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A SUPPLEMENTAL FUNCTION OF THE AVIAN EGG TOOTH

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Abstract. Hatchlings use egg teeth to help break through the shell during hatching, but these structures could have an additional function of increasing nestlings' visibility. I investigated the size, color, and persistence of egg teeth in woodpeckers, which nest in dark cavities. Many species of woodpecker have two egg teeth, one each on the tip of the maxilla and of the mandible, which, together with the pale flanges, frame the open mouth when nestlings gape. A spectrometer confirmed that reflectance of Northern Flicker (*Colaptes auratus*) egg teeth is higher than that of the flanges across a wide range of wavelengths, reaching nearly 100% reflectance in the wavelengths most visible to woodpeckers. Reflectance of flanges peaked in the ultraviolet, which is less visible to woodpeckers. Therefore, parent woodpeckers can probably see egg teeth better than flanges. Within a brood, the brightness of egg teeth or flanges was not dependent on nestlings' size (hatching order), suggesting these structures are not cues of nestlings' quality. Flickers retained upper egg teeth until fledging, but the size of egg teeth did not increase after hatching. A review of the literature suggests some burrow-nesting seabirds also retain egg teeth for a long time, reinforcing the idea that egg-tooth reflectance may have evolved independently in several phylogenetic groups in which parents must find nestlings in the dark.

Key words: Colaptes auratus*, color, detectability, egg tooth, nestling, Northern Flicker, reflectance, woodpecker.*

Una Función Suplementaria del Diente de Huevo de las Aves

Resumen. Los polluelos utilizan dientes de huevo para quebrar la cáscara del huevo al momento de eclosionar, pero estas estructuras podrían tener la función adicional de aumentar la visibilidad del polluelo. Investigué el tamaño, el color y la persistencia de los dientes de huevo en carpinteros que anidan en cavidades oscuras. Muchas especies de pájaros carpinteros tienen dos dientes de huevo, uno en la punta del maxilar y el otro en la punta de la mandíbula, los que junto a las comisuras de color pálido enmarcan la boca abierta de los polluelos que solicitan alimento. Un espectrómetro confirmó que la reflexión del diente de huevo de *Colaptes auratus* es mayor que la de las comisuras para un amplio rango de longitudes de onda, alcanzando cerca de 100% de reflexión en las longitudes de onda que son más visibles para los carpinteros. La reflexión de las comisuras fue máxima en el ultravioleta, que es menos visible para los carpinteros. Por esto, los padres probablemente pueden ver mejor los dientes de huevo que las comisuras. En una nidada, el brillo de los dientes de huevo o de las comisuras no dependió del tamaño del polluelo (orden de eclosión), lo que sugiere que estas estructuras no están señalizando la calidad de los polluelos. Los polluelos de *C. auratus* mantuvieron el diente de huevo superior hasta el emplumamiento, pero el tamaño del diente no aumentó después de la eclosión. Una revisión de la literatura sugiere que algunas especies de aves marinas que anidan en cuevas también mantienen el diente de huevo por un periodo largo, lo que refuerza la idea de que la reflexión del diente de huevo podría haber evolucionado de forma independiente en varios grupos filogenéticos en los que los padres tienen que encontrar a sus polluelos en la oscuridad.

INTRODUCTION

In altricial birds, brood size seems to be adjusted to the number of young that parents are able to nourish (Lack 1954), so there is strong selection for parents to collect, handle, and transfer food to the young efficiently. At the same time, offspring attempt to influence parental allocation of food through begging, which has been studied extensively (review by Wright and Leonard 2002). Until recently, the role of nestling color in directing food allocation has received less attention than vocal

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and postural components of begging displays (Kilner 2006). Bright red or yellow mouths and/or pale flanges with high reflectance in the ultraviolet (UV) could be signals of nestlings' health and quality, which parents prefer (Saino et al. 2000, 2008, De Ayala et al. 2007). Alternatively, bright colors could be conspicuous against the background of the nest and simply help parents to detect nestlings (Ficken 1965, Götmark and Olsson 1997, Heeb et al. 2003).

