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ORIGINAL ARTICLE

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Begging signals more than just short-term need: cryptic effects of brood size in the pied flycatcher (*Ficedula hypoleuca*)

Abstract The begging of nestling birds is known to reliably signal short-term nutritional need, which is used by parents to adjust rates of food delivery and patterns of food distribution within broods. To test whether begging signals reflect more than just short-term feeding history, we experimentally created 18 "small" (4-nestling) and 18 "large" (8-nestling) broods in the pied flycatcher (*Ficedula hypoleuca*). Compared to small broods, large broods were provisioned by parents at a greater rate, but at a lower visit rate per nestling and with no obvious differences in load mass per visit. However, lower rates of food mass delivery per nestling in large broods did not result in any measurable reduction in nestling growth (i.e. "long-term need") or in any increase in the begging effort per individual nestling whilst in the nest. Mid-way through the nestling period we also used hand-feeding laboratory trials to assess in more detail individual begging behaviour and digestive performance of the three mid-ranking nestlings from each brood. More food items were required at the start of each trial to satiate nestlings from large broods, but despite this initial control for "short-term need", nestlings from large broods went on to beg at consistently higher rates and at different acoustic frequencies. Large brood nestlings also produced smaller faecal sacs, which were quantitatively different in content but did not differ in frequency. We suggest that different nutritional histories can produce cryptic changes in nestling digestive function, and that these can lead to important differences in begging signals despite controlling for short term need.

Keywords Brood size · Nestling begging · Parental care · Pied flycatcher · Signals of need

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Introduction

Theoretical conflicts of interest between parents and offspring lead us to expect that the optimal level of parental investment per offspring may be distorted by individual offspring seeking to benefit from more than their fair share of parental resources (Trivers 1974). This manipulation of parents is only possible because offspring control the information concerning their investment requirements. Consequently, attention has focused upon the nature of offspring solicitation signals and their use by parents when allocating care (MacNair and Parker 1979; Parker and MacNair 1979; Harper 1986). Of particular interest is the potential resolution of parent-offspring conflict via the evolution of costly, and therefore honest, signals of offspring "need" (Godfray 1991, 1995). Empirical evidence has so far confirmed the expectation that begging signals of individual nestling birds reliably reflect their recent feeding history (e.g. Redondo and Castro 1992; Kacelnik et al. 1995; Mondloch 1995; Cotton et al. 1996; Leonard and Horn 1996; Price et al. 1996; Lotem 1998a). In addition, parent birds appear to provision young according to the magnitude of such begging signals, whether allocating food items to individual nestlings within broods (Redondo and Castro 1992; Kacelnik et al. 1995; Kilner 1995; Mondloch 1995; Price and Ydenberg 1995; Cotton et al. 1996; Leonard and Horn 1996), or when adjusting provisioning rates to the brood as a whole (Bengtsson and Rydén 1983; Wright and Cuthill 1990; Ottosson et al. 1997; Davies et al. 1998; Wright 1998; Kilner et al. 1999).

A central issue in the study of honest solicitation signals between offspring and their parents is the definition

of offspring "need". Theoretically, need has been treated as the marginal benefits that offspring would gain from receiving food, simply in terms of an immediate increase in their fitness (e.g. Godfray 1991). In the context of nestling growth and development, such offspring need is most easily equated with nutritional state, but this is unlikely to be a simple linear variable, or even one-dimensional. There are many stages between a parental feeding event and any subsequent increase in nestling fitness. At the very least, there is the ingestion of different types of prey, absorption and storage of nutrients, as well as the growth and development of different tissues prior to fledging. Begging signals have been shown to reflect not just recent feeding history, or "short-term need", but also "long-term" requirements in terms of the stage of nestling growth attained (Price et al. 1996; Lotem 1998a). Smaller or younger nestlings within broods appear to beg at a greater rate for a given level of food intake or satiation, when compared with their larger or older nestmates (Lotem 1998a, b; Cotton et al. 1999). Such effects may be due to different competitive begging strategies, because smaller nestlings often have to beg at a greater rate for a given level of food reward when in the nest (Price and Ydenberg 1995; Cotton et al. 1999). It may also be the case that chicks in large broods are simply hungrier, having a greater short term need. Conversely, an investment in gut residence times and/or increase in digestive efficiency could help smaller nestlings compensate for their comparatively reduced resources (Kilner 1996). "Long-term need" has been defined simply as the relative amount of growth achieved by a nestling over days and weeks prior to some target value at fledging (Price and Ydenberg 1995), whilst "short-term need" usually equates to stomach fullness and changes over time in the order of minutes (e.g. the obvious and immediate effect of satiation on begging effort). Although easy to measure, long-term growth and short-term feeding history are in themselves unlikely to reflect all aspects of nestling need (Stamps et al. 1985; Hussell 1988; Lotem 1998a, b; Cotton et al. 1999). Begging effort is probably also mediated by additional factors operating on intermediate time-scales (i.e. between a few hours and one or two days), such as total gut content, digestive efficiency, fat stores and learning. Hussell (1988) provides an appropriate theoretical framework for just this level of adaptive temporal flexibility in nestling demands, coupled with parental ability to supply foods, but few studies have investigated these issues directly.

