The manipulation of food resources reveals sex-specific trade-offs between parental self-feeding and offspring care

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Parent Palestine sunbirds (*Nectarinia osea*) feed on flower nectar that is not fed to their nestlings. This phenomenon provided a unique opportunity to manipulate self-feeding rates of parent birds independently of the rate at which they feed arthropod prey to their offspring. Based on provisioning models, we predicted that parents would invest more in their young as the energy content of their own food increased. From our earlier work, we also predicted that the levels of sex-specific activities of males and females would differ as the energy content of their food increased. Sunbird pairs with two or three nestlings were provided with feeders containing a low-, medium- or high-concentration sucrose solution. As the sugar concentration increased, the females delivered arthropods at a greater rate to their nestlings, removed proportionally more faecal sacs and spent longer at the nest, while the males increased their mobbing effort. Nestling food intake and body mass, but not tarsus length or bill size, were larger in small broods than in large broods, and increased with increasing feeder sugar concentration. These results imply that increasing the energy content of food consumed by parent sunbirds allows them to increase the rate at which other foods are delivered to their young and to increase other parental care activities as well. The results also add credence to the idea that behavioural decisions reflect life-history trade-offs between parental self-feeding and investment in current young.

Keywords: parental care; nestling feeding; mobbing; cost of reproduction; sunbirds; life history

1. INTRODUCTION

An important life-history question concerns the trade-off between parental investment in current young and surviving to invest in future young (Williams 1966; Charnov & Krebs 1974; Stearns 1976; Ricklefs 1977; Calow 1979). One manifestation of this trade-off is the parental allocation of food between self and offspring (Kacelnik & Cuthill 1990). This is because any benefits gained from feeding the current young must be traded off against the parent's need to maintain its own body condition and to survive for future breeding attempts (see reviews in Reznick 1985; Partridge & Harvey 1985, 1988; Nur 1988), or retain future fecundity (Gustafsson & Part 1990). Parental allocation of resources should therefore evolve as an optimal balance between present and future reproductive investment to maximize lifetime reproductive success (Kacelnik & Cuthill 1990). In partial support of this idea, Antarctic petrel (*Thalassoica antarctica*) parents were shown to adjust the amount of food delivered to their current chick according to both the chick's needs and their own body condition, which will allow the parents to maximize their chances to survive for future breeding bouts (Tveraa *et al.* 1998).

The amount of food allocated to the nestlings is not simply a function of food available after the parent has eaten. It also depends critically upon the discretionary energy gained by the parent that can be dedicated to pro-

visioning young (Houston 1987; Ydenberg 1994, 1998; Ydenberg *et al.* 1994).

Several studies have shown that single-prey-loading parents selectively transport large prey to their nestlings, while they themselves eat smaller prey (Carlson 1985; Krebs & Avery 1985; Sonnerud 1989), as predicted by optimal foraging theory (Stephens & Krebs 1986). This may lead to different ranges of prey types being consumed by parents and nestlings, which has consequences for both the foraging and resource allocation decisions made by parent birds. To determine the effect of food consumed only by the parent upon its provisioning rates, one needs to manipulate experimentally parental self-feeding independently of nestling provisioning. The effects of self-feeding on parental activities have yet to be tested, probably because in most bird species the provisioning parent often eats and delivers the same food type (Ydenberg 1994), which makes it difficult to control these two activities independently.

A recent model that deals with the provisioning of young was based on the assumption that the forager has one set of foraging options associated with feeding itself ('self-feeding') and another set of foraging options associated with provisioning the young (McNamara & Houston 1997). For example, in the case of a parent bird feeding its young, the parent may go to one location to look for one prey type to bring back to the young (i.e. the so-called provisioning option), and may go to another location to look for other items to eat (i.e. the so-called self-feeding option). A central prediction of this model is that, as the net energy gained while self-feeding increases, the parent

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will maximize its rate of food delivery to the young. To test this prediction empirically, and to examine earlier provisioning models that also made this prediction (Houston 1987, 1995; Kacelnik & Cuthill 1990; Ydenberg 1994; Ydenberg *et al.* 1994), we used a system in which the food eaten by parent birds is in part different from that eaten by their young.

