Behav Ecol Sociobiol (2001) 49:322–329
DOI 10.1007/s002650000295

ORIGINAL ARTICLE

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Does supernormal stimulus influence parental behaviour of the cuckoo’s host?

Received: 11 August 2000 / Revised: 12 September 2000 / Accepted: 26 August 2000 / Published online: 1 February 2001

Abstract The supernormal stimulus hypothesis (SSH) states that a cuckoo chick should obtain more parental care than host young by means of exaggerated sensory signals. We tested the SSH by comparing parental care by reed warblers at parasitized and non-parasitized nests. A comparison of feeding rates to parasite and host chicks of the same size showed that parasitized nests received more food than non-parasitized ones with one host chick. There was an interesting relationship between average prey length and the mass of a cuckoo chick: prey length first increased with chick mass, but decreased after the cuckoo chick outgrew the average-sized host brood (three to four young at fledging). This might be expected if fosterers reduced the selectivity of their foraging behaviour when trying to satisfy the supernormal food demands of the parasitic chick. This suggestion is supported by the finding that the relationship between nestling mass and proportion of less economical small prey is inverse to the relationship between nestling mass and prey size. These results suggest that the parental behaviour of reed warblers is adjusted by selection to the needs of an average-sized brood. The overall proportion of insect orders was significantly different between the parasitic and host chicks. This result probably reflects the opportunistic foraging habits of the host. The qualitative difference (proportion of insect orders) between host and cuckoo nestling diets is partly a by-product of unequal length distribution of members of different taxonomic groups. The results of this study are consistent with the SSH.

Communicated by T. Czeschlik

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Keywords Brood parasitism · Supernormal stimulus · Parental care · Feeding · *Cuculus canorus*

Introduction

There are two main strategies to pass on genes to future generations: obligatory child-bearing and facultative species-specific child-caring (Dawkins 1989). Several species use the obviously beneficial strategy of exploiting the child-care behaviour of other species. The common cuckoo, *Cuculus canorus*, provides one of the best-known examples. After hatching, the cuckoo nestling evicts the host young and exploits the parent-young communication system by tuning into the sensory predispositions of its fosterers (Kilner et al. 1999).

The cuckoo chick has traditionally been reported as a compelling example of supernormal stimulus (e.g. Lack 1968; Dawkins and Krebs 1979; Wyllie 1981; Dawkins 1989; Alcock 1998; Manning and Dawkins 1998). The supernormal stimulus hypothesis (SSH) predicts that a cuckoo chick should provide exaggerated sensory signals for its fosterers and elicit a higher level of parental care than host young under similar conditions (Dawkins and Krebs 1979). Surprisingly, until the last few years, there was no reliable experimental confirmation of the SSH in the common cuckoo. By the end of the 1980s, the SSH had only been tested twice. The two papers (Davies and Brooke 1988; Brooke and Davies 1989) which reported having tested the supernormal effect of the cuckoo nestling in the nest of the reed warbler, *Acrocephalus scirpaceus*, rejected the SSH. The hypothesis was verified for the first time by Soler et al. (1995a) for the great spotted cuckoo, *Clamator glandarius*, parasitizing magpie, *Pica pica*, nests. Recently, the SSH was tested in a series of experiments in several main host species of the common cuckoo (Davies et al. 1998; Kilner and Davies 1999; Kilner et al. 1999). They showed that cuckoo chick begging calls imitate the calling of an entire brood of host young (Davies et al. 1998). Cuckoo vocal begging is a supernormal stimulus; however, the colour of the nestling gape does not influence the feeding rate of either reed warblers or two other host species (Noble et al. 1999; personal observations in reed warblers). On the other hand, the success of brown-headed cowbird, *Molothrus ater*, nestlings in competition for food with yellow warbler, *Dendroica petechia*, young is not caused by the supernormal effect of the parasitic chick (Lichtenstein and Sealy 1998).

In a preliminary study (Grim and Honza 1997), we studied the food of cuckoo and reed warbler nestlings. In the present study, we test the SSH. Cuckoo nestling attains sixfold higher mass than the reed warbler during its occupation of the host nest, although its nestling period is less than twice as long (Kleven et al. 1999). Cuckoo food demands should be higher than those of host nestlings. Therefore, a parasitic chick should obtain more food (mass expressed in grams) than a same-sized host chick. We also predicted that fosterers should modify their foraging behaviour to satisfy high parasite demands. Namely, they should became less selective and collect less economical food items they would not otherwise take. Lower selectivity could be reflected in the relationship between prey and chick size. Finally, a supernormal effect of the parasitic nestling, could, through the changed food selectivity of its fosterers, lead not only to quantitative (see above) but also qualitative differences (i.e. in dominances of diet groups) in the composition of food delivered to parasitic versus host nestlings.

