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## Begging as competition for food in Yellow-headed Blackbirds

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Theoretical models suggest that chicks compete with one another for food by begging (MacNair and Parker 1979, Harper 1986, Parker et al. 1989, Price 1994, Price et al. 1996). Several comparative studies support this idea by illustrating a positive correlation between brood size and begging level interspecifically (e.g. Cotingidae; Harper 1986), and between brood size and the ratio of begs to feeds intraspecifically (e.g. Cattle Egrets, *Bubulcus ibis* [Fujioka 1985]; Budgerigars, *Melopsittacus undulatus* [Stamps et al. 1989]), although Henderson (1975) found no brood size effect in Glaucous-winged Gulls (*Larus glaucescens*). No one has demonstrated changes in begging in response to experimental changes in brood size.

Experimental evidence that chicks change their begging behavior in relation to sibling competition comes from Smith and Montgomerie's (1991) study of begging in American Robins (*Turdus migratorius*). Smith and Montgomerie deprived individual nestlings of food and then returned them to their brood mates. Deprived chicks begged relatively more and were fed more than their "control" nest mates, which had remained in the nest during the deprivation period. The control chicks also altered their begging level, apparently in response to the changed begging

of their hungry nest mate. Smith and Montgomerie (1991) did not monitor parental provisioning to control chicks during the deprivation period, however, and the response of these controls may have been confounded by changes in hunger level. Similarly, Yellow-headed Blackbird (*Xanthocephalus xanthocephalus*) chicks tended to increase begging following the temporary food deprivation of a nest mate (Price and Ydenberg 1995), but again, the behavioral change might have followed changes in hunger level. Young Zebra Finches (*Taeniopygia guttata*) increased begging upon hearing played-back begging calls (Muller and Smith 1978), but Yellow-headed Blackbirds did not, likely because they were well fed and satiated (Price 1994).

In this paper, I return to the first approach and experimentally investigate the effect of brood size on begging to extend the comparative studies and to complement the begging manipulation studies. I assess the effect of increased competition on sibling behavior. I do not compare the behavior of individual nestlings of differing need and abilities, nor do I examine the relationship between begging and provisioning (other than as a potential confound), which forms the focus of many studies of nestling begging (e.g. Litovich and Power 1992).

Yellow-headed Blackbirds lay two to five eggs that hatch asynchronously within one to three days; brood reduction is common (Willson 1966, Richter 1984).

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Parents feed nestlings primarily with emergent odonates (Orlans 1966, Willson 1966). Yellow-headed Blackbird nestlings thus experience changes in brood size and fluctuations in food availability. Herein, I ask whether broods of Yellow-headed Blackbirds increase their begging levels when faced with increased competition for food in the form of an extra nest mate.

**Methods.**—I studied begging and provisioning in Yellow-headed Blackbirds from May through July, 1990 to 1993, on the Creston Valley Wildlife Management Area, a 7,000-ha managed marsh in southeastern British Columbia, Canada. The study sites (three colonies, each with >100 nesting adults) contained islands of cattails (*Typha* spp.) growing in 0.5 to 1.2 m of water. I monitored the hatching and growth of 100 to 200 broods each year, visiting nests once per day near hatching and every second day subsequently. Chicks were marked with paint for identification (color randomly assigned). I performed two chick-addition experiments: (1) in 1992, I added single nestlings to natural broods under field conditions; and (2) in 1993, I added single nestlings to artificially created broods in the laboratory, while attempting to control nestling hunger level. All experimental nestlings had known histories.

In the field experiment I used 11 broods in two nesting areas as subjects. I placed a sham video camera in front of the nest one day before manipulation to allow parental habituation and replaced it with a real video camera on the day of the trial. I chose families randomly from among those observable by camera (i.e. not in the center of a clump of cattails), and with three nestlings alive on the day of the experiment. Nestling ages ranged from five to nine days, with a one- to two-day spread within each brood. At this age, chicks beg loudly and do not fledge prematurely (most chicks fledge at 11 to 12 days). Some broods hatched from clutches of three ( $n = 7$ ) whereas others had lost one chick through starvation ( $n = 4$ ). I reduced the effect of such among-nest variation by performing all comparisons within broods.

I added one chick to each brood for half of a 2-h observation period, and observed the natural three-chick brood during the other half (treatment order randomly assigned). The added nestling, from a nearby three- or four-chick brood, was selected to have a mass and age within the range of the chicks in the experimental brood. The mean mass of added chicks (measured immediately before each trial) was  $28.7 \pm$  SD of 5.6 g; those of brood mates were  $35.2 \pm 6.8$  g for the heaviest,  $30.8 \pm 7.4$  g for the middle, and  $25.0 \pm 6.4$  g for the lightest. The mean age of added chicks was  $6.5 \pm 1.2$  days; those of brood mates were  $7.4 \pm 0.9$  days for the oldest and  $5.9 \pm 0.8$  days for the youngest. I did not add sick or starving chicks, nor those infested with mites.

