation for the two parents is less if, for the male, reduced relatedness means increased opportunity costs, since the male is then constrained to give less to the offspring, meaning that the female is pushed into giving more. (Throughout Figs 3 and 4, changing p from 1 (no opportunity cost) to 0 (high opportunity cost) decreases the ESS input from the male, and increases ESS input from the female.) If we look at the offspring's ideal allocation, these effects become magnified: the offspring would 'prefer' to take much higher food amounts from the male provider than from the female, because of both parental asymmetries (unequal depletion costs and relatedness to brood).

For the present experiments, we are most interested in how the difference between the ideal allocations of the two parents increases with V (because V is what we sought
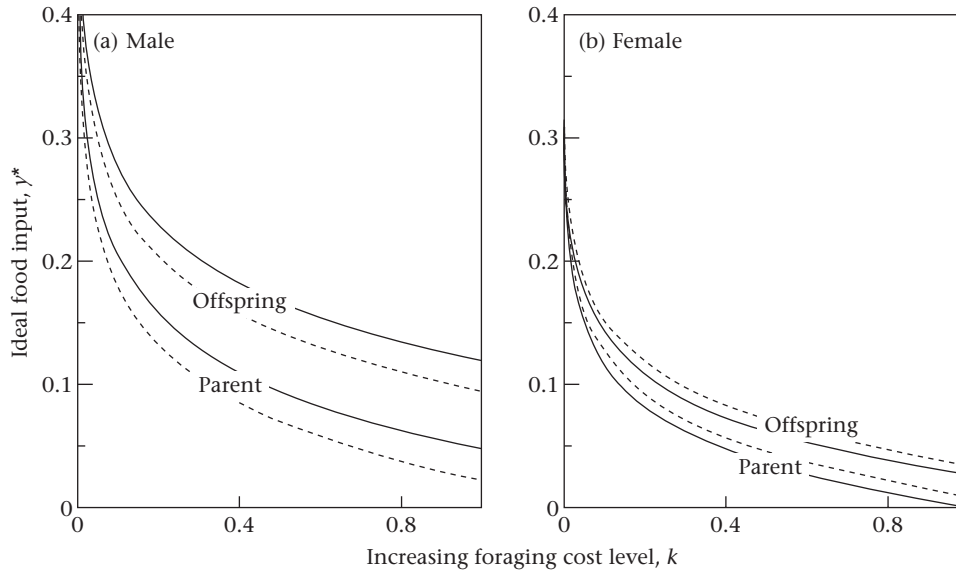

Figure 4. Parent–offspring battleground in relation to parental foraging costs, k (i.e. habitat quality). The habitat is richest when k is least (i.e. where the time costs of provisioning are minimal). As before, broken curves are for $p = 0$ (i.e. the male cost scaling h_m is inversely related to r_m) and continuous curves are for $p = 1$ (i.e. $h_m = h_f$). Parameters are $a = 1.5$, $b = 2$, $c = 5$, $r_m = 0.4$, $r_f = 0.5$, $n = 4$, $V = 1$. (a) Ideal evolutionarily stable strategy, ESS, food inputs for the male to supply per chick (lower two curves), and for each chick to demand from him (upper two curves) in relation to increasing foraging costs, k. (b) Ideal ESS food inputs for the female to supply per chick (lower two curves), and for each chick to demand from her (upper two curves) in relation to increasing foraging costs, k.
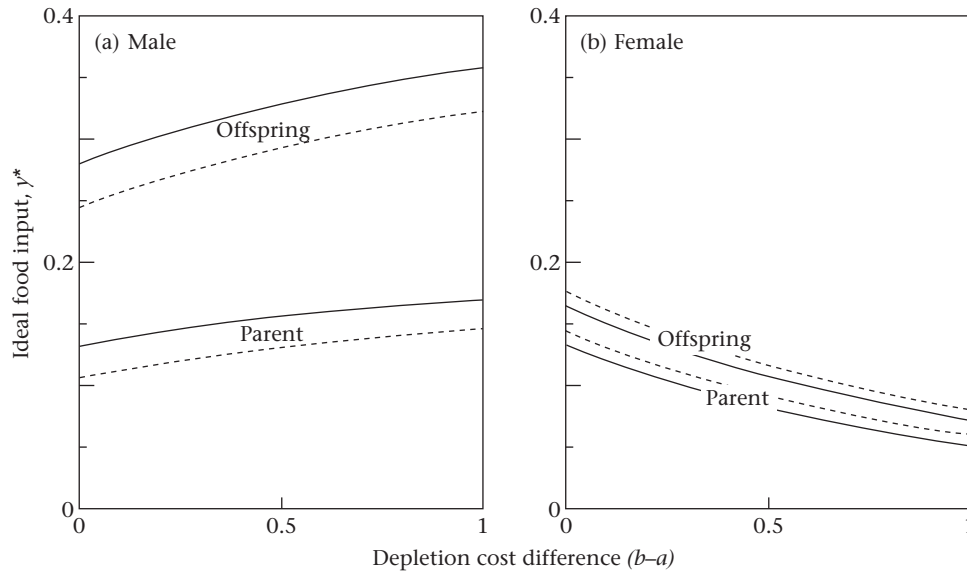
Figure 5. The parent–offspring battleground in relation to the difference between parents' depletion costs: female constant b minus male constant a. Broken curves are for $p = 0$ (i.e. the male opportunity-cost scaling h_m is inversely related to r_m) and continuous curves are for $p = 1$ (i.e. $h_m = h_f$). Parameters are $a = 1.5$, $V = 5$, $c = 5$, $r_m = 0.4$, $r_f = 0.5$, $n = 4$, $k = 1$. (a) Ideal evolutionarily stable strategy, ESS, food inputs for the male to supply per chick (lower two curves), and for each chick to demand from him (upper two curves) in relation to the difference between the parental depletion cost constants. (b) Ideal ESS food inputs for the female to supply per chick (lower two curves), and for each chick to demand from her (upper two curves) in relation to the difference between the parental depletion cost constants.