Detectability may be a particular challenge for birds nesting in dark cavities where the parent must adjust its eyes quickly after entering from bright light outside. Consistent with the idea that parents have difficulty seeing in dim light, nestlings of species that nest in tree cavities often have paler flanges than those of species that nest in the open (Ingram 1920, Kilner and Davies 1998, Hunt et al. 2003), and the flanges of cavity nesters contrast more with their gapes and body skin than do those of nestlings in open-cup nests (Avilés et al. 2008). In addition to pale whitish flanges, other structures of the mouth could enhance the visibility of nestlings in cavities.

The egg tooth is a small calcareous protuberance on the bill tip of the maxilla and, rarely, mandible, of most hatchlings (Clark 1961). In most species, the egg tooth seems to fall off or wear away a few days after hatching, and its function is thought to be to help the embryo puncture the egg's thick membranes and shell during hatching (Clark 1961). Nevertheless, in some species, the size and persistence of the egg tooth suggest an alternative or additional function. In a review of egg teeth, Wetherbee (1959:120) noted "the neonatal Yellow-shafted Flicker (*Colaptes auratus*) has the most peculiar egg tooth, or teeth, encountered . . . the tips of both mandibles have an extensive, thick, gleaming white covering that appears as if they had been dipped in enamel . . . the necessity for this armour is puzzling." Short (1982) suggested that egg teeth of woodpecker nestlings could enhance their bearers' visibility.

Visibility is a function of both nestling color ("brightness" = amount of reflectance at various wavelengths) and the parent's visual sensitivity to those wavelengths (Avilés and Soler 2009). The potential importance of UV reflectance, and not only colors visible to the human eye, was raised after the discovery that nestlings' skin (Jourdie et al. 2004) and especially flanges (Hunt et al. 2003) reflect maximally in the UV range. Although all birds can probably detect UV reflectance to some degree (Håstad 2003), woodpeckers have limited capacity to do so with their "VS-type" of visual pigment with a maximum sensitivity between 402 and 426 nm (Cuthill et al. 2000). In contrast, many passerines have a "UVS-type" of retinal pigment that is more sensitive to shorter wavelengths and is maximally sensitive at 355–376 nm.

Here, my first goal was to measure the potential effectiveness of egg teeth as a visual signal by quantifying the spectral reflectance of the both the flanges and egg teeth of the Northern Flicker, a woodpecker nesting in deep and dark cavities. I was interested in determining whether egg teeth might be equally or even more visible than flanges to parent flickers by comparing reflectance in the UV and in visual wavelengths, assuming UV wavelengths are less visible to woodpeckers.

A second goal was to see whether the brightness of mouth colors is correlated with nestlings' quality. In many birds, nestlings within a brood hatch asynchronously, with the last-hatched nestling representing a marginal offspring whose chance of death is greater (Mock and Forbes 1995). Last-hatched nestlings are smaller, and often physically weaker, than older nest mates. Flicker broods usually contain a nestling that hatches a day or two later than its siblings (Wiebe and Moore 2008), so I tested whether the brightness of flanges and egg teeth of the oldest (heaviest) nestling were greater than those of the youngest (lightest) nestling in a brood. I also measured the size and retention of egg teeth throughout the flicker's nestling period and reviewed the literature for similar data on other woodpeckers to see whether egg teeth serving as a signal are widespread in this family.