We recently demonstrated that adult Palestine sunbirds (*Nectarinia osea*) feed on flower nectar and arthropods, but feed only arthropod prey to their young (Markman *et al.* 1999). Thus, nectar is eaten exclusively by parent Palestine sunbirds. This example of food-type separation between parent and nestling birds allowed us to test the effect of self-feeding on food delivery to the young as well as on other parental activities. In this study, we investigated the parental care responses of monogamous Palestine sunbird pairs with different brood sizes to experimental manipulation of their food energy content. We hypothesized that the level of parental care invested in their current brood will depend upon the quality of the food available to the parents and thus on their self-feeding rates; parents should invest more in their young as the energy content of their own food increases. We further hypothesized that males and females would differ in how their parental care levels change as the energy content of their food increases in accordance with their sex-specific roles. This is based on the assumption that each sex will tend to invest more in the activity that it performs more efficiently or that it is more predisposed to perform. For example, Markman *et al.* (1995, 1996) showed that male sunbirds participate more in anti-predator behaviour, while females are more involved in feeding young. Therefore, we predicted that as the energy content of parent food increases:

- (i) males will increase their mobbing effort more than females; and
- (ii) females will increase their food delivery rate to young more than males, and will also increase the time spent at the nest and performing nest sanitation.

We quantified the effects of parental behaviour upon nestling growth by daily measurements of mass, tarsus length and bill length.

2. MATERIAL AND METHODS

(a) *Study species*

The Palestine sunbird is a small (6–7 g) passerine that rears its young in hanging nests of woven grass, leaves, hair and spider webs (Harrison 1975). In Israel, it breeds in natural habitats from open woody areas to dry wadis in the desert, but also in areas of human habitation where introduced flowering plants make nectar readily available. Sunbirds are territorial, monogamous and multiple brooded in any one season (Goldstein & Yom-Tov 1988). We studied this species during the 1996 breeding season in the Sede Boqer area in the Central Negev Desert (31°02' N, 34°46' E, 475 m above sea level), Israel.

(b) *Experimental procedure*

Before the experiments, we captured and colour ringed the adult sunbirds in the study area to allow individual identification.

All pairs used were feeding their first successful brood of the season. The nests contained naturally sized broods of two or three nestlings, with no hatching failures (i.e. the brood sizes equalled the clutch sizes).

We used artificial feeders to manipulate the parental food supply. A feeder was placed consistently near each nest as a permanent food source. We manipulated the birds' energy intake by filling the feeders with solutions of different concentrations of sucrose.

The feeders were hung *ca.* 5 m from each nest to enable simultaneous observation of both the nest and its associated feeder. To attract birds to feeders and to habituate them to their use, we initially filled all feeders with the same high-concentration sucrose solution (1.25 mol kg⁻¹). The feeders were presented in all territories 3 days before the nestlings were expected to hatch, and until the nestlings were 6 days old.

On day 7, we randomly assigned pairs to one of three treatment groups (i.e. feeder sucrose concentration) within the two natural brood sizes as follows:

- (i) low concentration—0.25 mol kg⁻¹;
- (ii) medium concentration—0.75 mol kg⁻¹;
- (iii) high concentration—1.25 mol kg⁻¹.

The selected sucrose concentrations are within the range of concentrations that Palestine sunbirds consume in nature (Nahari 1980). To measure the amount of sucrose solution that the birds consumed from the feeders, next to each one we placed an inaccessible control feeder, and used it to calculate the effects of evaporation and spillage. Both accessible and inaccessible feeders were weighed (± 0.01) before and after each observation session. All the feeders used in this experiment were maintained full, and contained much larger amounts of food than could be consumed by the parent sunbirds in a day. The experimental protocol spawned six sugar concentration and brood-size combinations. We used 36 sunbird pairs in total with six pairs in each of the six treatment groups. We provided the designated sugar solutions to these pairs until the nestlings were 13 days old.

