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Release of gaping in hummingbirds (Trochilidae).—Gaping is an instinctive behavior of many altricial birds in which the nestling displays a widely opened bill and, in most cases, produces loud begging calls to stimulate feeding by the parents (Stresemann 1927–1934). Gaping may be elicited by non-specific or specific stimuli (Skutch 1976, Bischof and Lassek 1985). At one time, gaping was considered to be restricted to passerines, but it has also been documented in certain non-passerines, e.g., woodpeckers (Picidae), cuckoos (Cuculidae), and mousebirds (Coliidae) (Stresemann 1927–1934).

Within the non-passerine order Apodiformes, Lack (1956) describes gaping in swifts (Apodidae), and Wagner (1945) and Schuchmann (1983) studied gaping in hummingbirds (Trochilidae). Here, I describe ontogenetic variation in gape-release stimuli in hummingbirds and discuss its ecological significance for nesting behavior. The results discussed are based on field and laboratory studies of 14 trochilid species (Table 1) over an observation period of 8–23 days, during which the behavioral interactions between adults and chicks were recorded. I also studied reproductive biology of four of these hummingbird species in the laboratory, using hand-reared young. In all cases, experiments described below were conducted on chicks which had recently been fed, thereby increasing the threshold of any gape-release response to its maximum.

Generally, hummingbirds build open, cup-shaped nests, often placed in an exposed location on the terminal branches of trees and shrubs. The female builds the nest alone, and in all species studied thoroughly to date, rears the young without the help of her mate. From studies on North, Central, and South American species, it appears that they can achieve, at most, two successful broods per year.

For all hummingbird species studied here, three well-differentiated stages of development were identified:

Stage I.—From day 1 to about day 5 after hatching, the nestling is unfeathered except for two dorsal rows of neossoptiles about 5 mm long (Collins 1978), and its eyes are still closed. During this stage the chicks, generally two in hummingbirds, are inactive in the nest.

For all 14 species studied, when the female arrived with food, she landed on the edge of the nest and touched the nestlings behind the eye-bulges with her beak. In response to this stimulus, the young birds always gaped and were fed by the female. Indeed, gaping could be induced 4–6 times successively in nestlings of this age by touching the eye-bulges (e.g., with a match-stick). Because feeding did not follow gaping in these experiments, a latent period of about one minute had to pass until a similar reaction could again be triggered in the offspring. No begging calls were heard at this stage.

Stage II.—Day 6 to day 9 was the period of major feather development on wings, tail and back. The dorsal neossoptiles were not shed but remained attached to the contour feathers. Begging calls were still not heard at this stage.

Stage III.—This period of the nestling development covered day 10 until fledging, i.e., days 17–19. By this time, chicks were almost completely feathered and often sat on the edge of the nest with their backs turned away from the nest cup, but still failed to give begging calls.

During stages II and III, the female gradually approached the nest and began to hover over the feathered young with an increased wing-beat frequency that was acoustically perceptible. When the dorsal neossoptiles attached to the chicks' contour feathers were visibly agitated by the resulting air movement, chicks invariably began to gape. In fact, gaping was easily triggered in the chicks at this stage of development by blowing on their dorsal neossoptiles (e.g., with a straw). No touching of the eye-bulges was observed during these stages. Thus, it appeared that the gape-releasing stimulus had changed. When gaping, and also during feeding, the chicks raised themselves only slightly and remained in a rather stooped position in the nest.

With increasing age (from about day 15 onwards), the chicks often sat at the edge of the nest during the day, mostly with their backs turned away from it. At feeding time, the female hovered just above the chicks, causing movements of their dorsal neossoptiles. Only after this stimulus would the nestlings gape and then be fed by the female. In all species observed, begging calls were still not heard at this developmental stage.

When the dorsal neossoptiles for seven chicks of four species (marked with asterisks in Table 1) were plucked out with forceps from laboratory-reared hummingbirds on day 10 after hatching, gaping reactions were not elicited by the female's hovering closely over their

TABLE 1

NEST SITE AND NEST CHARACTERISTICS OF 14 HUMMINGBIRD SPECIES

Taxa	Place of study	Habitats	Nest architecture	No. of nests
Glaucis hirsuta	ASA Wright Nature Centre, Trinidad	tropical rain forest	open, hanging	17
Phaethornis ruber	Voltzberg Mts., Surinam	tropical rain forest	open, hanging	1
Colibri coruscans[a]	Quito, Ecuador;	cultivated area	open, on branch	2
	laboratory	—	open, on branch	2
Chlorestes notatus	Arima Valley, Trinidad	garden	open, on branch	2
Thalurania furcata[a]	NW Cali, Colombia;	subtropical wet forest	open, on branch	1
	laboratory	—	open, on branch	3
Coeligena coeligena	NW Cali, Colombia	cloud forest	open, on branch	1
Eriocnemis luciani	E Quito, Ecuador	subpáramo	open, on branch	1
Haplophaedia aureliae	NW Cali, Colombia	cloud forest	open, hanging	2
Metallura tyrianthina	Pan de Azucar, Colombia	subpáramo	semi-domed	2
Aglaiocercus coelestis[a]	Nariño, Colombia;	cloud forest	completely domed	2
	laboratory	—	completely domed	3
Trochilus polytmus[a]	Greenhills, Jamaica;	elfin forest	open, on branch	8
	laboratory	—	open, on branch	14
Philodice evelynae	Andros, Bahamas	pine forest	open, on branch	7
Calypte anna	San Bernadino Mts., California	pine forest	open, on branch	5
Archilochus alexandri	Averill Park, L.A., California	park	open, on branch	6

[a] Dorsal neossoptiles removed to study gaping reactions.

backs. However, when a hovering female landed on a chick's back, it gaped immediately and was fed. Two days after neossoptiles were removed, gaping reactions could once again be observed with the approach of the female. The absence of tactile stimulation suggests that optical signals may now have become adequate stimuli.