METHODS

I studied flickers at Riske Creek in central British Columbia, Canada (51° 52′ N, 122° 21′ W), in a study area of approximately 100 km^2 where 80–160 nests have been monitored annually since 1998. The habitat consists of a mosaic of open grassland and small ponds interspersed with clumps of quaking aspen (*Populus tremuloides*) and larger patches of mixed forest. Most (>95%) flicker nests are in aspen trees. Wiebe and Swift (2001) and Fisher and Wiebe (2006a) summarized their attributes and placement on the landscape. Active territories were found in late April and early May by playing of tape-recorded territorial calls and checking of old cavities since flickers often reuse nests (Wiebe et al. 2007). After laying began, a small replaceable "door" was cut into the tree trunk near the base of the cavity to provide access to the nestlings, but it did not affect reproductive success of the pair or subsequent nest reuse (Fisher and Wiebe 2006b).

Flicker broods, which contain eight young on average, hatch slightly asynchronously, typically over 1–2 days, and so I measured the color of the largest and the smallest nestlings within broods in which no nestling had died. In 2008, when the oldest nestling was 4–6 days old, I transported the two nestlings per nest indoors to where a spectrometer was set up and then returned them immediately to their nests after measuring them, the whole transportation and measuring process taking 15–30 min. Parents did not abandon the nests, and average rates of fledging from measured broods (84%) were similar to those of other nests in the population that year (82.8%). Reflectance spectra of nestlings, in the 300- to 800-nm range, were recorded with an Ocean Optics (Dunedin, FL) model USB 2000 spectrometer with a PX-2 pulsed xenon light source and OOIBase 32 software. I calibrated the spectrometer with a Labsphere (North Sutton, NH) reflectance standard before measuring each nestling. The probe, which was encased in a black matte sheath to prevent external light from entering, was placed flush against the nestling's flange and egg tooth at about an angle of 90° from the flat surface.

For each nestling, I made two recordings of the flanges, one of the left flange and one of the right. Similarly, I took two readings of the (upper) egg tooth, one reading on the left side of the culmen and one on the right since the ridge along the center line of the egg tooth prevented flat placement of the probe. For analyses, for each nestling, I averaged the two readings of the flange and of the egg tooth. Since the flicker's visual sensitivity to UV drops off below 400 nm and it probably can't detect wavelengths shorter than about 350 nm (Cuthill et al. 2000), I divided the resulting spectrograms into the region below 400 nm, which conveniently corresponds to what is considered UV (300–400 nm), and the region above 400 nm, the wavelengths visible to the human eye (400–700 nm). I assumed that flickers have good visual perception above the UV threshold but weak detection below 400 nm in the UV range. Following Andersson et al. (1998), I calculated an index of "overall brightness" in the zones above and below 400 nm by summing the reflectance values. I used a paired *t*-test to assess differences in reflectance between the large and small nestlings within a brood and compared their brightness in the spectrum above and below 400 nm.

In 2009 only, I took digital photographs of egg teeth of nestlings at various ages opportunistically as I visited nests. To avoid pseudoreplication, I used only one photo per nestling per brood. The nestling's head and mandible were placed flat against a dark surface beside a ruler. Using the macro (close focus) setting on a Canon A80 camera, I took a picture of the head and egg tooth from directly above. I estimated the length of the culmen (from base) and the maximum length of the egg tooth along the center line of the culmen to the nearest 0.05 mm from the photos by comparison with the ruler in the photograph. I noted the presence or absence of upper and lower egg teeth as the nestlings aged.

To see whether upper and lower egg teeth are prevalent among woodpeckers and persist until late in the nestling period, I searched for published information on the egg teeth and depth of tree-cavity nests of 21 North American woodpeckers from the accounts in the *Birds of North America*. For European species, I checked Cramp et al. (1985). I also solicited unpublished information from other researchers studying woodpeckers and searched the Internet for additional photographs of young nestling woodpeckers.

STATISTICAL ANALYSES

Statistics were done in SPSS version 16.0 (SPSS, Inc., Chicago), and all tests were two-tailed with significance set at $P < 0.05$. Values reported under Results are means ± SD.

