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EPIZOOTIC OF BEAK DEFORMITIES AMONG WILD BIRDS IN ALASKA: AN EMERGING DISEASE IN NORTH AMERICA?

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Abstract.—The sudden appearance of a large cluster of animals with gross abnormalities may signal a significant change in an ecosystem. We describe an unusual concentration of beak deformities that appear to have arisen rapidly within Alaska and now extend southward along the Pacific Coast. In Alaska we have documented 2,160 Black-capped Chickadees (*Poecile atricapillus*) and 435 individuals of 29 other species of birds, primarily during the past decade, with grossly overgrown and often crossed beaks. The annual prevalence of beak abnormalities among adult Black-capped Chickadees in south-central Alaska varied from 3.6% to 9.7% and averaged 6.5 ± 0.5% between 1999 and 2008. Only 0.05 ± 0.05% of nestlings and 0.3 ± 0.2% of juveniles <6 months old had abnormal beaks, which suggests that this is either a latent developmental or an acquired condition. We documented 80 cases in which a Black-capped Chickadee captured with an apparently normal beak was subsequently recaptured with a beak abnormality and 8 cases in which a beak deformity was no longer detectable upon recapture. Necropsy and histopathology of a sample of affected individuals provided no conclusive evidence of the etiology of this condition. Deformities appear to affect primarily the keratin layer of the beak and may result from abnormally rapid growth of the rhamphotheca. Some affected birds also exhibited lesions in other keratinized tissues of the skin, legs, feet, claws, and feathers, which may represent a systemic disorder or secondary conditions. Additional studies are currently underway to determine diagnostic signs and the underlying cause of this avian keratin disorder. *Received 29 April 2010, accepted 3 July 2010.*

Key words: abnormality, Alaska, avian keratin disorder, bill, Black-capped Chickadee, deformity, emerging disease, lesion, passerine, *Poecile atricapillus*.

Difformités du bec épizootiques chez les oiseaux sauvages d'Alaska : une maladie émergente en Amérique du Nord?

Résumé.—L'apparition soudaine d'un groupe important d'animaux comportant de graves anomalies peut témoigner d'un changement significatif dans un écosystème. Nous décrivons une concentration inhabituelle de difformités du bec qui semblent avoir surgit rapidement en Alaska et qui s'étendent maintenant vers le sud le long de la côte du Pacifique. En Alaska, nous avons documenté, principalement au cours de la dernière décennie, 2 160 individus de *Poecile atricapillus* et 435 individus de 29 autres espèces d'oiseaux dotées d'un bec manifestement surdéveloppé et souvent croisé. La prévalence annuelle des anomalies du bec parmi les adultes de *P. atricapillus* dans le centre-sud de l'Alaska variait entre 3,6 % et 9,7 % et atteignait en moyenne 6,5 ± 0,5 % entre 1999 et 2008. Seulement 0,05 ± 0,05 % des oisillons et 0,3 ± 0,2 % des juvéniles âgés de moins de 6 mois possédaient des becs anormaux, ce qui suggère qu'il s'agit soit d'un développement latent ou d'une condition acquise. Nous avons documenté 80 cas pour lesquels un individu de *P. atricapillus* capturé avec un bec apparemment normal était subséquemment recapturé avec une anomalie du bec, et 8 cas pour les quels une difformité du bec n'était plus détectée lors d'une recapture. L'autopsie et l'histopathologie d'un échantillon d'individus affectés d'une anomalie n'ont fourni aucune preuve concluante de l'étiologie de cette condition. Les difformités semblent affecter principalement la couche de kératine du bec et peuvent résulter d'une croissance anormalement rapide de la rhamphothèque. Certains oiseaux affectés présentaient aussi des lésions dans d'autres tissus kératinisés de la peau, des pattes, des pieds, des serres et des plumes, ce qui peut représenter un trouble systémique ou des conditions secondaires. Des études complémentaires sont actuellement en cours afin d'identifier des indices diagnostiques et la cause sous-jacente de ce trouble de la kératine aviaire.

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Avian beaks are remarkable for their diversity in shape and size and provide elegant illustrations of the process and power of natural selection (Darwin 1859, Amadon 1947, Newton 1967, Grant 1986, Grant and Grant 2006, Badyaev et al. 2008, Badyaev 2010). Gross abnormalities of the beak have long drawn the attention of scientists not only because they are inherently intriguing but also because their debilitating effects engender their rarity in the wild. Even small differences in beak morphology can critically affect what foods are accessible to individuals (e.g., Boag and Grant 1981, Benkman and Lindholm 1991, Temeles and Kress 2003) and how well they can defend against ectoparasites (Clayton et al. 2005). Because beaks are under such strong selection pressure, there has been great interest in understanding the mechanisms that control their morphology. Recent research has revealed that changes in a few, key morphogenetic proteins can result in a broad diversity of beak shapes by influencing the embryonic development of the underlying bones (Schneider and Helms 2003; Abzhanof et al. 2004, 2006; Wu et al. 2004, 2006; Schneider 2005; Campàs et al. 2010). The shape and function of the avian beak are controlled, however, by more than just the underlying skeletal structure.