(c) *Data collection*

Each pair was observed for 1 h per day between 08.00 and 14.00 with the aid of 7 × 50 binoculars. We recorded the time that was spent feeding at the feeder, the amounts consumed from the feeder, parental visitation rate (and assumed that the visitation rate is equivalent to nestling feeding rate), the time that was spent at the nest (but not including time that was spent brooding), the number of faecal sacs removed and the time that was spent mobbing. Mobbing times were recorded as the mean time (in seconds) that individuals approached and made their particular 'mobbing call' at any potential predator that came within 5 m of the nest. Some nest sites may have been more prone than others to the types of natural nest disturbances measured here, thereby eliciting a greater mobbing effort from those parents. However, these differences should be unbiased because of the random assignment of the experimental groups. This was confirmed by the lack of any significant difference in the time of disturbance caused by potential predators between the experimental feeder groups ($F_{2,30} = 0.346$, $p = 0.710$) or between the brood sizes ($F_{1,30} = 0.311$, $p = 0.581$), and in the lack of any interaction term between disturbance time in the experimental feeder groups and brood sizes ($F_{2,30} = 1.169$, $p = 0.324$).

The order of observation was rotated every day, balancing any time-of-day effects. The random and alternate assignment of

Table 1. The effects of the experimental feeder sugar concentration (sucrose), brood size (brood) and parental sex (sex) in Palestine sunbirds on (a) the mean time that was spent feeding at a feeder per hour, and (b) the mean volume of sugar solution consumed per hour.

(The results of the ANOVA models are presented with d.f., MS, *F*-ratios and *p*-values.)

source	d.f.	MS	<i>F</i>	<i>p</i>
(a) time spent feeding				
sucrose	2	37960.18	30.26	< 0.001
brood	1	696.89	0.56	0.459
sex	1	50.00	0.04	0.842
sucrose × brood	2	4.35	0.00	0.996
sucrose × sex	2	198.04	0.16	0.854
brood × sex	1	272.22	0.21	0.643
sucrose × brood × sex	2	425.93	0.33	0.712
error	60	1254.39		
(b) volume consumed				
sucrose	2	9.26	77.80	< 0.001
brood	1	0.35	2.99	0.088
sex	1	0.04	0.33	0.566
sucrose × brood	2	0.00	0.06	0.938
sucrose × sex	2	0.06	0.50	0.610
brood × sex	1	0.04	0.33	0.566
sucrose × brood × sex	2	8.42	1.15	0.325
error	60	0.11		

pairs also meant that any differences between observation days, caused by time of year (day length) or differences in the weather, would be balanced across the experimental and brood-size groups. This was confirmed by the lack of any significant difference in hatching dates between experimental feeder groups ($F_{2,30} = 0.006$, $p = 0.994$) or between brood sizes ($F_{1,30} = 0.071$, $p = 0.792$), and in the lack of any interaction between hatching dates in the experimental feeder groups and brood sizes ($F_{2,30} = 0.001$, $p = 0.999$).

All nestlings were weighed daily (usually between 14.00 and 16.00) to ± 0.01 g with an electronic field balance (Ohaus, Model CT200). The lengths of the tarsus (from the joint between tibia and tarsus to the first joint of the toes) and bill (from the tip of the bill to the rear end of the nostrils) were measured to the nearest 0.1 mm using Vernier calipers.

All data were collected daily for each nest from nestlings aged 7–13 days. Data were not collected after this, because nestlings older than 13 days usually do not gain mass and are also too mature to handle without causing premature fledging.

(d) Statistical analysis

Prior to analysis, data were reduced to single parameter estimates (i.e. means) for each parent or nest. To estimate the effects of experimental feeder or brood size on variables such as nest visitation rate, the unit for analysis was the mean number of visits per hour for each bird. In the case of the proportion of visits in which faecal sacs were removed from the nest, the data were normalized using an arcsine-square-root transformation, and these were then subjected to the same ANOVA with respect to the experimental feeder, brood size and parental sex. ANOVA was also used to test the effects of experimental feeder and brood-size groups on nestling growth variables, but here each brood served as a unit of analysis.