RESULTS

Hatchling flickers had calcareous egg teeth on both the upper and lower bill tips (Fig. 1a), and the upper egg tooth remained visible on nestlings 20–21 days old, a few days from fledging (Figs. 1b, 2). The lower egg tooth disappeared between the ages of 13 and 14 days or about halfway through the nestling period, although the tip of the mandible continued to be pale whitish. The length of the upper tooth decreased with nestling age (regression, $n = 69$, slope $= -0.035$, $r^2 = 0.29$, $P < 0.001$) at the same time the culmen obviously grew (Fig. 2). Within the first two days of hatching, the length of the egg tooth averaged 3.07 mm ± 0.39, $n = 23$, while at 20 days it was 2.57 mm ± 0.30, $n = 8$.

I measured the reflectance of 20 nestlings (large and small from 10 nests) when the oldest nestling in the brood was 5 or 6 days old and the younger nestling was 1–1.5 days younger. Reflectance spectra of egg teeth did not show a peak but were very bright across a wide range of wavelengths and declined in the UV wavelengths below about 350 nm (Fig. 3). In contrast, the reflectance of the flanges peaked in the UV at an

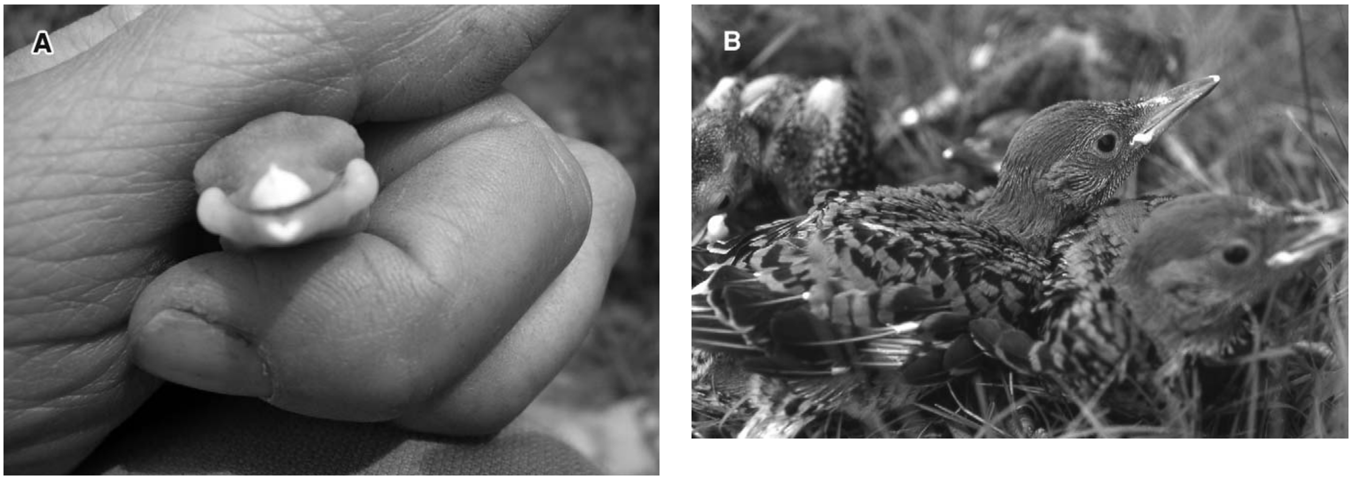

FIGURE 1. Northern Flicker (*Colaptes auratus*) nestlings, showing the extensive calcareous egg tooth on the maxilla and the smaller calcareous covering on the mandible of a 1–day-old nestling (a) and the persistence of the egg tooth on the maxilla of nestlings 19–20 days old (b).