The video tapes were transcribed by an observer naive to the purpose of the experiment but experienced with watching nests of Yellow-headed Black-

birds. Measured aspects of begging included loudness, intensity, and total duration (s) of vocalizations during and between parental visits. Loudness was measured from the tapes using a decibel meter placed at a constant distance from the speaker (levels 1, 2 and 3 were roughly equivalent to  $\leq 50$  dB, 50–70 dB, and  $\geq 70$  dB; because cameras were not equidistant from broods, these measurements are consistent within and not between trials). Intensity was measured on a ranked scale of perceived begging effort: (0) no visible effort; (1) movement only; (2) movement + single vocalization; (3) movement + several vocalizations  $\leq 1/s$ ; and (4) movement + several vocalizations  $> 1/s$ . This scoring system is similar to that used by Litovich and Power (1992), but focuses more closely on vocal behavior. I calculated brood mean loudness, mean intensity, and total duration of begging for the two treatment periods (one value for each brood of siblings for each hour) and analyzed these data between treatments within nests.

Under laboratory conditions where I attempted to control chick hunger level, I modified the addition experiment in June 1993. I removed eight chicks from one colony on each of five days for use in 10 experimental trials. I used only apparently healthy birds from 7 to 10 days old, generally removing one chick from natural broods of three or four to change the natural broods as little as possible. I returned all experimental chicks to their original nest at the end of each day. Parents accepted nestlings upon their return, and all chicks continued to grow normally.

The eight chicks constituted two artificial sets of four (three plus an "addition" chick). Each initial brood of three sat nestled inside a plastic basket ( $10 \times 10 \times 6$  cm) that was lined with clean tissue paper and placed in a heated container. The addition chicks sat alone in similar containers. I fed all nestlings to satiation with moistened pieces of cat food (from bulk dried pieces of similar size) until 30 min before experimental trials. I defined satiation as the point when a nestling either failed to gape in response to acoustic cues (taps on the container) on two consecutive attempts 5 s apart, or accepted food and did not swallow it within 10 s (criteria determined for a different experiment; Price 1994).

Each trial consisted of 2 h of observation (via video camera), 1 h with three chicks and 1 h with four chicks. In this experiment, treatments were randomly assigned in 0.5-hour blocks to allow subjects to experience brood augmentation and reduction repeatedly, and to decrease any bias due to trends in hunger over the 2-h period.

Feeding "visits" occurred every 5 min throughout the trials. I fed one chick per visit, sequentially, so that each received food every 15 min. Large chicks ( $\geq 35$  g) ate a  $5 \times 5 \times 7$  mm portion of moistened cat food ( $\frac{1}{2}$  of a piece), and small chicks ( $< 35$  g) ate a  $5 \times 5 \times 5$  mm portion ( $\frac{1}{4}$  of a piece). These quantities resulted in similar hunger levels over several hours

(measured as the number of  $5 \times 5 \times 5$  mm portions of food eaten before satiation at an hourly feeding; Price 1994). Prior to feeding, I passed a shadow over the brood and tapped the container. As soon as begging started, I used forceps to feed the chosen chick as quickly as possible and tapped the container again to simulate continued parental presence. In the four-chick treatments, I fed the three brood mates as before, and fed the added chick at the same time as feeding one of the regular chicks (i.e. with forceps held in each hand), so as not to increase the duration of the feeding visit while keeping feeding rate constant.

I calculated mean begging intensity and loudness and the total duration of vocalizations during and between feeding visits for each 0.5-h period (i.e. one value per variable for each three-chick set per 0.5 h). I also measured "rearing" height, estimated as the distance the base of the bill moved vertically (chicks did not rear before visits, but began with their heads at slightly different levels). I removed one nest from analysis due to an inconsistent feeding protocol that resulted in chicks not begging at all during most of the visits (15/18) over three of the four periods. I analyzed the data for the remaining nine trials using an analysis of variance blocked by trial and by time period, predicting that chicks would beg more in broods of four than in broods of three.