Methods

The field work was carried out from May to mid-July in 1996–1998 on two fish pond systems, 20 km apart, near the villages of Lednice and Lužice in the south-eastern part of the Czech Republic (47°40′ N, 16°48′ E), about 60 km south-east of the city of Brno. Both areas are ecologically very similar – ponds are situated in a flat agricultural lowland landscape and are surrounded by deciduous woods. All the nests used in this study were placed in *Phragmites australis* reed vegetation (Honza et al. 1998). Both the Lednice and Lužice study plots have a relatively high parasitism rate of cuckoos in the nests of reed warblers (Moksnes et al. 1993; Øien et al. 1998).

We examined reed warbler parental care in terms of the amount of food brought to nestlings. Number and size of prey items delivered during one feeding bout are very variable. Feeding frequencies may not give an accurate picture of true nestling consumption – there can even be a negative relationship between the frequency of feeding and the actual amount of food delivered (Royama 1966). Therefore, we used the neck-collar method which enables an accurate analysis of the quantity of food allocated to nestlings and precise prey identification. Plastic-coated wire ligature placed around the nestling neck hinders the swallowing of food but is loose enough not to strangle the chick (Soler et al. 1995a). Neck-collars were applied for 1 h, and food delivered by parents was removed every 20 min because food accumulated in the gape could influence nestling behaviour and, consequently, feeding rate. Food sampling had no effect on nestling growth parameters (chick mass, length and width of bill; unpublished data).

We measured several parameters of nestling size before the application of neck-collars. We weighed chicks to the nearest 0.1 g (reed warblers and small cuckoos) or 0.5 g (cuckoos above 10 g) with a Pesola spring balance. Gape length was measured as the maximum distance from the tip of the bill to the furthest point of the fleshy fold of the rictal flange. Gape width was defined as the maximum distance between the sides of the closed bill. Both width and length was measured to the nearest 0.1 mm with a thin ruler. Gape area (mm^2) was calculated from the length (L) and width (W) of the bill assuming a fully open bill according to the formula: $W\sqrt{[L^2-(W/2)^2]}$.

We used feeding rate (mg of food delivered during 1 h to one nestling) as a parameter of parental care. Because confounding variables (e.g. the size and number of chicks) have an effect on food delivery to the nest (e.g. Moreno 1987) we had to select a parameter of chick size for comparison of the intensity of parental care between species. Feeding rate of both parasitic and host nestlings was significantly positively correlated with age, gape area and mass of chicks (all correlations were significant even after a sequential Bonferroni test, $P<0.01$). Testing differences in the feeding rates of parasitic versus non-parasitic nestlings according to age would have introduced an important confounding variable (chick size) into the comparison. At the time of hatching, cuckoo nestlings were already significantly bigger (heavier) than host nestlings ($t=17.66$, $df=52$, $P<0.0001$) and this difference accelerates strongly during the whole nestling period. Therefore, we had to choose between gape area and mass. The gape area and mass of the nestling are strongly correlated because both are a function of time. Growth of gape area in relation to an increase in mass is allometric and differs between young reed warblers and cuckoos. A host chick of the same size (mass) as a cuckoo nestling has a larger gape area than the parasitic chick and this difference accelerates during the nestling period – the difference between the slopes of linear regression lines tested by Student's t-test (Zar 1984) is significant ($t=21.30$, $df=165$, $P<0.0001$). Because chick dietary need is determined more by body size (a nestling feeds its body not its gape) we chose body mass as a measure of nestling size. We compared feeding rates in nestlings of both species with ANCOVA, controlling for chick size. Here, we only used data for nestlings from a mass range where data for both species were available (from 3 to 12 g).

We only used nests with a single host chick because we were interested not in the cost of parasitism (i.e. parental effort of reed warblers to parasitic nestling vs their own entire brood) but in the supernormal stimulus (i.e. feeding rate to the parasitic chick vs its non-parasitic equivalent – one reed warbler nestling of the same size). Provisioning effort per nestling is affected by brood size in passerines (Rytkönen et al. 1996) and thus it is not possible to compare the feeding rate of the cuckoo chick with the average feeding rate per nestling from a brood of several nestlings because of the possible confounding effect of brood size. Therefore, brood sizes among non-parasitized nests were manipulated to obtain nests with only one chick. From naturally small broods of two to three nestlings one or two nestlings, respectively, were transferred to other nests with smaller than average broods of the same age to create broods with 1 or 4 nestlings. Only the former were used in the analysis.

