The role of nonvocal begging behaviour in food allocation in nestling Yellow Warblers (*Dendroica petechia*)

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Introduction

Begging is considered to be a form of communication between offspring and parent (Marler 1956; Hussell 1991; Litovich and Power 1992). Avian begging behaviour consists of both acoustical and visual components (Litovich and Power 1992; Redondo and Castro 1992). The begging calls of the chicks are believed to be a proximate stimulus for the parents' feeding rate (von Haartman 1953 cited in Hussell 1991; Bengtsson and Rydén 1983). If frequency and intensity of calling increase, this may result in an increase in the frequency of parental feeding trips to the nest (Muller and Smith 1978; Bengtsson and Rydén 1983). Nonvocal begging behaviour is thought to function in soliciting resources from parents and may influence the parent's decision regarding which chick to feed (Rydén and Bengtsson 1980; Kilner 1995); this would reflect sibling competition (Smith and Montgomerie 1991). Examples of avian nestling nonvocal begging, or solicitation behaviour include: gaping, raising the head, stretching the neck, elevating the body on the tarsi, wing flapping, and positioning oneself close to the parent (Rydén and Bengtsson 1980). Other studies have shown the nestling who is the first to gape, holds its head the highest, and positions itself closest to the parent is the first to be offered food (Kacelnik *et al.* 1995; Kilner 1995; Rydén and Bengtsson 1980; Smith and Montgomerie 1991; Stamps *et al.* 1989).

Through detailed analysis of video, I am quantifying Yellow Warbler nestling solicitation behaviours to determine whether the various components influence parental food allocation decisions among young. This report summarizes preliminary results obtained in 1996.

Methods

During the summer of 1996, G. McMaster and I found Yellow Warbler nests on the forested dune-ridge at the Delta Field Station and Portage Country Club near Delta, Manitoba. Nests were monitored from discovery until hatch. Yellow Warbler hatchlings were individually marked with a non-toxic marker on the skin under the wing.

At days 2, 5, and 8 after hatching of the first chick (i.e. early, middle, and late nestling stages), nests were videotaped. Brood size was noted and the nestlings were individually colour-marked with a dot of non-toxic paint on the crown. The camcorder, weatherproofed in a toolbox, was mounted on a tripod at least 1m away from the nest. Recordings were 1-hour bouts: 10 minutes to allow the adults to habituate to the equipment and 45 minutes of observations (n=46 hours). During later analysis of the video, parental activities and chick 'begging' behaviour were detailed (as per Redondo and Castro 1992). For the purpose of this report, I shall summarize nonvocal solicitation behaviours of nestling Yellow Warblers (Table 1).

Nest videos were initially transcribed and a subset was analyzed in greater detail. I concentrated on nests with a brood size of 4 nestlings. Sample sizes of analyzed nests are: 7 nests at day 2, 7 nests at day 5, and 6 nests at day 8 (20 total). These are the sample sizes for all figures. I concentrated on the identity and solicitation ranks of the nestling first offered food by a parent during a

Table 1. Categories of Yellow Warbler nestling solicitation behaviour detailed during video analysis.

Category	Description
START	Rank order in which a nestling begins to gape
	S1 to S4 - first to last to gape
HEAD	Rank order of relative height of nestlings' heads
	H1 to H4 - highest to lowest head height
INTENSITY	Measure of solicitation effort by a nestling
	INT1 - head up gaping
	INT2 - INT1 + neck stretched
	INT3 - INT2 + standing
	INT4 - INT3 + wing flapping
POSITION	Position of nestling in nest relative to adult perched on nest rim
	POS1 - closest to adult
	POS2 - intermediate distance
	POS3 - furthest from adult

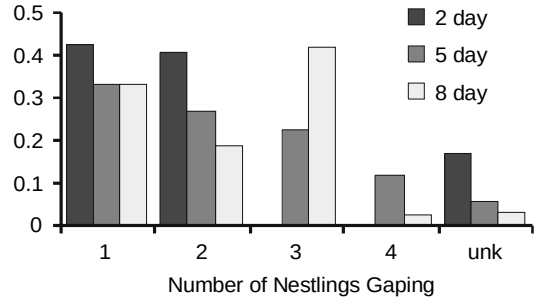

Figure 1. Average proportion of visits during which one or more nestlings gaped prior to the first food offer from a parent (unk=unknown).

feeding visit in order to determine the factor(s) assisting the parent in determining food allocation within its brood.