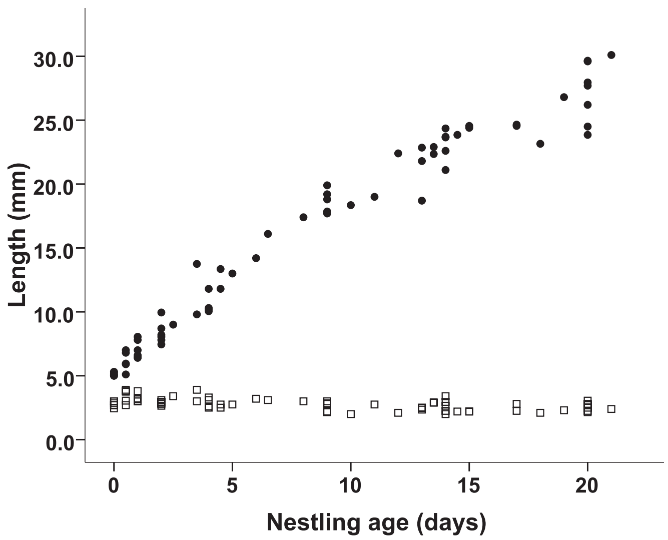

FIGURE 2. Length of the culmen (dark circles) increases steadily with nestling age while length of the egg tooth (white squares) tends to decline slightly. Each set of data points is from one nestling per flicker brood ($n = 69$).

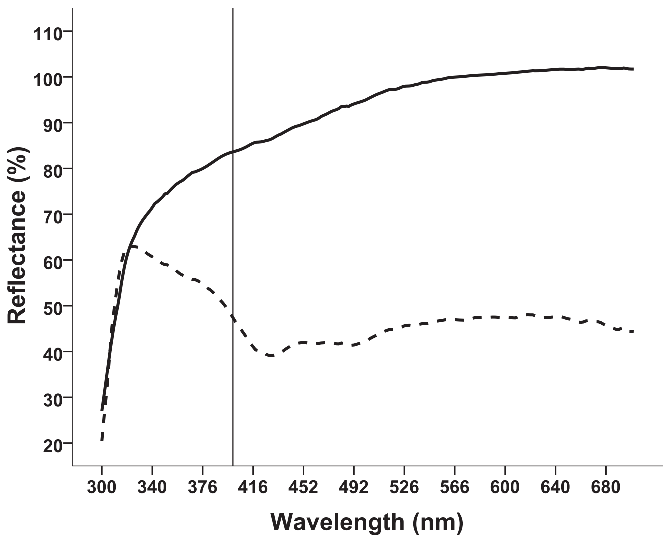

FIGURE 3. Average reflectance of the egg tooth (solid line) and flanges (dashed line) calculated from 20 Northern Flicker nestlings sampled at an age of 5 or 6 days. The visual sensitivity of flickers declines below the vertical line, which divides the spectrum at 400 nm.

average wavelength of 324 nm ± 3.1 ($n = 20$; Fig. 3). To the human eye, the flanges seemed unpigmented, and this was confirmed by the relatively flat shape of the reflectance curve in the part of the spectrum visible to the human eye (Fig. 3). Results from all nestlings pooled, the average maximum reflectance of flange skin was 48% ± 6.2, whereas the average maximum reflectance from the egg tooth was much higher at 97% ± 7.3.

Comparisons of the largest and smallest nestlings within a brood showed that, in the UV part of the spectrum below 400 nm, neither total flange brightness (paired *t*-test: $t_9 = 0.70$, $P = 0.51$) nor egg-tooth brightness ($t_9 = 1.2$, $P = 0.27$) differed according to the nestlings' hatching order. Similarly, in the visible part of the spectrum, the largest and smallest nestlings within a broods did not differ in total flange brightness ($t_9 = 0.42$, $P = 0.65$) or tooth brightness ($t_9 = 0.21$, $P = 0.83$). I combined results from all nestlings and compared brightness in the visible spectrum to body mass, but there was no correlation with flange brightness ($r = 0.23$, $n = 20$, $P = 0.29$) or egg-tooth brightness ($r = 0.25$, $n = 20$, $P = 0.28$).