All the nests were situated in identical habitat (reed beds) with homogenous forest surroundings. An effort was made to take food samples simultaneously from both parasitized and non-parasitized nests. Altogether, we took food samples from 33 non-parasitized and 29 parasitized reed warbler nests. To avoid any possible effects from repeated sampling, we analysed only one (the first) sample taken from each nest. We used all available data in every analysis (i.e. sample sizes are not the same in all analyses). We found no significant effect of year, locality and other measured variables on the composition of food (unpublished data), and therefore compare entire data sets for both species unless otherwise stated. Data not normally distributed were transformed before analyses with parametric statistics. All transformed data sets were normally distributed after transformations.

The term “sample” refers to the contents of one nestling crop. Cases when the chick was not fed were excluded from the analyses. Food samples (stored in 75% ethanol) from 1996 and 1997 were analysed further to examine both the qualitative and quantitative composition of the food and prey size (measured as length of body without appendages). To estimate biomass for calculating feeding rate, food samples from all years were dried to constant mass in an oven at 60°C for 48 h and then weighed on a precision balance to the nearest 0.0001 g.

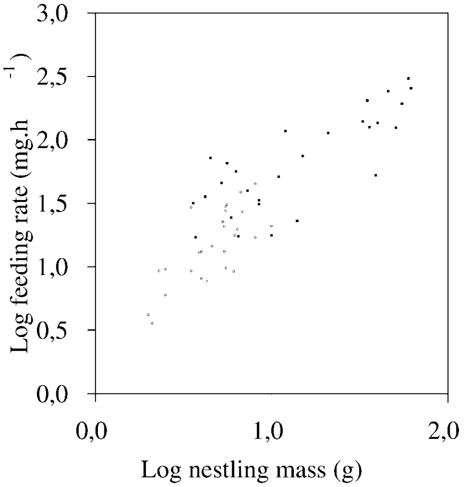

Fig. 1 The relationship between nestling mass and amount of food delivered to it per hour was linear both for the reed warbler (*open circles*) and cuckoo (*filled squares*) (see text for details)

Results

Quantity of food (prediction 1)

The feeding rates of both parasitic and host chicks were positively correlated with all measures of nestling size (see Methods). The relationship between nestling mass and feeding rate (both data log-transformed) was linear for both studied species (reed warbler: $y=1.139x+0.411$, $R^2=0.55$, $F_{1,27}=31.10$, $P<0.0001$; cuckoo $y=0.724x+0.988$, $R^2=0.64$; $F_{1,27}=46.87$, $P<0.0001$; Fig. 1). Reed warbler nestlings have disproportionately larger bills compared to same-sized cuckoos. Moreover, the reed warbler nestling gape area grew much faster than that of the cuckoo (see Methods). Therefore, we controlled for this difference by comparing chicks of the same mass (from 3 to 12 g). A comparison of feeding rates to reed warbler and cuckoo nestlings showed that parasitic nestlings obtained significantly higher amounts of food than same-sized host nestlings (ANCOVA, slopes: $F_{1,34}=1.00$, $P=0.324$; elevations: $F_{1,35}=13.99$, $P<0.001$).

Length of food (prediction 2)

In both years, there was a slight tendency for cuckoo chicks to be fed with smaller prey than reed warblers (5.4 vs 5.6 mm in 1996, 5.4 vs 6.0 mm in 1997). However, when nests were used as independent samples, the differences in average prey length were not statistically significant (Mann-Whitney test, 1996: $U_{14,15}=0.02$, $P=0.98$; 1997: $U_{11,8}=0.29$, $P=0.77$). Prey longer than 14 mm were rarely taken, the longest prey being *Ischnura elegans* (Odonata) which appeared in the food of nestlings of both species. Length distribution of food items was not significantly different between species (Kolgomorov-Smirnov two-sample test: $D=0.625$, $P=0.088$; see also Fig. 2).

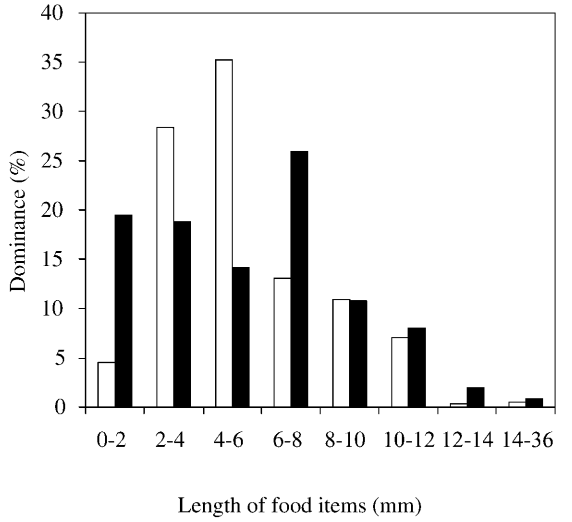

Fig. 2 Frequency distribution [dominance=(number of items of respective order/total number of items)×100] of length of food items delivered to reed warbler (*open bars*, $n=596$; 25 samples) and cuckoo (*filled bars*, $n=2{,}069$; 23 samples) nestlings