For the ANOVAs where particular between-treatment group comparisons were of interest (e.g. males that were rearing three nestlings and feeding on a high sugar concentration compared with males that were rearing two nestlings and feeding on a low

sugar concentration), we present the results of Tukey HSD pairwise comparisons (Sokal & Rohlf 1981; SYSTAT v. 7 1997).

3. RESULTS

(a) Feeder use

As the sucrose concentration in the feeder increased, the parents spent significantly more time feeding at the feeder and consumed more of the solution (table 1). However, there were no significant differences between males and females nor between parents rearing different brood sizes in the time that was spent feeding, or the amounts consumed from the feeder (table 1).

(b) Levels of parental care

Experimental feeder manipulation had a significant effect on the parental visitation rate (table 2a). Both females and males increased their visitation rates to the nest as the sugar concentration increased (figure 1a). Thus, the effect of the manipulation was to create different levels of parental self-feeding in terms of energy intake or time that was spent feeding. By increasing the energy intake from the feeders or changing the overall time that was spent self-feeding, we allowed parents to invest more in providing arthropods to their young.

There were significant effects of parental sex and brood size on the parental visitation rates (table 2a). The females had significantly higher visitation rates than the males (figure 1a). The greater number of visits to the larger broods was caused mainly by an increase in the male visitation rate, as indicated by the significant interaction term for brood size by parental sex (table 2a, figure 1a).

The males and females differed in how the sugar concentration affected their food delivery rate, as indicated by the significant interaction term for experimental feeder by parental sex (table 2a). As the sugar concentration increased, the delivery rate of arthropods to nestlings

Table 2. The effects of the experimental feeder sugar concentration (sucrose), brood size (brood) and parental sex (sex) in Palestine sunbirds on (a) mean parental visits per hour; (b) mean time that was spent at the nest per parental visit; (c) mean proportion of visits in which a faecal sac was removed; and (d) mean time that was spent mobbing near the nest per hour. (The results of the ANOVA models are presented with d.f., MS, *F*-ratios and *p*-values.)

source	d.f.	MS	<i>F</i>	<i>p</i>
(a) parental visitation rates				
sucrose	2	0.88	47.43	< 0.001
brood	1	0.55	29.61	< 0.001
sex	1	1.75	93.90	< 0.001
sucrose × brood	2	0.02	1.20	0.307
sucrose × sex	2	0.06	3.30	0.045
brood × sex	1	0.12	6.48	0.013
sucrose × brood × sex	2	0.03	1.90	0.159
error	60	0.01		
(b) time spent at the nest				
sucrose	2	44.48	6.05	0.004
brood	1	127.62	17.35	< 0.001
sex	1	1561.34	212.29	< 0.001
sucrose × brood	2	8.94	1.22	0.304
sucrose × sex	2	276.40	37.58	< 0.001
brood × sex	1	7.53	1.02	0.316
sucrose × brood × sex	2	8.42	1.15	0.325
error	60	7.35		
(c) faecal sac removal				
sucrose	2	0.02	11.75	< 0.001
brood	1	0.02	11.69	0.001
sex	1	0.35	183.80	< 0.001
sucrose × brood	2	0.00	0.85	0.432
sucrose × sex	2	0.00	3.28	0.045
brood × sex	1	0.01	5.54	0.022
sucrose × brood × sex	2	0.00	0.80	0.452
error	60	0.00		
(d) time spent mobbing				
sucrose	2	8180.40	33.31	< 0.001
brood	1	1597.82	6.50	0.013
sex	1	96682.49	393.70	< 0.001
sucrose × brood	2	443.31	1.81	0.173
sucrose × sex	2	6975.96	28.41	< 0.001
brood × sex	1	865.58	3.53	0.065
sucrose × brood × sex	2	240.69	0.98	0.381
error	60	245.57		

increased at a greater rate in the females than in the males. In addition, the males that reared broods of three nestlings and fed on the medium sugar concentration had a delivery rate similar to that of the males that reared three nestlings and fed on high sugar concentration (figure 1*a*; Tukey HSD-test, n.s.). The non-significant interaction term for experimental feeder by brood size suggests that there was no difference in the general trend of the food delivery rates between the two brood-size groups as the sugar concentration increased.