This paper investigates the consequences of differing competitive and nutritional experiences of nestling pied flycatchers (*Ficedula hypoleuca*) from large or small experimental brood sizes. We expected that in larger broods each chick would receive less food because of the increased demand on the provisioning parents. Comparing detailed growth parameters would then indicate whether this had caused an increase in long term need. Nestling digestion and begging behaviour were assessed over and above the obvious effects of short-term nutritional need and long-term growth experienced in broods of different sizes. Individual nestling begging behaviour and digestive performance were assessed in laboratory trials mid-way through the nestling period, in which short-term need was controlled for by hand-feeding nestlings to satiation at the start of the trials.

Methods

Clutch size manipulation

A nestbox population of pied flycatchers was studied at Abergwyngregyn National Nature Reserve on the North Wales coast, which consists of a 169-ha area of mixed deciduous and plantation coniferous woodland in a steep sided valley with acidic soils. The study was carried out on 36 of the 45 active nests during the 1998 breeding season. At 2–3 days of age, nestlings were moved between nests in order to create 18 experimentally "small" broods (mean=4.11, SE=0.08 nestlings) and 18 experimentally "large" broods (mean=7.94, SE=0.06 nestlings), each being roughly two nestlings either side of the mean brood size and within the natural range for this population (in 1998, mean=6.51, SE=0.19, range 4–9). Nestlings were matched for age and size within each experimental brood. Prior to the start of data collection at nestling age 3 days, there were no significant differences between the two experimental brood size groups in original clutch size, brood size or hatch date (all P-values >0.05), nor in nestling mass or tarsus length (for mean and coefficient of variation in values per brood, as well as for the largest or smallest nestling per brood, all P-values >0.126).

Laboratory trials

Experimental procedure

At 6–8 days of age (mean=7.23, SE=0.07, matched for brood size treatment), the three mid-ranking nestlings by body mass were temporarily removed from each nest, and replaced by substitute nestlings matched for age and size from non-experimental nests. This made it possible to maintain parental feeding rates and competitive conditions within the nest at all times. The three "test" nestlings were then taken to the field laboratory in the middle of the reserve and satiated with as many hand-fed dipteran larvae as they would eat (range 2–14). These dipteran larvae were of a standard size averaging 0.06 g, which was approximately half the mass of a normal parental load mass for typical prey items, such as caterpillars. The first larvae fed to test nestlings was accompanied by 40 µl of red food dye, and the last with 40 µl of blue food dye. Test nestlings were then placed into three separate test boxes each containing a heated artificial nest and a Sony Hi8 video camera (CCD-TR1100E) 0.25 m distance from the nestling. The begging behaviour of individual test nestlings was then recorded every 10 min for a total of 90 min.

Nestlings were encouraged to beg each time by removing a covering piece of material (used to keep them warm and in the dark between trials) and after a short delay (mean number of seconds=0.48, SE=0.05, range 0.20–1.39) tapping the side of the nest a number of times (mean number=13.72, SE=0.20, range 11–16) with the experimenter making repeated and regular "cheep" sounds (mean number=9.15, SE=0.09, range 8–10) which mimicked parental vocalisations at the nest. The stimulus was terminated by replacing the piece of material back over the nestling shortly after the vocalisations (mean number of seconds=2.17, SE=0.13, range 1.44–4.62). In this way, the stimulus to beg was kept standard during each begging trial for all test nestlings, and there were no significant differences in any measures of this stimulus between the two brood size treatments (P>0.161 in all cases). It is important to demonstrate this lack of any difference, given that the experimenter was sometimes aware of the brood size

treatment and, consciously or unconsciously, could have biased the stimulus received by different broods of nestlings.

At the end of 90 min and nine trials, each nestling was encouraged to beg one last time and its individual calls recorded using a DAT tape recorder (HHB PortaDat PDR100) and a small tie-clip microphone (Sony ECM-77B) placed 0.25 m directly above the nest. Test nestlings were then satiated once more with hand-fed dipteran larvae and offered larvae again every 10 min until blue faecal samples were produced. Any faecal samples produced during this time were collected and placed into an air-tight sealed container. Only post-trial faecal samples that appeared after the emergence of the red food dye were used in the subsequent analyses, because these were likely to be the result of digestion of hand-fed dipteran larvae, rather than natural food types received by the nestlings in the nest prior to the trials. Test nestlings were then returned to their natural nest. Test nestlings were out of the nest for between 3–5 h, and this had no significant effect on any of their growth parameters, or those of their nestmates, during the day of the begging trials as compared to normal growth of nestlings within and between nests (all P-values >0.05).

Data collection

Data were recorded during the laboratory hand-feeding begging trials on 93 test nestling from 31 broods (15 small broods; 16 large broods), and each begging trial included: latency to beg (seconds from stimulus to gape open); mean beg posture (scored 0–5 as below); vocalisation volume (scored by observer from video soundtrack 0–2); and vocalisation rate (calls per second). Sonograms of each test nestling at 90 min were then produced and parameters of three representative calls extracted per test nestling including: maximum frequency; minimum frequency; and call length. Post-trial faecal samples were measured in terms of: wet mass; dry mass (determined by drying at 55°C for 48 h); and percentage organic matter (determined by producing ash at 550°C for 20 h).

Nest observations

Experimental procedure

Each of the 217 nestlings in the brood size manipulation was individually measured for body mass (0.1 g accuracy) and tarsus length (0.1 mm accuracy) every second day between the ages of 4 and 12 days, after which time disturbance might have caused premature fledging. In addition, at 12 days of age all nestlings were measured for wing length and given a numbered metal ring.