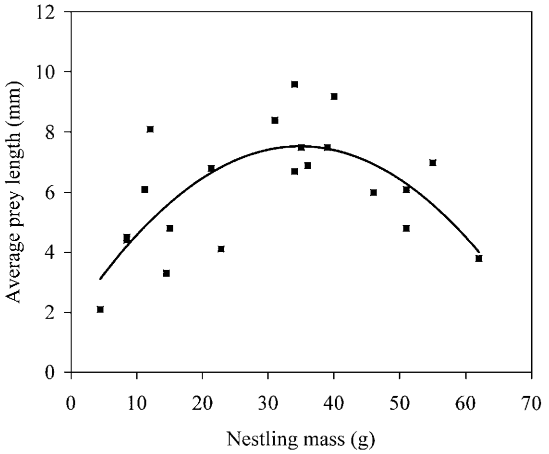

Fig. 3 Relationship between nestling mass and average length of food delivered by reed warbler fosterers to a cuckoo chick. Each *point* represents the average prey length in one sample taken from a cuckoo chick of known mass. A second-order polynomial regression ($R^2=0.50$, $F_{2,18}=8.83$, $P=0.002$) gives the best fit. Linear regression on the same data is not significant ($R^2=0.09$, $F_{1,20}=1.81$, $P=0.19$)

No significant linear relationship between chick size and mean prey length was found. However, for cuckoo (but not reed warbler) nestlings, a second-order polynomial regression significantly fitted the relationship between nestling mass and prey length ($y=-0.005x^2+0.335x+1.704$; $R^2=0.50$, $F_{2,18}=8.83$, $P=0.002$; first-order regression coefficient: $t=4.13$, $P<0.001$; second-order regression coefficient: $t=3.81$, $P<0.01$; Fig. 3). The relationship between nestling mass and presence of small prey (0–2 mm) in food samples was the opposite {logistic regression: $y=1/[1+\exp(-0.005x^2+0.328x-1.405)]$, $R^2=0.22$, $\chi^2=422.556$, $df=2$, $P<0.0001$}. A similar significant effect was found for the presence of aphids {logistic regression: $y=1/[1+\exp(-0.004x^2+0.205x+1.199)]$, $R^2=0.23$, $\chi^2=430.095$, $df=2$, $P<0.0001$; all regression parameters in both regression equations were significant, $P<0.0001$}. These results indicate that the lower average size of prey delivered to older cuckoo nestlings was caused by an increase in the proportion of the smallest prey size category (0–2 mm) and specific prey types (small aphids).

These relationships could be artefacts of uneven sampling of different-sized nestlings or could be caused by a changing food supply during the season (e.g. large size of nestlings later in the season might coincide with a higher proportion of aphids in the food supply). However, there was no seasonal trend in either prey length (linear regression: $R^2=0.04$, $F_{1,19}=0.75$, $P=0.40$; polynomial regression: $R^2=0.07$, $F_{2,18}=0.70$, $P=0.51$) or proportion of small prey (linear regression: $R^2=0.096$, $F_{1,19}=2.02$, $P=0.17$; polynomial regression: $R^2=0.11$, $F_{2,18}=1.16$, $P=0.34$) or aphids (linear regression: $R^2=0.01$, $F_{1,19}=0.25$, $P=0.62$; polynomial regression: $R^2=0.07$, $F_{2,18}=0.63$, $P=0.55$). Moreover, there was no relationship between the size of sampled nestlings and the date (linear regression: $R^2=0.06$, $F_{1,19}=1.14$, $P=0.30$; polynomial regression: $R^2=0.27$, $F_{2,18}=3.32$, $P=0.06$). Almost significant polynomial regression for the nestling size and date relationship is caused by the fact that more *small* nestlings were sampled during the second half of breeding season (this confirms that the relationship between chick size and prey size is not an artefact of uneven sampling). Thus, there was an increasing trend in prey length with age, which turned to a negative relationship between length of food and nestling size in older cuckoo chicks. The declining trend in prey length with nestling mass in large cuckoo chicks is consistent with prediction 2 (see Discussion).