The females spent significantly more time at the nest than the males (figure 1*b*, table 2*b*). Furthermore, the time that the females spent at the nest increased as the sugar concentration in the feeder increased, with the opposite response in the males. This resulted in a significant interaction term for parental sex by experimental feeder (table 2*b*). However, both females and males spent longer at the nest when feeding larger broods (figure 1*b*).

Females removed faecal sacs more often than males (figure 1*c*, table 2*c*), and they increased the proportion of

visits to the nest in which faecal sacs were removed as the sugar concentration increased. Males did not do this, as indicated by the significant interaction term for parental sex by experimental feeder. There was also a significant interaction term for parental sex and brood size because females increased the proportion of visits in which the faecal sacs were removed, especially from the larger broods, and males did not.

Parental sex and experimental feeder both affected mobbing effort, and the time that the males spent mobbing was significantly greater than that for the females (figure 1*d*, table 2*d*). As predicted, the males were more involved in mobbing activity than the females, and they increased their mobbing time with increasing feeder sugar concentration (figure 1*d*), while the females did not, as implied by the significant interaction term for parental sex by experimental feeder (table 2*d*). There was also a significant effect of brood size on mobbing time, with more mobbing effort for larger broods (table 2*d*).

Figure 1. Relationships between parental care by Palestine sunbirds and sucrose concentration in artificial feeders, brood size and parental sex (white areas, males; hatched areas, females). The experimental period was for days 7–13 of nestling age; the feeder sucrose concentrations were: low, 0.25 mol kg⁻¹; medium, 0.75 mol kg⁻¹; and high, 1.25 mol kg⁻¹; the brood size was two or three. Overall means ($\pm$ s.e.) are given for (a) parental visits per hour; (b) time that was spent at the nest per parental visit; (c) proportion of visits in which a faecal sac was removed; and (d) time that was spent mobbing near the nest per hour.

(c) Parental visits per nestling

After examining parental visits from the point of view of parental care behavioural strategies, we tested for differences in the number of parental visits received per nestling and found that it increased significantly with increasing sugar concentration in the feeders (figure 2a, table 3a). Although the total number of visits to the larger broods was higher than to the smaller broods, the number of visits per nestling was significantly less in broods of three than in broods of two (figure 2a, table 3a). In addition, there was no significant difference in the number of visits per nestling in broods of three, when parents fed on the high sugar concentration, than in broods of two, when parents fed on the low sugar concentration (Tukey HSD-test, n.s.).

(d) Nestling body mass and body size

The growth rate of the nestlings was directly related to the level of care per nestling. Mean nestling mass attained at 13 days of age increased as the sugar concentration in feeders increased (figure 2b, table 3b). The mean nestling mass at 13 days of age in broods of two was significantly higher than those of broods of three. The fact that broods of three nestlings, whose parents fed on the high concen-

tration sugar solution, received the same number of parental visits as broods of two, whose parents fed on low sugar concentration, resulted in nestlings of both these groups attaining similar maximum mass (Tukey HSD-test, n.s.).

Neither the maximum bill and tarsus lengths attained at 13 days of age were affected by sugar concentration nor by brood size (table 3c,d), although there was a significant brood-size effect, with nestlings of smaller broods having greater tarsus lengths on average (table 3d).

4. DISCUSSION

As the sucrose concentration in the feeders increased, both parents consumed significantly more of the solution. This meant that parents who were offered higher sucrose concentrations, in fact obtained more energy from the feeders. In response to artificial manipulation of their available dietary sugar, parent sunbirds provisioned their young at rates proportional to their own energy intake from the feeders. In general, the increase in provisioning rate with the increase in concentration of the sugar solution that was available for self-feeding agrees with the predictions of the theoretical models of the food-allocation