Results

The proportion of adult feeding visits during which one or more nestlings gaped prior to the first food offer is summarized in Fig. 1; rarely did all four nestlings gape after the parent arrived at the nest. The mean proportion of first-offers graphed in Figures 2-5 are taken from feeding visits with more than one chick gaping (i.e. some degree of sibling competition occurring) (Fig. 1). Table 1 describes the solicitation ranks and scores summarized below. At both day 5 and 8, most first-offers were made to the nestling that gaped shortly after the parent arrived (start: S1 and S2, Fig. 2a), held its head the highest (head: H1, Fig. 2b), and was positioned closer to the side of the nest on which the adult was perched (relative position: POS1, Fig. 2d). Solicitation intensity levels did not seem to affect the proportion of first food offers at day 5 or 8 (Fig. 2c). The 'unknown' values are due to the parent's body obstructing the view of the nest, but were included to ensure the sum of the proportions equaled one.

The identity of the chick first offered food was summarized to determine the proportion of the first-offers that were made to the largest versus the smallest chick. In general, the largest chick was offered food first more frequently (31.2%) than the smallest (20.8%) [n=10 nests in total at days 5 and 8].

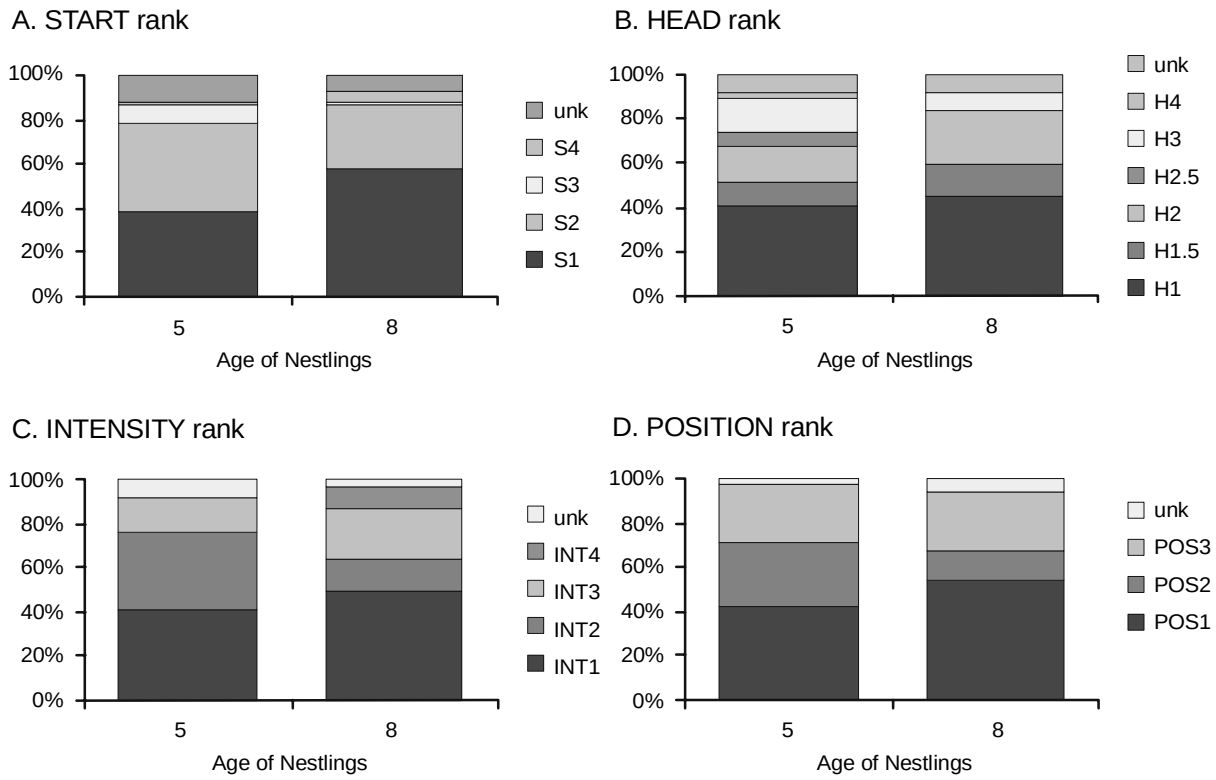

Figure 2. Proportion of first-food offers a nestling received according to its solicitation rank scores: a) START rank (S1 = first to gape); b) HEAD rank (H1 = head held up the highest relative to the brood); c) INTENSITY rank (INT1 = lowest intensity level); d) POSITION rank (POS1 = closest to parent). See Table 1 for a description of the rank scores.

Discussion

The arrival of a parent at the nest is not always met with gaping, posturing, and vocalizing nestlings (as per Kilner 1995). At all three ages, at least 30% of the feeding visits had only a single nestling gaping (Fig. 1). If this trend exists after sample sizes are increased, it is possible that sibling competition is less of a factor in food allocation than originally suspected (see Kacelnik *et al.* 1995; Smith and Montgomerie 1991; Teather 1992).