For 19 of the 36 experimental broods in 1998 (10 small broods; 9 large broods), parent and nestling behaviour was recorded in the nest over the period of one day between nestling ages 6 and 10 days. This was done using a Sony Hi8 video camera (CCD-TR1100E) in the nestbox and an electronic balance (Mettler PB3001 or SM3000) placed under the nest. Parents were habituated to the larger nestbox set-up for 24 h prior to data collection. Video recording inside the nestbox included a view of the balance read-out to measure nest mass (0.1 g accuracy), and was carried out at six different times spaced out throughout the day, each for 1.5 h at a time. For each nest, recording started in the early afternoon of day one and finished at the same time on day two (approximate video times: 1500–1630, 1730–1900, 2000–2130, 0500–0630, 0800–0930, 1100–1230 hours) – i.e. videos and balances were moved between boxes just after midday.

Data collection

Provisioning data per parental visit included parental entrance and exit times (to nearest second), parental sex, load mass, and faecal sac removal. For two recording times in the morning (0800–1230 hours, totalling 3 h) data were also recorded concerning the begging effort of nestlings during each visit (scored 0–5,

where: 1= gaping, neck not extended; 2= gaping, neck extended, head raised; 3= gaping, neck extended to full extent; 4= gaping, neck extended to full extent, front of body raised; and 5= gaping, full neck extension and body raised; adapted from Redondo and Castro 1992; Kilner 1996).

Analysis

Data for all variables were reduced to values per brood prior to statistical analysis. In the case of parental provisioning and nest begging variables, this involved producing a mean per minute per brood for the duration of the video data collected. In 5 of the 19 nests measured (i.e. 2 small and 3 large broods), only one parent was ever observed provisioning the young, including four lone females which probably reflected a proportion of polygynous nests, and a lone male possibly representing at least one instance of female parent mortality during the early nestling period. All analyses concerning parental provisioning are presented with these single parent nests included, because the significance and direction of tests were unaffected by their exclusion (i.e. using only the 14 bi-parental nests would make no difference to the main results presented here).

Nestling growth per brood was calculated using all the data per individual, and fitting logistic growth curve models to mass and tarsus measurements. Parameter estimates were then extracted for: asymptote (A) towards which the young grew prior to fledging; the growth rate constant (K); and the inflexion point (I) of the growth curve (Ricklefs 1973; O'Conner 1984). For the hand-feeding begging trials, the gradual increase in begging effort by each test nestling over the 90 min was characterised by fitting either linear or second-order polynomial curves to the data as appropriate (as determined by entering time into a regression equation, and then using a step-wise procedure to assess the need for the second order term – i.e. the significance of time^2). A reliable value for each begging variable at 90 min was then derived for each nestling separately using these regression equations. Analyses were then performed on the measures of begging and faecal sac contents using the mean values per brood calculated from all three test nestlings.

Data were analysed using parametric tests whenever possible (i.e. homogeneity of variance and normality confirmed using F-tests and Kolmogorov-Smirnov tests respectively). In the case of proportional variables, arcsine square-root transformations were required to normalise prior to analysis. The categorical nature of some begging variables, and the large number of zero begging scores, necessitated the use of non-parametric statistics in much of the nestling begging and hand-feeding trial data. Exact two-tailed P-values are given throughout.

Results

Levels of parental provisioning

When compared to small broods, large broods were fed at a significantly greater rate, but received a significantly lower visit rate per nestling and fewer grams of food per nestling per time interval (Fig. 1, Table 1). The duration of parental visits, the proportion of visits in which faecal sacs were removed, and mean load mass did not differ significantly between experimental brood sizes (Table 1).

Nestling growth

The logistic curves fitted very closely to the growth data for nestlings from both small broods (mass mean
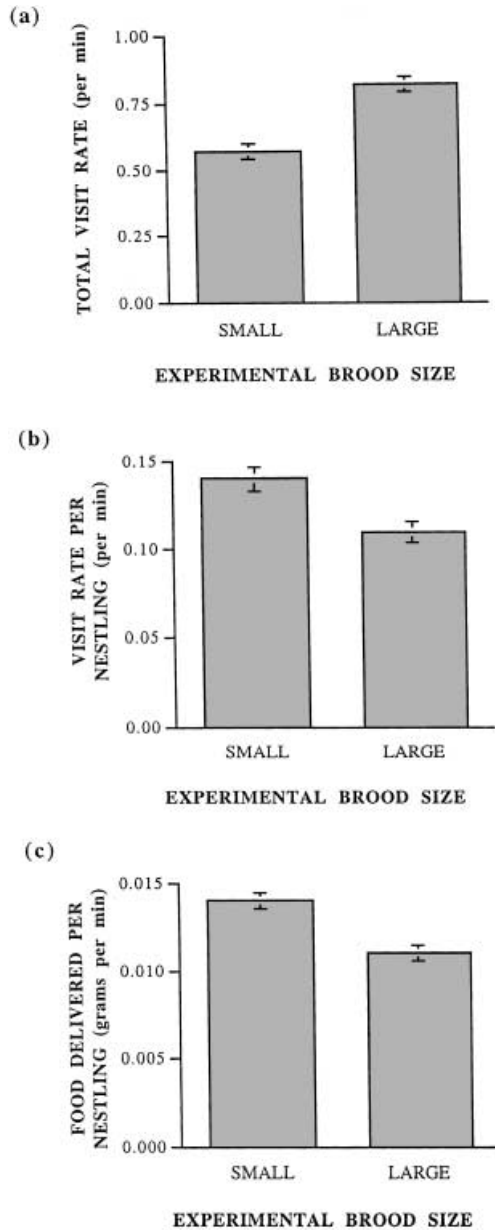
(a)