Figure 2. Relationships between (a) parental care and (b) nestling growth in Palestine sunbirds and sugar concentration in artificial feeders and brood size. The feeder sucrose concentrations were: low, 0.25 mol kg^{-1} ; medium, 0.75 mol kg^{-1} ; and high, 1.25 mol kg^{-1} ; the brood size was two or three. Overall means ($\pm$ s.e.) are given for: (a) parental visits per nestling per hour and (b) mean nestling mass at the end of the manipulation (when nestlings were 13 days old).

decisions (Kacelnik & Cuthill 1990; Beauchamp *et al.* 1991). Kacelnik & Cuthill (1990) and Beauchamp *et al.* (1991) predicted that parents would allocate the food they find between themselves and their young based upon maximizing their lifetime reproductive success. This means that parents should allocate food to their current young in a manner that will allow them to maintain their own body condition and to survive for future reproductive attempts. The present study confirms that parents that consume higher-quality food or feed themselves more efficiently should have more energy and time to invest in feeding their nestlings.

By contrast, provisioning models (Houston 1987, 1995; Ydenberg 1994; Ydenberg *et al.* 1994; McNamara &

Houston 1997) do not use the long-term calculation of lifetime reproductive success. Much more in line with the findings of the present study, these models predict that, as net energy gain from self-feeding in the parents increases, energy delivery to the chicks will also increase. However, we do not know how the increased feeder sugar concentrations actually resulted in greater parental deliveries of arthropod prey to the nestlings. Self-feeding from the feeders may have saved the parents' time, or increased their total daily energy intake, or both. The parent birds in our experiments also consumed floral nectar and some arthropod prey. Thus, it is possible that the different sugar concentrations in the feeders allowed parents variable levels of time or energy saving, while not affecting their total daily energy intake. It is also possible that the parents spent the same overall time self-feeding in all three treatment groups. Therefore, the overall energy intake, both from the feeders and the floral nectar, of the parents was higher if they were feeding on higher sugar concentrations from the feeders. Thus, the feeders may have saved parents both time and energy, and possibly increased their total daily energy intake.

In this study, we manipulated the parents' energy source without affecting the amount of arthropods that was available for the nestlings. As arthropods could also serve as an energy source for parents, the parents that were fed higher sugar concentrations might not have needed to consume as many arthropods to fulfil their energy requirements. Therefore, these parents may have allocated a higher proportion of arthropods that they captured to their young than to themselves, indicating that we might have indirectly influenced the quantity of arthropods available to the nestlings.

Our data show that, principally, the sunbird female cared for the nestlings, at least in terms of provisioning activity, removal of faecal sacs and time that was spent at the nest. This was also found to be the case in a non-desert population of sunbirds previously investigated by Markman *et al.* (1995, 1996). When females had access to high-energy foods for themselves, they tended to use this extra energy and time for greater delivery rates of food to their young, to spend more time at the nest and to increase the proportion of faecal sacs removed. By contrast, males supplied with high-concentration sugar solution showed smaller increases in their provisioning rate than their mates. As a result, males that were rearing three nestlings and feeding on a high sugar concentration delivered food at a similar rate to males supplied with the medium concentration. One reason for this might be that the males rearing three nestlings and feeding on high sugar concentration spent more time mobbing potential predators, and were therefore unable to invest extra effort in provisioning. This might be due to a time constraint on the maximum rate at which food can be collected (Wright & Cuthill 1990a), or because the males were working at some physiological maximum (Drent & Daan 1980). In addition, Markman *et al.* (1995) showed that male sunbirds trade off provisioning effort against mobbing time. This suggests that, when the brood is sufficiently well fed, males benefit more from increasing time that was spent mobbing than increasing their provisioning activity.

Concurrent with their increase in nest visitation rates

Table 3. The effect of experimental feeder sugar concentration (sucrose) and brood size (brood) in Palestine sunbirds on (a) mean parental visits per nestling per hour; (b) mean nestling mass; (c) mean nestling bill length; and (d) mean nestling tarsus length, at the end of the manipulation (day 13).