to manipulate). The offspring presumably 'knows' that it received extra nutrients, which should not affect its perception of its own quality. A parent is perhaps more likely to misjudge offspring quality if it measures nestling growth in relation to the parentally delivered input of food: essentially, the offspring has grown better than expected (because it has been supplemented without parental participation). Figure 3 supports the notion that, for a given increase in V, the male parent should escalate food deliveries more sharply than the female, provided that his foraging costs, g_m, climb less steeply than hers, mainly due to his lower depletion-cost constant ($a < b$). This, in turn, offers a testable (but untested) prediction: if our reasoning is correct, then the observed escalation of male deliveries must hinge on lower overall foraging costs for that parent.

Sexual conflict and parent–offspring conflict also relate to the way that opportunity costs change for the two sexes (Fig. 4). As k, our indirect expression of local habitat quality, increases, the time required to fetch each food item lengthens, pulling the foraging opportunity costs up with it. For the present experiments, we are most interested in how the offspring should view the optimal division of labour (vis-à-vis food deliveries) between the two parents as a function of habitat richness (here, k). Suppose that the quality of the habitat improves (i.e. k decreases by some increment). If an offspring interprets increased food input as indicating higher habitat quality, then it would be best served by increasing its absolute demand from its male parent more than that from its female parent (compare the offspring curves in Fig. 4a with those of Fig. 4b): it 'wants' its male provider to be the main donor of the increased provisioning, and especially so when relatedness between the male and

offspring does not affect the male's opportunity costs (i.e. if $p = 1$).

Thus, both of the model's predicted effects of food supplementation (parents assessing offspring as having higher quality; offspring assessing the environment as having higher quality) could account for the experimental results observed.

These effects are relatively insensitive to assumptions about the difference in depletion-cost constants between male and female parents (Fig. 2b), provided that these are sufficiently greater for the female than the male (for Figs 3, 4, $a = 1.5$, $b = 2.0$). Figure 5 shows how the ideal food inputs vary with the difference between depletion-cost constants ($b - a$), by raising the female's constant b above the male's level of $a = 1.5$, with other parameters fixed. The offspring's ideal food input from the male parent is much greater than the male is selected to supply at all ($b - a$) values shown in Fig. 5a. The disparity between parent and offspring ideals is much lower from the female perspective (Fig. 5b), because of the higher relatedness between the female and offspring. Provided that the difference between depletion-cost constants is sufficiently large, the male's ideal food input level is greater than the female's, and increasingly so as the difference between them increases. However, at sufficiently small positive difference values, the female may ideally supply more food than the male, especially when $p = 0$. In the example shown in Fig. 5, when $p = 0$, the depletion-cost difference in ideal food inputs for the male and the female are equal at 0, but when $p = 1$, they are equal at 0.2. So, if the male sustains only slightly lower depletion costs than the female, he may be selected to supply less food than the female if feeding the present brood increases his opportunity costs in terms of extrapair fertilizations ($p = 0$).

The evidence for sparrows suggests a relatively high depletion-cost difference between the sexes. In free-living North American house sparrows, for example, female body mass and fat deposits decline during the nestling feeding phase (see Figure 2 in Hegner & Wingfield 1986a), whereas male mass and fat scores show no similar, or even consistent, patterns (see Figure 2 in Hegner & Wingfield 1986b).

Conclusions

In house sparrows, at least, the primary behavioural effect on parents of unexpectedly high nestling condition is a substantial acceleration of the male's delivery rate. The logic explored by our ESS model indicates that such responses could stem from how the experimental manipulation was (mis)interpreted by the parental and/or the offspring generations within the nuclear family, mediated through asymmetries between the two parents' capacities for further investment and genetic relatedness to the progeny. Several earlier studies have shown unequal feeding strategies by male and female parents (e.g. Gottlander 1987; Stamps et al. 1989; Christe et al. 1996). For example, superb fairy-wren, *Malurus cyaneus*, females normally increase nest visits to broods that are enlarged or contain older nestlings, whereas male visits remain constant across these variations; but if offspring vocal begging signals are exaggerated experimentally (via additional playbacks), the males then respond positively, but not the females (MacGregor & Cockburn 2002). These and other studies suggest that the two sexes may often operate on different cues emanating from offspring. Nevertheless, differences in male and female investment decisions are most commonly attributed to the lower mean relatedness of males to their broods and/or to broader male opportunities for extrapair fertilizations (e.g. Whittingham et al. 1992; Westneat & Sherman 1993; Whittingham & Dunn 2001), with scant consideration to how the sexes differ in residual parental effort (Dawkins & Carlisle 1976), or to offspring interests. At this point, we have only a slight indication that supplemented broods increased the magnitude of their begging signals to parents, and thus we cannot distinguish between the mechanisms of offspring signals or parental responses, as outlined in this model. If offspring in unusually good condition do intensify their begging activities, that would seem to be at odds with the view that such signals are 'honest' indications of neediness (Godfray 1991; Kilner & Johnstone 1997; Wright & Leonard 2002), but more in keeping with the alternative models of begging as a form of scramble competition (Parker et al. 2002; Royle et al. 2002).

Acknowledgments

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