(b)

(c)

Fig. 1 Mean provisioning (±SE) to experimental small and large pied flycatcher (*Ficedula hypoleuca*) broods for: **a** total visit rate per minute; **b** visit rate per nestling per minute; and **c** amount of food delivered per nestling (g/min)

Table 1 Parental care received per hour by experimental small versus large broods of pied flycatcher (*Ficedula hypoleuca*). Results are given for *t*-tests with 17 *df*, and *P*-values

Variable	t	P
Total visit rate	−4.37	0.007
Visits per nestling	2.95	0.009
Food per nestling	3.13	0.004
Visit duration	0.59	0.570
Faecal sac removal	−0.51	0.610
Load mass	−0.97	0.350

Table 2 Analysis of logistic growth curve parameters for nestlings in small and large broods, including growth rate (*K*), age at inflexion point (*I*) and asymptotic growth (*A*) for (*a*) mass and (*b*) tarsus (see methods for details). Results are given *for t*-tests and *P*-values, with 34 *df* in all tests, with means ± SE for large and small broods

Parameter	t	P	Small broods		Large broods	
			Mean	SE	Mean	SE
(a)						
K	0.75	0.456	0.54	0.03	0.52	0.04
I	−0.58	0.564	4.43	0.24	4.66	0.30
A	−0.82	0.417	14.11	0.38	14.01	0.43
(b)						
K	1.39	0.173	0.43	0.01	0.42	0.03
I	−1.23	0.226	3.17	0.20	3.32	0.25
A	−0.16	0.873	17.84	0.17	17.97	0.14

Table 3 Analysis of brood size effects on nestling measurements at age 12 days per brood for mass, tarsus and wing length for (*a*) mean values per nest; (*b*) the smallest nestling; (*c*) the largest nestling; and (*d*) CV of values per brood. Results are given for *t*-tests and *P*-values, with 34 *df* throughout, except for wing length which had 26

	t	P	Small broods		Large broods	
			Mean	SE	Mean	SE
(a)						
Mass	0.21	0.833	13.64	0.17	13.69	0.20
Tarsus	0.28	0.781	17.08	0.08	17.13	0.08
Wing	−0.36	0.721	46.09	0.93	45.73	0.49
(b)						
Mass	0.93	0.358	13.12	0.25	12.72	0.19
Tarsus	1.11	0.275	16.76	0.11	16.54	0.11
Wing	0.53	0.602	44.33	0.56	43.92	1.34
(c)						
Mass	−0.91	0.367	14.22	0.20	14.51	0.18
Tarsus	−2.08	0.046	17.51	0.09	17.66	0.08
Wing	−1.63	0.114	47.13	0.46	48.54	0.63
(d)						
Mass	−1.02	0.315	3.68	0.66	4.45	0.29
Tarsus	−2.66	0.012	1.91	0.19	2.32	0.19
Wing	−1.12	0.272	2.76	0.30	3.65	0.81

r^2=0.96; tarsus mean r^2=0.98) and large broods (mass mean r^2=0.98; tarsus mean r^2=0.96). However, there were no significant differences between the brood sizes in the magnitude of any of the mean nestling growth parameters (Table 2).

Measurements of nestlings at age 12 days were consistent with the non-significant effects of experimental brood size from the growth curve analysis. Mean nestling mass, tarsus and wing lengths were not significantly different between small and large broods (Table 3, a). These results for mean values per brood also held for analyses using values from only the smallest or only the largest nestling per brood (as defined by the measure itself on