Quality of food (prediction 3)

An analysis of food samples showed that both cuckoo and host chicks obtained a generally similar diet (Table 1). Nevertheless, the proportion of invertebrate orders in the diet of parasitic and non-parasitic nestlings was statistically significantly different ($\chi^2=79.34$, $df=8$, $P<0.0001$). Members of Diptera (especially Chironomidae) were the dominant part of the diet in both parasitized and non-parasitized nests followed by Sternorrhyncha (especially aphids) and Araneida. Within Diptera, the proportion of main groups was not significantly different between the cuckoo and reed warbler diet (Chironomidae: $\chi^2=1.50$, $df=1$, $P=0.22$; Syrphidae: $\chi^2=1.91$, $df=1$, $P=0.18$; Empididae: $\chi^2=1.27$, $df=1$, $P=0.25$). Regarding prediction 2, it is interesting that the proportion of smallest prey (aphids) was higher in the cuckoo diet both in 1996 (19.81 vs 8.25%) and 1997 (15.61 vs 11.03%). However, a comparison of aphid dominance (each nest used as an independent sample) showed that the differences were not statistically significant either in 1996 (Mann-Whitney test, $U_{14,15}=1.27$, $P=0.21$) or 1997 (Mann-Whitney test, $U_{11,8}=0.56$, $P=0.58$).

Table 1 Composition of food delivered to reed warbler and cuckoo nestlings. Total number of food items is 596 for reed warbler (25 samples) and 2,069 for cuckoo (23 samples) [*D* dominance=(number of items of respective order/total number of items)×100; *F* frequency=(number of samples in which items of respective order appeared/total number of samples×100]

	Reed warbler		Cuckoo	
	D (%)	*F* (%)	*D* (%)	*F* (%)
Diptera	67.45	96.00	58.72	95.65
Sternorrhyncha	9.56	40.00	18.85	60.87
Araneida	9.06	68.00	5.70	91.30
Auchenorrhyncha	4.36	44.00	2.17	52.17
Coleoptera	3.36	36.00	2.90	43.48
Heteroptera	0.84	20.00	2.27	43.48
Gastropoda	0.50	12.00	2.46	52.17
Hymenoptera	1.68	4.00	0.63	26.09
Others	3.19	48.00	6.28	65.22

The overall qualitative difference in diet composition is partly explicable in light of the finding that there is a negative relationship between the length of food and chick mass in large cuckoos. If fosterers become less selective when they have a large cuckoo chick, they will feed smaller prey to parasitic nestlings. The distribution of size categories of insect bodies is clearly different among various taxonomic groups in the food supply – small prey are predominantly aphids. Thus, a primary difference in the length of food secondarily affects the qualitative composition of the diet of parasitic nestlings.

These results show that (1) a cuckoo chick obtains more food than a same-sized reed warbler chick, (2) hosts presumably reduce the selectivity of foraging behaviour when feeding a large parasitic chick and (3) reduced selectivity leads not only to differences in the length of prey delivered but also, secondarily, to qualitative changes in food composition.

Discussion

Quantity of food (prediction 1)

Cuckoo nestlings parasitizing reed warbler fosterers were fed with larger amounts of food than host nestlings of the same size. In contrast, Kilner et al. (1999) comparing the number of feedings delivered to cuckoos and the broods of four reed warblers found no significant difference between the two species. The discrepancy between Kilner et al. (1999) and our results is probably explained by the different measure of parental investment used in the two studies: feedings delivered per hour in the former and feeding rate (mg food/h) in the latter. The amount of food obtained in one feeding is very variable (Royama 1966) and it is possible that highly variable feeding rates did not allow differences in food consumption between the nestlings of the species studied by Kilner et al. (1999) to be revealed. We measured the amount of food fed to nestlings directly and it is possible that cuckoo nestlings in the study by Kilner et al. (1999) also obtained slightly more food than same-sized host chicks. The finding that brood size can affect per-individual feeding rate (Rytkönen et al. 1996) could provide another explanation for this discrepancy – Kilner et al. (1999) tested broods of four reed warblers while only one nestling was present in our experimental nests.

By the end of the 1980s, the SSH had only been tested twice in the common cuckoo. In the first study, Davies and Brooke (1988) found that reed warblers showed no preference for a cuckoo chick when presented with a simultaneous choice between feeding their own versus parasitic chicks. It is possible that the absence of preference was due to the short duration of the test, small sample size or the learning ability of reed warblers (see discussion on the great spotted cuckoo below). Soler et al. (1995a) recalculated the data from Davies and Brooke (1988) and found that the cuckoo chick was fed on average 4.5 times per hour whilst reed warbler chicks received only 3.5 feedings. This recalculation supports the SSH but is not compelling for the reasons already mentioned.