After the arrival of the parent, the food is transferred to a nestling(s) almost immediately (unpublished data). The time span during which the parent evaluates the nestling situation and 'decides' on which nestling to feed is short (0.4 - 8 seconds; unpublished data). Therefore, the first-offered nestling must exhibit some characteristic(s) that attracts the parent's attention and succeeds in obtaining at least a food offer. By examining the mean proportion of first-offers made to chicks gaping at the various combinations of solicitation parameters, the strongest factor(s) affecting the food allocation decision may be illuminated. If only one chick gapes, it is offered the food; the parent rarely eats it or flies away with it (personal observation). Therefore, these figures (Figs. 2a-d) illustrate feeding visits where more than one chick is gaping. In Yellow Warblers, it appears that the "first-offered nestling" is often the one that starts gaping earlier, with its head higher, and is positioned closer to the parent than the other nestlings. Apparently, the start, head, and position parameters have a greater influence on the proportion of first-offers at day 8 than at day 5. Similar results have been obtained in several other studies (Kacelnik *et al.* 1995; Kilner 1995; Rydén and Bengtsson 1980; Smith and Montgomerie 1991; Stamps *et al.* 1989). Most of these studies did not find only one factor determining the probability of being fed; the parents may be cueing in on a number of different components when more than one nestling is 'begging' during a feeding bout.

The largest Yellow Warbler nestling obtained the first-food offer in just over 30% of the feeding bouts. However, a distinct competitive advantage was not obvious. Sample sizes must be increased before any concrete conclusions can be made regarding this factor. Price and Ydenberg (1995) found the largest Yellow-headed Blackbird nestling received the most food loads. Size is also important in the acquisition of favourable nest positions (Kilner 1995) and the height to which the head is held up (Teather 1992). However, mother budgerigars will search out and feed the smallest nestling, whereas the males feed according to begging rates (Stamps 1993).

The solicitation intensity of the chicks does not seem to play an important role in food allocation in Yellow Warblers. Nestlings exhibiting a higher and supposedly, more energetically costly, level of solicitation did not receive a greater proportion of first food offers; in fact, high intensity solicitation levels were not as common as the lower levels (Fig. 2c). Redondo and Castro (1992) summarized a basic positive relationship between begging intensity and the probability of being fed. However, much variation exists in how parent birds respond to intensely begging nestlings, again pointing to a more flexible and complex system deciding food allocation.

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