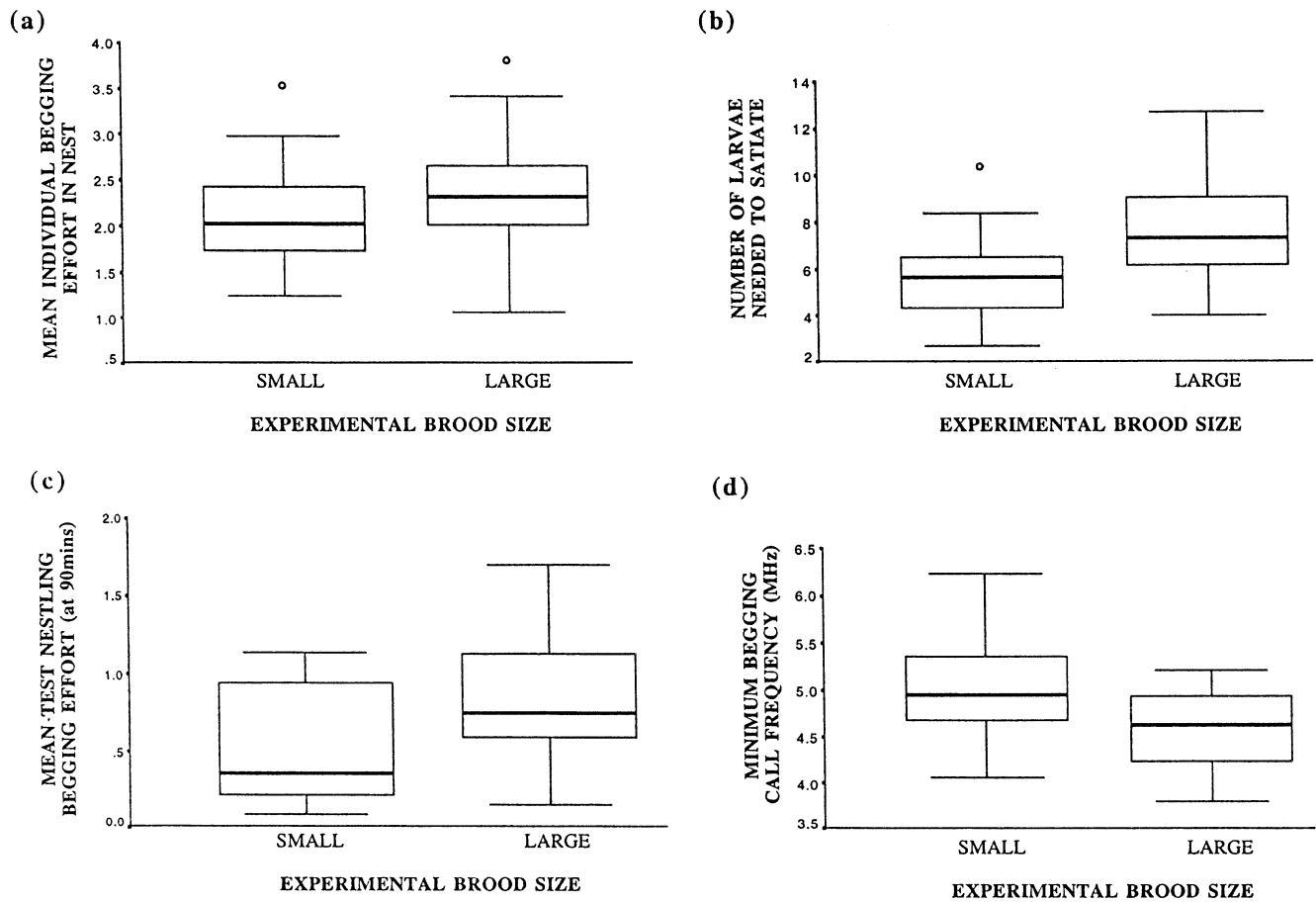**(a)**

(b)

(c)

(d)

Fig. 2 Median values for begging and hand-feeding data (*box* indicates interquartile range, and *bars* indicate 95% percentiles with *outliers* shown) for experimentally enlarged and reduced broods: **a** individual nestling begging scores in the nest; **b** number of larvae required to satiate test nestlings; **c** nestling begging score of test nestlings after 90 min in trials; and **d** minimum frequency of begging calls of test nestlings at 90 min

Table 4 Comparisons of begging parameters for broods whilst in the nest (see text for details) for 11 small versus 10 large broods. Results and *P*-values are given for Mann-Whitney *U*-tests

Parameter	U	P
Begging effort per nestling	46.00	0.557
CV of begging in broods	28.00	0.061
No. of nestlings begging	1.50	<0.001
% of nestlings begging	34.00	0.152

day 12), as well as for the coefficient of variation (CV) of measurements within broods (Table 3). However, the CV in tarsus length was significantly greater within large broods, as a result of the largest nestlings having slightly longer tarsus length, with no corresponding effect on the mean and smallest nestling tarsus lengths (Table 3).

This general lack of an experimental brood size effect on nestling growth also held for the sub-set of test nestlings taken from each brood for use in the hand-feeding trials (mass: $t_{23}=0.32$, $P=0.748$; tarsus: $t_{23}=1.35$, $P=0.182$; wing: $t_{23}=-0.83$, $P=0.408$). This confirms that the three mid-ranking nestlings within each brood selected for the hand-feeding trials were representative of the larger experimental sample of nestlings in terms of their physical growth.

Begging in the nest

Whilst in the nest, the mean begging effort per individual nestling did not appear to differ significantly between small versus large broods (Fig. 2a, Table 4). However,

there was a tendency for greater variation in the individual begging effort of nestlings within small broods as compared to large broods (Table 4). From observation, this probably reflects the likelihood of temporary satiation of individual nestlings periodically within the small broods. Overall, at any one time there were significantly more nestlings actively begging in larger broods (Table 4), but with a similar proportion of the brood begging in small versus large broods (Table 4).