In the second study, reed warblers were able to increase their feeding rates when faced with experimentally enlarged broods (Brooke and Davies 1989). The authors asked why the cuckoo nestling did not use this spare feeding capacity. One of the suggested solutions (cuckoos are physiologically not able to grow faster) to this puzzle has already been falsified – cuckoo nestlings reared by the great reed warblers, *A. arundinaceus*, grew much faster than when fostered by reed warblers (Kleven et al. 1999). Suprisingly, this accelerated growth does not reduce the nestling period. Therefore, more probable than physiological constraint is the effect of signalling constraint, i.e. the cuckoo is not able to increase its begging call rate (Brooke and Davies 1989). Reed warbler parents integrate visual and vocal information from begging nestlings and adjust their feeding rate accordingly (Kilner et al. 1999). A begging cuckoo nestling compensates its subnormal visual display (small gape) by supernormal vocal begging. The cuckoo possibly cannot beg more frequently and use the ability of reed warblers to increase the intensity of their parental care. The great reed warbler may have different feeding rules than reed warblers and may feed the cuckoo nestling more than this smaller host even when the cuckoo nestling provides the same signals of need. This hypothesis needs testing.

On the other hand, we think that the results of both our study and the data of Brooke and Davies (1989, Fig. 1d) show that the cuckoo chick actually uses this spare feeding capacity but only after it has outgrown the average reed warbler brood. Nevertheless, there must be a physiological limit to the growth rate of a young cuckoo. We have not tested this idea directly, but it is interesting to note that older cuckoo nestlings usually have full crops of food before the application of neck-collars. They were evidently not able to consume all the food delivered by the fosterers. A similar observation was obtained in great spotted cuckoo chicks (Redondo 1993). Moreover, Kilner and Davies (1999) have found that common cuckoo nestlings consumed more food relative to their daily energy budget than blackbirds, *Turdus merula*, even though blackbirds grow faster than cuckoos.

Length of food (prediction 2)

There was a tendency for cuckoos to obtain smaller prey items than host young. In our previous study, we also found reed warblers provisioned parasitic chicks with smaller prey than their own nestlings (Grim and Honza 1997).

If fosterers try to satisfy supernormal parasite food demands they should modify their foraging behaviour – they should become less selective and collect less economical food items. Thus, there could be a relationship between nestling size (mass) and prey size (average length of prey in sample), namely larger cuckoo chicks should be fed smaller prey than younger chicks because of the hypothesized reduced selectivity in host foraging behaviour. An analysis of the food delivered to cuckoos showed that for small nestlings there was a trend towards increasing length of food items. For larger cuckoos, the trend was the opposite (Fig. 3). No such relationship was found in the reed warbler.

Average prey length is most strongly influenced by small diet items (they are usually numerous when present in a food sample), so we expected an increasing trend in dominance of the smallest food category (0–2 mm) and aphids to larger cuckoos. An increased dominance of small prey (aphids, juvenile spiders, Psocoptera) for older cuckoo nestlings (but not reed warbler chicks) was as expected if fosterers reduced their selectivity when feeding an older and more intensively begging parasitic chick. Foraging on small prey is considered less economical (e.g. Lifjeld 1988; McCarthy and Winkler 1999; Matyjasiak et al. 2000), which is clear for prey not distributed in groups. Foraging on aphids, which are typically social organisms, should not be less economical. Although a substantial proportion of the small prey in our samples was formed by aphids, we think that their collection, in contrast to that of larger prey types, is less economical for two reasons : (1) aphids are not always in compact groups (species *Hyalopterus pruni* in our study area) and (2) reed warblers often bring only one prey item in one feeding bout – even aphids are bought in very small loads of five to ten (personal observation; data not included in this study). More important is the fact that aphids formed 96.3% of the smallest prey (in the category 0–2 mm) in reed warbler nestling food, while only 62.3% of that in the food to the cuckoo chick. The category of smallest prey (0–2 mm) was formed not only by aphids, but also by e.g. small Psocoptera (included in “Others” in Table1) and juvenile spiders. Thus, the increase in the proportion of small prey delivered to a cuckoo nestling was partly caused by the rise in the percentage of aphids. However, prey items other than aphids had an important effect on the higher proportion of small prey in food delivered to cuckoo nestlings.