**Results.**—The three experimental nestlings vocalized for longer during parental visits when a fourth chick was present, but did not beg for longer between visits (Fig. 1; during visits,  $t = 2.72$ ,  $P = 0.02$ ; between visits,  $t = 0.33$ ,  $P > 0.5$ ; paired  $t$ -test,  $df = 10$ ; mean increase of  $51.1 \pm 18.8$  s per chick). When accompanied by an extra chick, nestlings begged more intensely in all 11 broods (three-chick broods,  $\bar{x} = 2.68 \pm 0.16$ ; four-chick broods,  $\bar{x} = 2.96 \pm 0.17$ ;  $z = 2.95$ ,  $P = 0.003$ ; Wilcoxon matched pairs; proportion of visits when chicks gave multiple vocalizations: three-chick broods,  $\bar{x} = 0.69 \pm 0.09$ ; four-chick broods,  $\bar{x} = 0.85 \pm 0.07$ ), and more loudly in 8 of 10 broods (one tie; three-chick broods,  $\bar{x} = 2.21 \pm 0.15$ ; four-chick broods,  $\bar{x} = 2.42 \pm 0.16$ ;  $z = 2.4$ ,  $P = 0.02$ ).

I calculated feeding rate to judge if chicks likely grew hungrier due to treatment. Parental provisioning rate did not increase to broods of four (number of visits: three-chick broods,  $\bar{x} = 11.82 \pm 1.95$ ; four-chick broods,  $\bar{x} = 11.64 \pm 1.61$ ;  $t = 0.06$ ,  $P > 0.5$ ; including visits where the added nestling was fed). Hence, the number of feeds per chick tended to decrease (three-chick broods,  $\bar{x} = 4.0 \pm 0.5$  visits per chick; four-chick broods,  $\bar{x} = 3.5 \pm 0.4$  visits per chick;  $F = 2.63$ ,  $df = 1$  and  $21$ ,  $P = 0.12$ ; repeated-measures ANOVA blocked by nest, on feeds to the three siblings), and chicks may have been hungrier with an extra nest mate.

In the laboratory experiment, nestlings begged significantly longer during the four-chick treatment (three-chick broods,  $\bar{x} = 187.72 \pm 18.63$  s per chick;

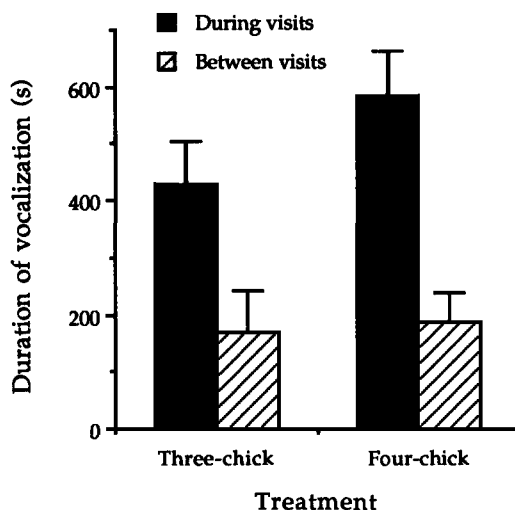


FIG. 1. Time spent vocalizing by broods of three siblings (summed per brood) with and without an extra nest mate. Bars show mean duration of vocalization in 11 broods ( $\pm$  SE) during parental visits and between visits.

four-chick broods,  $\bar{x} = 205.11 \pm 16.86$  s per chick;  $F = 12.14$ ,  $df = 1$  and  $23$ ,  $P = 0.002$ , blocked by trial and period; Fig. 2). The high error associated with begging length results from strong trial and period effects (trial effect,  $F = 13.29$ ,  $df = 8$  and  $23$ ,  $P < 0.001$ ; period effect,  $F = 17.66$ ,  $df = 3$  and  $23$ ,  $P < 0.001$ ). Eight of nine broods begged less during the first 0.5-h treatment than during the following three periods, and the former was responsible for the significant effect (orthogonal contrasts).

Chicks did not beg significantly louder in four-chick broods (mean loudness: three-chick broods,  $\bar{x} = 2.27 \pm 0.13$ ; four-chick broods,  $\bar{x} = 2.32 \pm 0.13$ ;  $F = 2.41$ ,  $df = 1$  and  $23$ ,  $P = 0.13$ ). Nor did they change their begging intensity (three-chick broods,  $\bar{x} = 2.08 \pm 0.12$ ; four-chick broods,  $\bar{x} = 2.02 \pm 0.08$ ;  $F = 0.00$ ,  $df = 1$  and  $23$ ,  $P = 1.00$ ), the length of between-visit begs (three-chick broods,  $\bar{x} = 38.83 \pm 15.96$  s per chick; four-chick broods,  $\bar{x} = 42.89 \pm 9.93$  s per chick;  $F = 1.16$ ,  $df = 1$  and  $23$ ,  $P = 0.29$ ) or rearing height (three-chick broods,  $\bar{x} = 92 \pm 6$  mm; four-chick broods,  $\bar{x} = 86 \pm 5$  mm;  $F = 0.00$ ,  $df = 1$  and  $23$ ,  $P = 1.00$ ). I examined changes within broods excluding the first period for patterns obscured by the period effect (using a mean value for treatments observed in two periods). Eight of nine broods begged for longer with four chicks ( $t = 2.79$ ,  $P = 0.02$ ; paired  $t$ -test), five of nine begged louder ( $z = 0.89$ ,  $P = 0.37$ ; Wilcoxon matched pairs), five of nine begged more intensely ( $z = -0.06$ ,  $P > 0.5$ ), seven of nine begged for longer between visits ( $t = 1.01$ ,  $P = 0.34$ ) and three of nine reared more ( $z = -0.89$ ,  $P = 0.37$ ). Again, only begging duration increased significantly.