A survey of the literature and personal communication with other researchers suggested that some, but not all, species of woodpeckers have distinct egg teeth on both the upper and lower bill tips, as does the flicker (Table 1). For most woodpeckers, quantitative information on retention of egg teeth was imprecise, but on the basis of photographs, some species seem to retain upper egg teeth when nestlings are fully feathered and near fledging, while others seem to lose egg teeth at earlier stages. Generally, the presence of two egg teeth seems to be correlated with long time of retention of at least the top tooth, and prominent egg teeth seem to be present among species nesting in the deepest, and presumably darkest, cavities.

DISCUSSION

FUNCTION OF EGG TEETH IN FLICKERS

As do other birds, flicker hatchlings may use egg teeth to break through the egg shell, but several features of the teeth suggest these structures have also evolved in woodpeckers to enhance the detectability of nestlings' mouths in the dim light of a cavity nest. First, the teeth are relatively large compared to those of many other species, yet flickers have thin eggshells (Wetherbee 1959; Fig.1a). Most birds have a small protuberance on the maxilla (Clark 1961), but the flicker's large upper tooth and the additional calcareous tip on the mandible means that when the nestling's the mouth is open, its gape is distinctly framed in four corners by the pale flanges and egg teeth. Second, spectrometry confirmed that at all wavelengths the egg teeth are brighter (reflect more light) than the flanges. Furthermore, while the peak reflectance of flange skin was in the UV part of the spectrum and thus less visible to the parents, reflectance of egg teeth was high in the visible spectrum, approaching a remarkable 100% (Fig. 3). Third, flickers retained the upper egg tooth through nearly the entire nestling period. Finally, in an experiment, in dim light adult flickers avoided feeding nestlings with egg teeth and flanges painted black but did not in bright light, suggesting parents had difficulty finding dull-colored nestlings in the dark (Wiebe and Slagsvold 2009).

It is not uncommon that at least one nestling in a brood of flickers, usually the smallest (last hatched), dies of apparent starvation early in the nestling period (Wiebe and Moore

TABLE 1. Location and persistence of egg teeth in species of woodpeckers (family Picidae). An egg tooth is defined as a distinct, calcareous coating, not only a "lightish bill tip." Species are sorted according to average cavity depth (reported from the literature; see Methods) or approximate body size when cavity dimensions are not available.

Species	Cavity depth (cm)	Lower egg tooth present?	Time retained[a]	Source
Dryocopus pileatus	48	yes	long	Hoyt 1944
Campephilus sp.		yes	?	Beebe and Beebe 1910
Dryocopus martius	40	yes	long	Friedmann 1955
Colaptes auratus	40	yes	21 days	Wetherbee 1959; this study
Melanerpes formicivorus	40	yes	12 days	Koenig et al. 1995
Picus viridis		yes	long	Wetherbee 1959
Melanerpes erythrocephalus	38	yes	long	Smith et al. 2000; Lori Blanc, pers. comm.
Melanerpes lewis	35	?	long	J. Dudley, photo
Melanerpes carolinus	27	yes	15–21 days	Lori Blanc, pers. comm.; Stickel 1965
Picoides tridactylus	27	yes but small	short	Friedmann 1955
Sphyrapicus thyroideus	26	yes? but small	moderate	Les Gyug, pers. comm.
Picoides villosus	25	no	short	pers. obs.
Dendrocopos medius	24	no	short	K. Ruge, video
Sphyrapicus nuchalis	24	no	short	pers. obs.
Picoides borealis	21	no	short	Deborah Jensen, photo
Picoides pubescens	21	no	short	Wetherbee 1959, Ritchison 1999

[a] Retention of upper egg tooth as either short (lost or much reduced within a week after hatching) or long (egg tooth is retained until near fledging).

2008). Neither the brightness of the egg tooth nor the brightness of the flanges in the visible or UV range was associated with the hatching order or presumably the health or reproductive value of young flickers. Living skin tissue, which can contain blood, carotenoid pigments, and collagen arrays (e.g., Kilner and Davies 1998) is probably more likely to signal health than is reflectance of an inert chemical deposit such as an egg tooth. I did not measure intrabrood variation in size of egg teeth, so it is still possible that their size indicates proximate constraints such as availability to the embryo of calcium or other nutrients and is a reliable cue of nestling quality.