Begging during hand-feeding trials

As might be expected from the food delivery rates per nestling (Table 1), at the start of the laboratory hand-feeding trials, it took a significantly greater number of larvae to satiate test nestlings from large broods as compared to those from small broods (Fig. 2b; Mann-Whitney
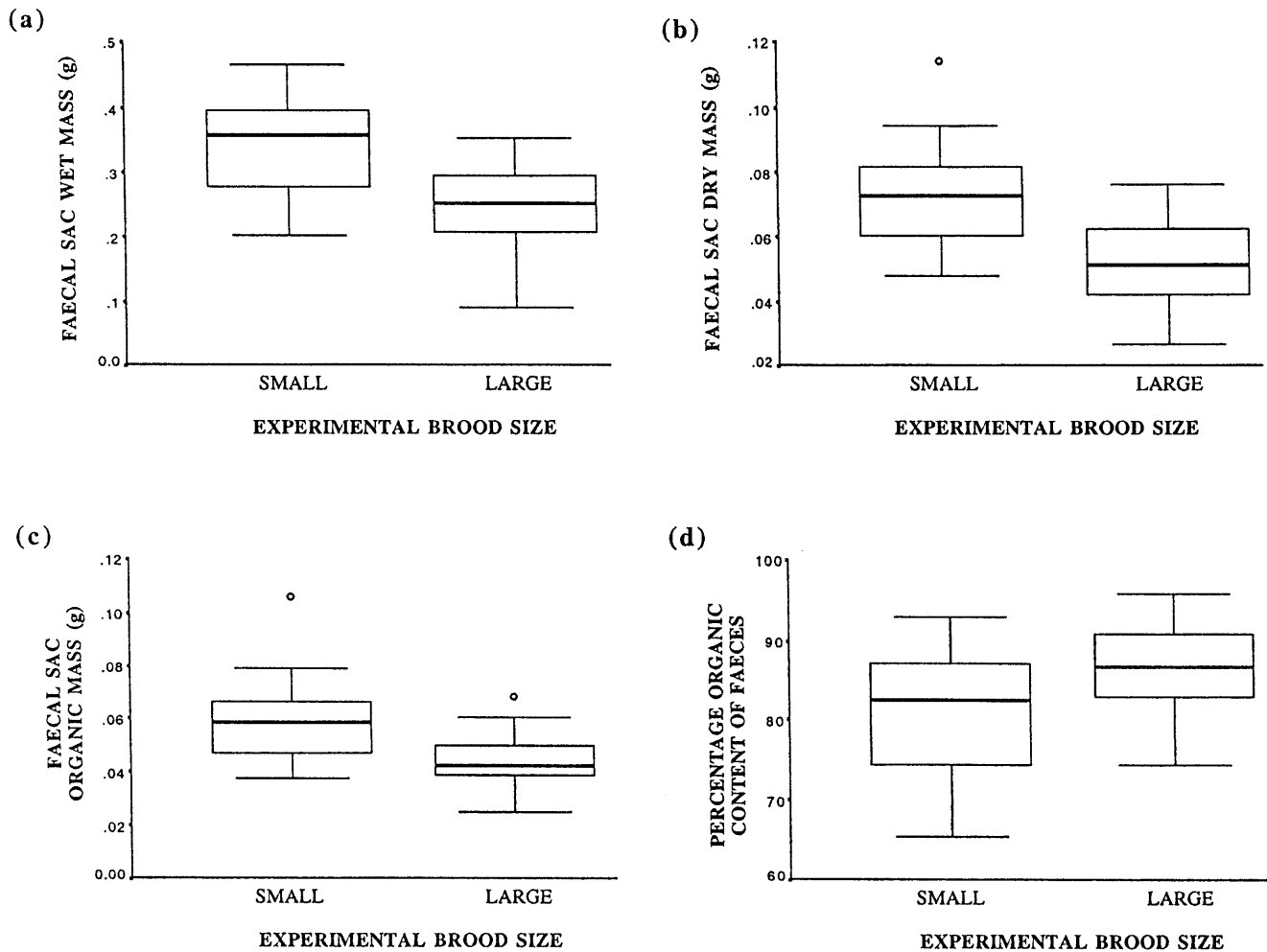
(a)

(b)

(c)

(d)

Fig. 3 Median values for contents of faecal sacs of test nestlings after 90 min in hand-feeding trials (*box* indicates interquartile range, *bars* indicate 95% percentiles with *outliers* shown) for experimentally enlarged and reduced broods: **a** wet mass; **b** dry mass; **c** organic mass; and **d** percentage organic content

Table 5 Results of laboratory hand-feeding trials on test nestlings from small versus large broods after 90 min for: (*a*) begging variables (31 broods); (*b*) parameters from sonograms of begging calls (29 broods); and (*c*) analysis of faecal contents (29 broods). Results and *P*-values are given for Mann-Whitney *U*-tests

	U	P
(a)		
Latency	45.00	0.003
Beg posture	62.00	0.022
Vocalisation volume	69.00	0.044
Vocalisation rate	65.00	0.030
(b)		
Maximum frequency	86.00	0.407
Minimum frequency	55.00	0.029
Individual call length	95.00	0.663
(c)		
Wet mass	42.00	0.006
Dry mass	36.00	0.003
Organic mass	48.00	0.013
% Organic matter	66.00	0.089
Gut passage time	67.00	0.020
Number of sacs	95.50	0.683

U=65.00, *n*=31, *P*=0.029). Following this satiation, test nestlings from large broods showed a faster increase in their begging effort during the 90 min as compared to those nestlings from small broods, with the result that at 90 min they were begging at a significantly greater effort in every measure of latency, posture and vocalisation (Fig. 2c, Table 5 a). In addition, there was a significant difference in the minimum frequency of calls made by nestlings from the different sized broods (Fig. 2d), although there were no significant differences in maximum call frequency and call duration (Table 5 b).