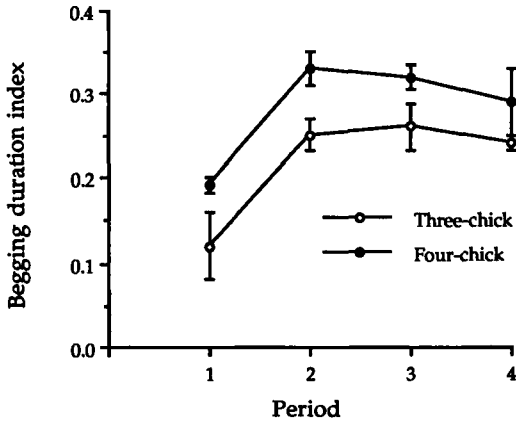


FIG. 2. Begging duration for nestlings in three-chick and four-chick broods. Data are expressed as time spent begging in a period as a proportion of total time spent begging over all four periods for each nest ( $\bar{x} \pm SE$  for nine nests), graphically controlling for trial and period effects. Because each brood appears in some three- and some four-chick means, proportions do not sum to one.

*Discussion.*—In the field, chicks faced with an added competitor in the nest significantly increased their begging length, loudness, and intensity. Because feeding visits in the field did not compensate for the presence of an extra mouth, chicks were likely hungrier during this period. Hungry chicks beg more (Smith and Montgomerie 1991, Litovich and Power 1992); hence, the change in begging may have reflected an increased hunger level rather than potential food competition. Hungry Yellow-headed Blackbirds, however, increase the duration of their begging both during and between parental visits (Price and Ydenberg 1995). In the addition experiment, chicks did not increase the length of their between-visit begs, suggesting that they were not much hungrier. Laboratory measurements of begging and hunger suggest that the given increase in hunger could account for 25% of the observed increase in begging (Price 1994).

The laboratory experiment provides evidence that nestlings increase at least one aspect of begging level in response to an increase in brood size, independently of hunger level. Chicks significantly increased their begging duration during visits. They did not, however, significantly increase begging loudness, intensity, the length of between-visit begs, or rearing height. These results suggest that the increase in begging loudness and intensity seen in the field may have reflected hunger, while the increase in begging duration reflected competition. The more complex design and smaller sample in the second study reduced its power; a larger sample might detect effects of competition other than begging duration.

Chicks changed their begging behavior between the first and subsequent periods of the laboratory

experiment. They responded less readily to taps on their container during the first period, and may have taken time to learn the relationship between an unfamiliar sound and a feeding visit. A 30-min learning period might have reduced this effect. Alternatively, chicks may have been insufficiently deprived of food before the first period. The second possibility is more troubling, as it suggests that hunger levels changed over time. The experiment was designed, however, to reduce the correlation between hunger level and competition seen in the field. If any correlation existed between hunger and competition in the laboratory, it was negative, because six of the nine broods experienced augmentation during the first period. If hunger level increased over time, these chicks experienced higher levels of competition while the least hungry. Analysis excluding the anomalous first period did not reveal any new patterns.

Stamps et al. (1989) found an effect of brood size on begging level in an observational study comparing singletons and larger broods. These investigators were unable to detect any effect in broods of more than two, but since they did not manipulate brood size, variation in provisioning between families may have obscured any pattern. The addition experiments presented here show that, within families, Yellow-headed Blackbird nestlings in broods of three beg more in response to the presence of an extra nest mate.

Siblicidal egrets do not reduce aggression directed at siblings if food availability increases (Mock et al. 1987), but fight less in reduced broods (two versus three chicks; Mock and Lamey 1991). Food levels are unpredictable from day to day in egrets, and brood size may be a better indicator of future food demands than hunger level (Mock and Lamey 1991). Non-aggressively brood-reducing species faced with unpredictable food supplies may also use the number of nest mates as an indicator of future competition. Yellow-headed Blackbirds fall into this category because they provision their young with emergent insects—a resource depending strongly on unpredictable weather patterns. The increase in begging with increased brood size shown here suggests that Yellow-headed Blackbirds can assess the potential competition within their brood and that they respond to increased competition with increased begging.

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