Flicker nestlings have pale palates and flanges, but the bright carotenoid colors of some passerine nestlings' mouths are positively correlated with their health, immunocompetence, or body mass (Saino et al. 2000, de Ayala et al. 2007, Ewen et al. 2008). The UV reflectance of nestling flanges may also signal quality but results of experiments differ. De Ayala et al. (2007) did not find the UV reflectance of the flanges of Barn Swallows (*Hirundo rustica*) to be correlated with a nestling's condition within a brood, but Bize et al. (2006) and Soler et al. (2007) documented such a relationship for experimentally stressed broods of starlings and swifts. Nevertheless, variation in nestlings' flange color is greater among broods than within a brood (Soler et al. 2007), so the reflectance of flanges is probably not sensitive enough for the parents to distinguish among the relatively small differences in age or condition within typical broods of flickers.

FEATURES OF EGG TEETH IN OTHER SPECIES

Many, but not all, species of woodpeckers have two egg teeth and retain them through most of the nestling period (Table 1). Within the Picidae, it is unlikely that phylogeny explains the presence of the lower tooth, as the trait occurs in various genera in all three of the main clades of the family identified in a molecular phylogeny (Webb and Moore 2005). Instead, the number and persistence of egg teeth may be correlated with cavity size and amount of ambient light. Data are few, but those in Table 1 suggest a pattern where woodpeckers nesting in the larger, and presumably darker, cavities, such as *Dryocopus*, *Campephilus*, and *Colaptes*, have prominent egg teeth while some of the smaller species, such as those of *Picoides* and *Sphyrapicus*, do not. Detailed and quantitative measures of egg teeth are needed not only in woodpeckers but also other avian species to more rigorously test the hypothesis that the size and persistence of egg teeth is related to ambient light conditions at the nest site.

Unfortunately, in other species comparative information on egg teeth is often vague or sometimes involves conflicting reports based on live birds and museum specimens. For example, Clark (1961) mentioned egg teeth on the mandible of avocets, thick-knees, and thrushes, but subsequent observations of more avocet specimens failed to confirm the existence of lower egg teeth (Parkes and Clark 1964). Sealy (1970) reported "egg teeth" on the mandible of seven seabirds but described these as "swollen protuberances"; only two species, the Ancient Murrelet (*Synthliboramphus antiquus*) and Marbled Murrelet (*Brachyramphus marmoratus*), were confirmed to have a calcareous coating on the egg teeth. Sealy (1970) assumed the function of the seabirds' lower tooth to be to protect the lower mandible during hatching, as did Jehl (1968) for shorebirds. Nevertheless, many seabirds nest in burrows or crevices, so the white egg teeth on the mandible of the murrelets could also be important for visibility of nestlings in low ambient light.

In most birds, the egg tooth seems to disappear within the first week of hatching. It is retained longer in some species (Clark 1961), but for most, quantitative data on the persistence of egg teeth is lacking. The young flickers I studied seemed to hatch with full-size teeth that wore away very gradually during the nestling period (Fig. 2). Apparently, calcareous deposits are not added to the bill tip after hatching, but the deposits there at hatching can persist for >20 days. Interestingly, some seabirds that may nest in burrows or crevices with little ambient light also have egg teeth that persist until fledging (Sealy 1970).

In summary, the calcareous coating on the bill tips of birds at hatching is highly reflective and may have evolved a secondary function as a signal between offspring and parents. In woodpeckers, it seems to enhance nestlings' detectability, and it may have a similar convergent function in other families that nest in conditions of dim light. With careful observations, future workers in the field can add to the knowledge of the form and function of egg teeth across a wide array of species to test the idea that egg teeth enhance the detection of nestlings or signal nestling quality.

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