The bones of the beak are covered by the rhamphotheca, a thick, modified layer of the integument that in most birds is hard and heavily cornified, consisting of closely packed, keratinized cells (Lucas and Stettenheim 1972, Stettenheim 2000). The structure of the rhamphotheca itself shows remarkable morphological adaptations for foraging, including specialized sensory organs for detecting prey (Piersma et al. 1998) and surfaces for straining, cutting, tearing, and cracking foods (Storer 1971, Stettenheim 2000). The bill tip and tomia (cutting edges of the beak) are worn down through normal processes such as feeding and pecking, and the rhamphotheca is continually being replaced as keratinized cells are worn off (Lüdicke 1933, Cooper and Harrison 1994, Lumeij 1994). Several studies of passerines have related seasonal changes in bill length to changes in diet and the concomitant rates of wear and abrasion of the rhamphotheca (Clancey 1948; Davis 1954, 1961; Gosler 1987; Morton and Morton 1987). Little is known, however, about the mechanisms that control the growth of the rhamphothecal tissues.

Causes of beak abnormalities are often difficult to determine, but they can arise from improper bone growth, malocclusion (misalignment) of the maxilla and mandible, or disruption of the germinative layers of the beak (Stettenheim 1972, Lumeij 1994). Beak deformities among wild and domestic birds have been attributed to a broad array of factors, most commonly trauma or improper wear of the rhamphotheca (Pomeroy 1962, Lumeij 1994, Olsen 2003); nutritional deficiencies, particularly related to vitamins or calcium metabolism (Romanoff 1972, Stevens et al. 1984, Tangredi 2007); and bacterial, viral, fungal, or parasitic infections (Gartrell et al. 2003, Mans and Guzman 2007, Keymer 2008, Galligan and Kleindorfer 2009). Less commonly documented causes include exposure to extreme heat (West 1959), liver disease (Lumeij 1994), toxins (Bassir and Adenkunle 1970), radiation (Møller et al. 2007), and neoplasms (Owen et al. 2007).

The published literature is replete with records of generally isolated cases of wild birds with abnormally grown bills from all over the world (for summaries, see Pomeroy 1962, Craves 1994). An extraordinary specimen of an Ivory-billed Woodpecker (*Campephilus principalis*) with a decurved, grossly overgrown upper beak >40 cm long was collected in Cuba as early as the mid-19th century (Cory 1886, Jackson 2002). Few studies have documented the rates at which such deformities occur within normal wild populations, likely because estimating rare events requires large sample sizes (Rockwell et al. 2003). In the few populations that have been systematically examined for morphological abnormalities, frequencies of beak deformities have generally been <1% (Hicks 1934, Pomeroy 1962, Hays and Risebrough 1972, Sharp and Neill 1979, Tweit et al. 1983, Nogales et al. 1990, Rockwell et al. 2003, Badyaev 2010).

Although scattered reports of such beak abnormalities are not unexpected, the sudden appearance of a large geographic cluster of morphological abnormalities in a wildlife population can be an early sign of a much larger underlying ecological problem. Beginning in the mid-1970s, high rates of crossed beaks and other congenital malformations were documented in aquatic birds around the Great Lakes, an area where increased levels of persistent organochlorine contaminants were documented (Gilbertson et al. 1976, 1991; Fox et al. 1991; Yamashita et al. 1993; Bowerman et al. 1994; Ludwig et al. 1996; Ryckman et al. 1998; Custer et al. 1999). During the 1980s, a high incidence of gross abnormalities, including beak malformations, was found among embryos and hatchlings of aquatic birds exposed to elevated levels of selenium from agricultural runoff in California (Ohlendorf et al. 1986a, b, 1988; Hoffman et al. 1988). These epizootic clusters were among the first indicators that teratogenic compounds had accumulated in the environment in ecologically significant concentrations.

Here, we document an unusual concentration of beak abnormalities among a broad suite of bird species in Alaska. We were first alerted to the phenomenon in 1998 when we received reports of single Black-capped Chickadees (scientific names of all Alaskan species discussed are given in Table 1) with grossly elongated beaks at bird feeders in two widely separated areas in Alaska. We began compiling observations and historical records of similar deformities in the region. When it became clear that these constituted a significant cluster, particularly for the Black-capped Chickadee, we began a multifaceted study of the problem. The objectives of this study were to (1) describe the types of beak abnormalities observed among all species in Alaska, (2) document the geographic distribution and timing of abnormalities observed, (3) estimate the prevalence of beak abnormalities in different age cohorts of Black-capped Chickadees to determine whether this condition was more likely congenital or acquired, and (4) conduct pathological examinations of a sample of affected individuals to determine the etiology of the disorder.