Faecal sac analyses from hand-feeding trials

At the end of the hand-feeding begging trials, test nestlings from large broods produced smaller faecal sacs than test nestlings from small broods, as reflected in significantly lower wet mass, dry mass and organic mass

(Fig. 3, Table 5c). There was also a non-significant tendency for nestlings from large broods to produce faeces with a higher percentage organic matter, suggesting less efficient digestion by nestlings in large as compared to small experimental brood sizes (Fig. 3d, Table 5c). It was not possible to detect differences in gut passage time prior to the red marker (onset of hand feeding) because this was almost always produced at 90 min – the first time the chicks were fed after the begging trial. The blue marker (given at the end of hand feeding) emerged significantly later in small as compared to large broods. Chicks from small broods were retaining food for longer even though they had received less in the hand feeding trials. The number of faecal sacs produced did not differ between nestlings from large (mean=1.46, SE=0.16) versus small (mean=1.32, SE=0.45) brood sizes (Table 5c).

Discussion

Pied flycatcher nestlings raised in experimentally reduced or enlarged broods demonstrated contrasting begging behaviours and digestive performance, and this requires an explanation beyond the effects of short-term feeding history and long-term growth. What aspects of nestling competitive and nutritional experiences can account for these results, and how do such responses fit within the current adaptive framework concerning honest signalling of offspring need?

The greater number of parental visits to large broods was probably the result of the greater number of nestlings actively begging and producing greater apparent total brood begging effort in those broods (Bengtsson and Rydén 1983; Wright and Cuthill 1990; Ottosson et al. 1997; Davies et al. 1998; Wright 1998; Kilner et al. 1999). The increase in parental visits with experimental brood size was not, however, proportional to the number of nestlings and visit rates per nestling declined in larger broods, as expected from previous studies on parental care in birds including pied flycatchers (e.g. Nur 1984b; Lifjeld 1988; Wright and Cuthill 1990; Martins and Wright 1993; Moreno et al. 1995; Wright et al. 1998). Contrary to earlier studies, the decrease in visits per nestling was not compensated for by any change in the mass of the loads delivered to nestlings in enlarged broods (see Wright et al. 1998, and references therein). Therefore, consistent with general predictions from life history theory (e.g. Sibly and Calow 1983; Nur 1984a), the amount of food delivered per nestling decreased with increasing brood size (Klomp 1970; Nur 1984a, 1988; but see Wright et al. 1998).

Compared to similar studies (e.g. Gustafsson and Sutherland 1988; Lunberg and Alatalo 1992; Moreno et al. 1995), the present dataset produced surprisingly few measurable differences in nestling growth parameters in broods of different sizes. The greater mass of food delivered per time interval to nestlings in small broods did not result in any apparent differences in nestling mass. A similar lack of effect of experimentally manipulated food

intake rates on the body mass of pied flycatcher nestlings has also been recorded by Verhulst (1994). The measurements of body size (tarsus and wing length) also demonstrated little effect of experimental brood size upon nestling growth, which suggests that there may be more to "long-term need" (sensu Price and Ydenberg 1995) than simple morphometric measurements.

The lower rates of food intake per nestling in larger broods probably explains the greater numbers of larvae needed to satiate test nestlings from large broods at the start of the hand-feeding trials. Test nestlings coming from large broods could have been experiencing consistently greater short-term need, whilst nestlings from small broods probably contained a greater amount of natural food items already in their intestines. However, despite the fact that short-term need (i.e. immediate hunger in the form of stomach distension) was controlled for via satiation at the start of the trials, there might have been a difference in the amount of food already held lower down in the digestive systems of test nestlings. These differences in "medium-term" feeding history could therefore provide one explanation for our finding that, despite the lack of differences in external morphometric measurements, test nestlings from large broods begged at consistently higher rates and appeared to get hungrier quicker than nestlings from small broods.

It appears that nestlings from large broods may not have invested equivalently in their gut or digestive efficiency. Total gut passage time was comparatively shorter, the organic content of faeces was higher and they became hungrier sooner after satiation. Nestlings from large broods may have become hungrier quicker during the hand-feeding trials because of a smaller stomach and/or a shorter gut length (although the longer gut passage time would suggest otherwise). It has been found that adult birds which process more food per day have longer guts (Savory and Gentle 1976; Al-Joborae 1980), suggesting that the gut of nestling birds may develop so as to attain a length appropriate to their rate of food consumption. Our large brood nestlings could therefore have developed smaller stomachs and/or shorter guts as a result of receiving consistently lower food intake rates in the nest, thereby becoming hungrier quicker. In the nest, however, chicks from large broods did not appear to beg at a significantly greater rate than those in small broods. Although it is possible that in the nest the narrower range of nestling states between satiation and hunger created few distinct differences, such that they were only revealed in the extremes of our hand-feeding trials.

In work on nestling house sparrows (*Passer domesticus*), Lepczyk et al. (1998) showed that during periods of food restriction, food was retained in the gut for longer (i.e. in line with models of optimal digestion in adult birds; Sibly 1981; Karasov 1996). However, during temporary periods of higher food intake they found no compensatory increases in growth, and concluded that the guts of nestling birds have little spare capacity to deal with increased food intake during growth and following longer periods of food restriction.

The differences in digestive function may simply reflect differences in the quality of diets during the hand-feeding trials. As compared to small brood nestlings, satiated large brood nestlings will have consumed a greater proportion of the poorer quality hand-fed dipteran larvae versus high quality natural food items. Indeed, recent experiments demonstrate that faecal sacs produced by hand-fed flycatcher nestlings become progressively smaller the longer they are out of the nest and the more they are fed on such poor quality dipteran larvae (J. Wright and R. Yarnell, unpublished data). Hence, smaller faecal sacs in large brood nestlings may indicate a slowing of gut passage rates, reflecting a digestive response to a poor quality of diet. It is therefore unclear whether all of the differences in nestling digestive function in the present study can be attributed to differences in gut physiology. Either way, this study suggests that more attention should be paid to diet and its influence on medium-term differences in digestive function when assessing nestling begging signals.