It is especially interesting to note that the curve (Fig. 3) begins to turn downwards when the mass of the cuckoo nestling reaches the equivalent of the total mass of an entire reed warbler brood (three to four nestlings on average, each weighing about 11 g). This result could indicate that reed warblers are adjusted by selection to feed an average-sized brood. Consequently, larger parental effort (for a big cuckoo chick or a larger-than-average brood) results in abnormal foraging behaviour, namely reduced food selectivity. However, this interesting result should be interpreted with caution even though the regressions are significant, because of the small sample size. Whether the fosterers really do change their foraging behaviour when working for a large cuckoo chick could be tested simply by a pair-wise experiment: to observe the foraging behaviour of fosterers and the composition of food delivered to small and big cuckoo chicks in two nests and then to cross-foster these chicks between the two nests and look for changes in food composition.

We have found no published data for prey length for the cuckoo. In great tits, *Parus major* (Royama 1966), pied flycatchers, *Ficedula hypoleuca* (Lifjeld 1988) and tree swallows, *Tachycineta bicolor* (McCarthy and Winkler 1999), feeding frequency is negatively correlated with prey length, i.e. an increase in nestling hunger is accompanied with a decrease in parents' foraging selectivity. Fosterers trying to satiate a vigorously begging cuckoo nestling could be in a situation similar to parents who try to satisfy the need of (an experimentally enlarged) brood of their own (older) young. Thus, fosterers are forced to be less selective in prey choice and bring prey that is less profitable. Despite consuming smaller prey, cuckoo chicks obtained more food than same-sized warbler nestlings. Interestingly, Mayer (1971) found a higher percentage of aphids in the food of cuckoo chicks reared in great reed warbler nests (58.5% vs 8.1% according to number dominance). We found a similar difference in reed warblers caring for a cuckoo (Table 1). Reed warbler foraging behaviour is probably affected by environmental conditions in a similar manner – Bibby and Thomas (1985) reported that reed warbler nestlings obtained more small Homoptera in poor-quality habitat than in a high-quality environment (21.5 vs 13.6%). Interestingly, male barn swallows, *Hirundo rustica*, and female sand martins, *Riparia riparia*, handicapped by artificially elongated outermost tail feathers captured smaller insects than did controls (Møller 1989; Møller et al. 1995; Matyjasiak et al. 2000). Thus, an enlarged brood, old nestlings, poor environmental conditions, physical handicap and the presence of a cuckoo nestling in the nest can all impair foraging ability.

Food quality (prediction 3)

Information on the diet of cuckoo nestlings is scarce. Wyllie (1981) states without evidence that “nestling parasitic cuckoos are fed, of course, on whatever food each particular host species normally brings to its own young”. Brooke and Davies (1989) analysed nestling faeces and provided data on the frequency of main prey types delivered both to cuckoo and reed warbler chicks. Large differences between their and our data probably stem from the opportunistic feeding nature of the host species (Davies and Green 1976) and the fact that a faecal analysis underestimates the content of soft prey while increasing the prevalence of more chitinous prey. However, both studies have shown that Diptera are the most prevalent component of the diet. Brooke and Davies (1989) reported a higher frequency of beetles in the faeces of cuckoo nestlings. We also found a higher frequency (but not dominance) of Coleoptera (Table 1) but these results are hardly comparable because of the different methods used in collecting samples. Nevertheless, Soler et al. (1995a) also found a similar trend in the great spotted cuckoo.

The different qualitative composition of the diet fed to parasitic and host nestlings could, at least in part, be a by-product of uneven prey length distribution in different food groups (i.e. there are both small and big Diptera but no big aphids). Thus, the difference is primarily quantitative (in terms of food item length) and, secondarily, qualitative.

Can the supernormal effect be suppressed by learning?

The SSH has also been tested in the great spotted cuckoo. This species commonly parasitizes the magpie, *P. pica*, in southern Europe (Cramp 1985). The great spotted cuckoo chick does not show ejection behaviour and competes with the host brood by intense begging, thus drastically decreasing host reproductive success. Magpies allocate food preferentially to parasitic nestlings. This result corroborates the SSH (Soler et al. 1995a). On the other hand, magpies can discriminate a cuckoo chick if it is cross-fostered to their nest. This ability improves with the age of the alien chick – great spotted cuckoo chicks transferred to non-parasitized host nests at the end of the nestling period were neglected by fosterers at a higher rate than magpie nestlings cross-fostered to parasitized nests (Soler et al. 1995b). This result led Soler et al. (1995b) to the conclusion that the cuckoo nestling is not a supernormal stimulus. But magpies learn to recognize their young as those who hatch in their own nests. Therefore, the design of this experiment was asymmetrical: a young cuckoo moved to non-parasitized nest provided a novel stimulus but a magpie nestling cross-fostered to a parasitized nest did not. Therefore, we think that the great spotted cuckoo chick really does influence host parental behaviour by means of superstimulus (as shown in Soler et al. 1995a). At the same time, the supernormal effect of a cuckoo nestling can be reduced by the learning ability of magpies – but only under the unnatural conditions of experimental cross-fostering. Magpies cannot use their potential discriminatory ability under natural circumstances because they learn the appearance of their young after they hatch. Therefore, the success of an alien chick depends on exploiting the obligatory reaction of magpies to feed all the chicks hatched in their nest (Soler et al. 1995a). It should be noted that the negative result of a choice experiment between own and parasitic nestlings in reed warblers (Davies and Brooke 1988) suggests that the situation is similar in the common cuckoo. Reed warbler parents possibly learn the appearance of their young during the nestling period and refuse to feed alien nestlings at the end of the nestling period. In conclusion, the supernormal effect of both the common and great spotted cuckoo nestlings can be suppressed by the discriminatory ability of fosterers acquired during the nestling period. However, this hypothesis needs experimental testing in the common cuckoo.