Begging calls were given by the hummingbird chicks only after fledging. They gave loud begging calls, irrespective of the presence of the female, but called more vigorously when she was within view.

Details of chick-feeding behavior are known for many passerines which produce altricial young. As comparative ethological studies show, the release of gaping stimuli in passerines is relatively non-specific. For example, gaping can be stimulated in young finches through nest vibration caused by the parents' landing on the edge of the nest (Tinbergen 1951). Furthermore, by the time that chicks can perceive and react to supplementary visual stimuli, gaping in passerines continues to be relatively non-specific (Tinbergen op. cit.).

Although the begging behavior of chicks of many passerine species may easily alert the attention of a potential nest predator, this danger can be reduced through the choice of a concealed nesting site, protective nest construction (e.g., enclosed domed nests), and by camouflaging the nest with plant material from the immediate vicinity. The mortality rate of young passerines by predators is further compensated for by a relatively high reproduction rate of several broods per year (reviewed by Cody 1971).

Comparatively little is known about the chick-feeding behavior of those non-passerines whose young hatch as blind altricial birds. From observations of Lack (1956), European Swifts (*Apus apus*) gape in reaction to relatively non-specific tactile stimuli by the parents. In contrast, in hummingbirds, the closest modern relatives of swifts, non-specific tactile and acoustic stimuli appear to be rare.

Because hummingbirds forage while hovering, they can no longer climb with their feet which serve only for perching. Consequently, they build exposed but camouflaged nests easily accessible in flight. The exposed nest site and low reproductive output probably also favored the development of this very specific gape-response behavior. Loud begging calls of the offspring as well as uncontrolled begging and gaping movements through non-specific causes, e.g., vibration of nest by wind, would be types of behavior that could potentially betray the nest site to predators such as tree lizards, snakes, and birds. Thus, I suggest that the highly specific stimuli described herein which elicit gaping by unfledged hummingbird chicks are adaptations for reducing predation on exposed nest sites. Consistent with this hypothesis is the fact that chicks of those hummingbirds, e.g., sylphs (*Aglaiocercus* spp.) and metaltails (*Metallura* spp.) which build enclosed domed nests, give begging calls very shortly after hatching, presumably in response to tactile stimuli from the female as she enters the nest.

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Decline of the Long-eared Owl in New Jersey.—Long-term observations of the Long-eared Owl (*Asio otus*) in New Jersey suggest that numbers are decreasing at traditional winter roosts (Kane pers. obs.). Nesting activity is rare within the state and also may be decreasing. In this paper, we review the previous wintering records of Long-eared Owls in New Jersey and analyze Christmas Bird Count (CBC) data from 1956 to 1986, published annually in *American Birds.*

Methods.—We have monitored Long-eared Owls for 10 or more years in New Jersey, New York, Connecticut, and Pennsylvania. Most of our field work has involved checking of known roost sites (Smith 1981, Bosakowski 1984), as well as frequent reconnaissance trips of new areas. During the breeding season, intensive ground searches for raptor nests have been made primarily in northern New Jersey, southeastern New York, western Connecticut (e.g., Bosakowski 1982; Speiser and Bosakowski 1984, 1987, 1988; Bosakowski et al. 1989), and northeastern Pennsylvania, but no active nests of the Long-eared Owl have been discovered during these surveys. In addition to field observations of winter roosts, we summarized all winter Long-eared Owl sightings reported in "Records of New Jersey Birds" since 1966. We also summarized all CBC data for New Jersey from 1956–86. Only CBC stations that recorded at least one Long-eared Owl in their history were included in this analysis. Due to the increasing number of counts and observers since 1956, the data were normalized relative to a measure of field effort. Raynor (1975) found that party-hours had the highest correlation with numbers of birds observed. Since wintering Long-eared Owls are faithful to their day roosts (Smith 1981, Bosakowski 1984), some observers make special trips in advance to find these roosts for the CBC day, thus somewhat biasing the data. This effect reduces the value of normalizing factors such as party-hours and therefore we have presented the data using several different indices of abundance or effort.

Results.—We have observed a decrease in Long-eared Owls at many traditional winter roosts. Of 58 known winter roost sites during 1967–1988, six have been eliminated, and three have been thinned or affected by land development. With 49 roost sites remaining, most of the owls should also remain, but many roosts have had noticeable decreases or abandonment during the past decade. Unfortunately, long-term coverage at these roosts was too inconsistent to lend numerical support to our inquiry, although Smith (1981) has documented a decline at a traditional winter roost in central Pennsylvania that was checked annually for nearly 20 years. Prompted by these preliminary observations, we decided to search the regional literature and CBC records for evidence of a decline.