(The results of the ANOVA models are presented with d.f., MS, *F*-ratios and *p*-values.)

source	d.f.	MS	<i>F</i>	<i>p</i>
(a) parental visits per nestling				
sucrose	2	9.15	46.84	< 0.001
brood	1	33.48	171.50	< 0.001
sucrose × brood	2	0.00	0.02	0.982
error	30	0.20		
(b) nestling mass				
sucrose	2	1.92	26.32	< 0.001
brood	1	5.14	70.27	< 0.001
sucrose × brood	2	0.05	0.79	0.463
error	30	0.07		
(c) bill length				
sucrose	2	0.28	0.97	0.390
brood	1	0.11	0.39	0.540
sucrose × brood	2	0.01	0.05	0.954
error	30	0.29		
(d) tarsus length				
sucrose	2	0.39	1.71	0.198
brood	1	2.51	11.07	0.002
sucrose × brood	2	0.00	0.02	0.982
error	30	0.23		

with increasing feeder sugar concentrations, the females also spent more time at the nest. This was not necessarily because extra time was available to them, as they probably had met their energy demands, but likely because their higher delivery rate of arthropods also meant that their nestlings tended to defaecate more, and they spent more time at the nest waiting to remove faecal sacs. Indeed, as the sugar concentration increased, the females increased the proportion of visits in which a faecal sac was removed. By contrast, as the sugar concentration increased, the males spent less time at the nest. This may have been due to their allocating more time to alternative activities, such as patrolling their territory or extra-pair copulation. It is also possible that, as the females removed most of the faecal sacs when they were at the nest, the males did not need to remove any additional faecal sacs.

Although the males contributed less than the females to feeding the offspring, they have the potential to work harder with increasing brood size. This was seen when the males made up the extra feeding effort necessary for broods of three compared with broods of two (for similar results see Markman *et al.* (1995)). In general, male parental care may not always be 'necessary', especially when the female can cope with raising the young alone with no extra costs compared with when being assisted by a male (Gowaty 1983). However, paternal care may also be important in regulating the level of female reproductive effort (Searcy 1982; Gowaty 1983). In a multiple-brood species such as the sunbird, males may be more likely to gain some benefits from the fitness and survival of their partners because they are likely to breed again with the same females later in the season.

In a previous study, where male sunbirds were removed (Markman *et al.* 1996), the lone females did not change

their time that was spent mobbing compared with the assisted females, possibly because of their increased commitment to provisioning. The present study shows that, even if the females had the extra energy or time, they did not invest it in mobbing, but rather in provisioning, leaving the mobbing to the males. The increase in mobbing effort made by males with increasing sucrose concentration and brood size may serve females not only as a simple cue of increase in paternal activities, but also as a signal of male quality (Curio 1987) and body state (Wright *et al.* 2001).

The increases in provisioning rates and mobbing times as the sugar concentrations increased were not different between the two brood sizes. One possible explanation might be that we used natural brood sizes (i.e. not manipulated broods). Thus, it might be that the types of parents in the two brood-size groups were inherently different from the start. Natural brood sizes may have been adjusted (i.e. individually optimized (Gustafsson & Sutherland 1988; Pettifor *et al.* 1988)) according to individual territory quality or the provisioning ability of the pair (Wright & Cuthill 1992). Therefore, it might be that parents rearing broods of three nestlings were of higher quality in terms of their ability to rear nestlings. These parents worked harder from the start, so the increases in the sugar concentration encouraged them to increase their effort just a little, but at a similar rate to parents of lower quality rearing two nestlings. The differences between potential causes of similar increases in investment can only be resolved by experimentally manipulating the brood size (e.g. Wright & Cuthill 1990*a,b*).

Parents rearing broods of three nestlings and feeding on the high sugar concentration made the same number of visits per nestling as parents rearing broods of two and

feeding on the low sugar concentration. The result was similar mean nestling body masses in the two groups. Thus, the increase in the parental food quality allowed an equivalent increase in parental effort, roughly equal to that needed to raise an extra nestling.

We conclude that increased energy intake from self-feeding allowed parent sunbirds the extra time or energy to invest more heavily in their young. Although concerned with short-term behavioural decisions, these results have direct implications for long-term life-history trade-offs between parental investment in current versus future young.

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