It should be noted that our experimental design was also asymmetrical: unparasitized nests were manipulated to obtain nests with only one chick while parasitized nests remained unmanipulated. Perhaps it would be better to manipulate all experimental nests. However, in our study, parents were never confronted with foreign chicks: parents in parasitized nests were confronted with cuckoo nestlings that hatched in their nests and parents at unparasitized nests were confronted with reed warbler nestlings hatched in their nests (other nestlings were moved to other nests which were not used in this study). Thus we have studied parental behaviour under almost natural circumstances (e.g. under natural circumstances, brood size can be reduced to one by partial predation). Moreover, reed warblers are not able to discriminate between cuckoo and warbler nestlings; it is therefore highly improbable that our experimental design negatively influenced the results.

Lichtenstein and Sealy (1998) have tested the SSH in the brown-headed cowbird, *M. ater*, parasitizing the yellow warbler, *D. petechia*. The cowbird nestling is fed more than its nestmates but not because of the exaggerated stimuli preferred by the fosterers. It receives a higher level of parental care because it is bigger and, therefore, able to reach higher than host nestlings (see also Dearborn 1998). After controlling for height, cowbird chicks were not more successful than yellow warbler young at gaining feedings even when they were bigger. Thus, Lichtenstein and Sealy (1998) have concluded that the breeding success of parasitic chicks is explicable on the basis of nestling competition and that brown-headed cowbird chicks do not exploit their host with a supernormal stimulus.

Superstimulus as evolutionary artefact

We hypothesize that the evolution of ejection behaviour followed an evolutionary period when the cuckoo chick was reared together with host nestlings. Therefore, the exaggerated begging of a parasitic chick (Davies et al. 1998) could have originated as a means of competition with the host nestlings. After the evolution of ejection behaviour, exaggerated begging probably remained adaptive – chicks in open nests are at a high risk from predation, so shortening the nestling period (through higher intensity of parental care) is strongly adaptive. Moreover, the selection pressures against louder begging (intensity of predation is positively correlated with begging intensity: Redondo and Castro 1992) should have been reduced after evolution of the ejection behaviour because of the smaller brood size (i.e. reduced vocal output of the nest). Therefore, the supernormal stimulus of the cuckoo chick could be a “relic” from former competition with host nestlings while still remaining adaptive. This hypothesis could be tested using phylogenetic comparative methods when more information on the behaviour of ejecting and non-ejecting parasitic and non-parasitic cuckoos has been obtained.

Both before and after the evolution of ejection behaviour in the cuckoo nestling, young cuckoos have exploited the pre-existing parental behaviour of their fosterers which is itself adaptive in the absence of parasitism (Redondo 1993). A supernormal stimulus could be the mechanism (in terms of proximate explanation) used for exploitation by young cuckoos. We conclude that the cuckoo chick, through supernormal begging, changes the foraging behaviour of the fosterer and, consequently, both the quantitative and qualitative composition of food delivered.

Acknowledgements We are grateful to N.B. Davies, L. Gvoždík, V. Pavel and E. Tkadlec for helpful comments on various versions of the manuscript. Suggestions from two anonymous referees greatly improved the paper. We thank S. Sweeney for improving the English. We also thank O. Kleven, O. Mikulica, A. Moksnes, I. Øien, E. Røskaft and G. Rudolfsen for their help in the field. We are indebted to I. Míšek who allowed us to use the precision balance in his laboratory. Financial support was received from Ministry of Education grant VS-96019 and from the Grant Agency of the Czech Republic (grant no. A6087801). This study has been carried out under permission given to M.H. and in accordance with the laws and ethical guidelines of the Czech Republic.

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