Nestling birds faced with temporary reductions in food intake may do best by maintaining their skeletal and muscular growth, because shortfalls in these are largely unrecoverable (Schew and Ricklefs 1998). This would have to be done at the cost of reduced investment elsewhere, such as in gut development, and this may be preferable because it can always be recovered at a later date (Karasov 1996). Thus, nestlings in larger broods may have made the strategic adjustment to reduce their gut size and therefore sacrifice their capacity to hold onto and efficiently digest a greater mass of food if and when it became available. Hence, contrary to our initial prediction that disadvantaged chicks may try to invest in larger guts, the converse may be true. We suggest that such flexibility in gut physiology may represent a cryptic difference between nestlings from different sized broods. Such adjustments occur over a longer period than short-term need, and yet are not permanent in the sense of long-term need, and we suggest they represent an intermediate "medium-term need". Although the differences in nestling digestive development suggested here have yet to be quantified, similar cryptic differences in medium-term need have recently been demonstrated for an alternative nestling state, that of nestling immunocompetence (Saino et al. 1997; Birkhead et al. 1999). Therefore, pied flycatcher nestlings fed at different rates can show similar patterns of body growth but still retain cryptic differences in their physiological development, such as in their digestive or immune systems, and it is these that might explain differences in subsequent recruitment rates (Verhulst 1994).

As well as producing contrasting feeding and digestive histories, the brood size manipulation must have created differences in the competitive experiences of nestlings raised in large versus small broods. Previous authors have suggested that competitive experience in the nest may result in learnt responses and facultative adjustments in observed levels of nestling begging effort (Stamps et al. 1989; Cotton et al. 1999). This effect of learnt experience has recently been confirmed in specifically designed hand-feeding experiments on nestling house sparrows (Kedar et al. 2000). In the present study, nestlings in large broods will have experienced lower food rewards per begging effort, and may therefore have been maximising their net energy intake through a strategy of reduced begging effort for a given level of hunger. Hence, the lack of a brood size effect on the begging effort of individuals receiving differing rates of food intake whilst in the nest. Once in the hand-feeding trials, these same nestlings from large broods will have experienced a much improved return on their begging effort, which would have exceeded any improvement experienced by nestlings from small broods for whom the profitability of investment in begging effort was always high. It is therefore possible that nestlings from large broods begged at a greater rate following satiation because they experienced a greater increase in their expectation of reward. However, this interpretation remains speculative without specific field experiments of these effects within natural broods.

In the light of the results presented here, current definitions of nestling "need" may require elaboration. Long-term need represents components of permanent and relatively inflexible nestling growth, including obvious external states such as skeletal body size and feather growth (Price and Ydenberg 1995). The optimum long-term developmental strategy for any nestling would be to invest an appropriate proportion of food resources in to each component state at each stage in the nestling period so as to maximise its fitness upon fledging. Medium-term need can be defined as less permanent aspects of nestling state, growth and development, which are reversible, but which last longer than the short-term effects of one stomach full of food. Examples include: nutritional stores (e.g. fat reserves); components of gut plasticity and digestive efficiency; as well as possible effects of competitive experience on begging effort. It is exactly these types of cryptic medium-term changes in nestling state that Hussell (1988) predicted as compensating shifts in nestling demand functions, and which have the potential to explain differences in begging effort irrespective of short-term nutritional need (see Stamps et al. 1985; Hussell 1988; Lotem 1998a, b; Cotton et al. 1999). Short-term need can still usefully be defined via the mechanism of nestling hunger (i.e. stomach contents), which directly controls solicitation behaviours (Redondo and Castro 1992; Kacelnik et al. 1995; Mondloch 1995; Cotton et al. 1996; Leonard and Horn 1996; Price et al. 1996; Lotem 1998a). However, as demonstrated here, even nestling begging behaviour in controlled hand-feeding trials can be modified by (and reflect cryptic components of) medium-term need.

In conclusion, experimental brood size manipulations in the pied flycatcher produced the expected reduction in food delivery rates per nestling in large broods. However, these were insufficient to influence any of the nestling growth parameters previously used to define long-term need. Surprisingly, individual levels of begging in

the nest also revealed no differences with brood size. Controlling for short-term need in hand-feeding trials, we demonstrate that test nestlings from large broods begged at consistently higher rates and differed in gut passage time and digestive efficiency. Our results confirm earlier suggestions that begging demands can shift and reach some equilibria with levels of parental supply (Hussell 1988), and we additionally reveal a possible mechanisms via differences in their digestive performance. We therefore suggest three possible, but not mutually exclusive, explanations for these results on nestling begging behaviour: (1) differences in the quantity and/or quality of total gut contents, which may have influenced gut passage times and thus hunger; (2) cryptic differences in growth and strategic performance of the digestive system similarly influencing digestion and hunger; and (3) contrasting competitive experiences causing nestlings to adjust their begging effort over and above level of hunger. Nestling begging signals clearly incorporate aspects of recent individual competitive experience beyond the typical measure of short-term stomach fullness. By definition, such mechanisms provide us with the all-important link between nestling nutritional state and the particular aspects of offspring need that are of interest to parents when provisioning their young in the nest.

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