Methods

Distribution.—After our first observations of Black-capped Chickadees with grossly elongated beaks in Anchorage, Alaska, we solicited additional observations from biologists and the public through local chapters of the National Audubon Society and the media (print, radio, and television). We searched the published literature and continued to seek observations from across North America through colleagues, the national media, the Cornell Lab of Ornithology FeederWatch Program, and a variety of listservers used by banders, birders, and contaminants specialists. Via telephone or e-mail we contacted observers who had reported

TABLE 1. Minimum numbers of individual birds, by species, reported with crossed or elongated beaks in Alaska, ca. 1979–2009. These exclude probable resightings of the same individuals on the basis of proximity of observations and similarity of beak deformities from descriptions or photographs.

Species	Years reported	Number of individuals	Crossed[a]	Elongated[a]
Pacific Loon (*Gavia pacifica*)	2007	1	+	
Bald Eagle (*Haliaeetus leucocephalus*)	2000, 2007	2	+	+
American Kestrel (*Falco sparverius*)	2005	1		+
Peregrine Falcon (*F. peregrinus*)	2000	1	+	
Sandhill Crane (*Grus canadensis*)	2009	1	+	
Black-legged Kittiwake (*Rissa tridactyla*)	2007	1	+	
Glaucous-winged Gull × Herring Gull (*Larus glaucescens* × *argentatus*)	2008	1	+	
Downy Woodpecker (*Picoides pubescens*)	1979–2009[b]	33	+	+
Hairy Woodpecker (*P. villosus*)	1999–2008	12	+	+
Steller's Jay (*Cyanocitta stelleri*)	1997–2009	39	+	+
Black-billed Magpie (*Pica hudsonia*)	1997–2009	60	+	+
Northwestern Crow (*Corvus caurinus*)	1979–2009[b]	148	+	+
Common Raven (*C. corax*)	1992–2009	18	+	+
Black-capped Chickadee (*Poecile atricapillus*)	1991–2008	2,160	+	+
Chestnut-backed Chickadee (*P. rufescens*)	2008	1		+
Boreal Chickadee (*P. hudsonicus*)	1994–2002	5	+	+
Red-breasted Nuthatch (*Sitta canadensis*)	1998–2009	75	+	+
Ruby-crowned Kinglet (*Regulus calendula*)	1999	2	+	
American Robin (*Turdus migratorius*)	1999–2005	3	+	
Varied Thrush (*Ixoreus naevius*)	2001–2008	3	+	+
European Starling (*Sturnus vulgaris*)	2009	1		+
Orange-crowned Warbler (*Oreothlypis celata*)	2002–2004	2	+	+
Yellow-rumped Warbler (*Dendroica coronata*)	1998–2007	3	+	+
American Tree Sparrow (*Spizella arborea*)	2002	1	+	
Savannah Sparrow (*Passerculus sandwichensis*)	1999	1	+	
Lincoln's Sparrow (*Melospiza lincolnii*)	2002	1	+	
Dark-eyed Junco (*Junco hyemalis*)	2002	1	+	+
Pine Grosbeak (*Pinicola enucleator*)	1999–2007	6	+	+
Common Redpoll (*Acanthis flammea*)	1999–2004	6	+	+
Pine Siskin (*Spinus pinus*)	1999–2004	6	+	+

[a]+ = Condition observed in at least one individual.
[b]Earliest report was from the late 1970s or early 1980s, specific date unknown.

deformed birds and requested the following information: species, detailed description and photographs of the morphological abnormality, date(s) observed, location, and behavior. We carefully screened all reports for accuracy and entered all verified observations into a database and geographic information system to produce maps of distribution. We excluded probable duplicate sightings of individuals on the basis of locations, dates, and descriptions of the deformities.

Prevalence.—To estimate prevalence in breeding adult and nestling Black-capped Chickadees, we erected nest boxes across residential areas (n = 164), large tracts of rural property (10–70 ha; n = 66), and municipal and state parks (18–200,000 ha; n = 266). These sites were established in south-central Alaska around Anchorage and the Matanuska-Susitna Valley, areas where large numbers of Black-capped Chickadees with abnormal beaks had been reported. We monitored the boxes from late March through early July during the summers of 2000–2004. Once nest building had begun, we checked boxes every 2–4 days to determine the date of initiation of egg laying and final clutch size. We monitored most nests every 4–6 days during incubation and 1–2 days around the expected date of hatch to document chronology, hatching success, and any congenital defects. We captured adults inside the nest box during incubation (females) or when provisioning nestlings (males) and banded, weighed, measured, and examined each individual for gross abnormalities. We measured, weighed, and examined nestlings for malformations on day 0 (date of hatch) or 1 and generally at days 4, 7, 10, 12, and 14; chicks were individually marked by clipping claws at hatch and were banded on day 12.

From 2001 to 2008 we conducted a systematic capture–recapture study to monitor the prevalence of deformities by sex and age during the nonbreeding season. We used modified funnel traps (Senar et al. 1997), sometimes augmented with mist nets, to capture Black-capped Chickadees every 2 months between September and April on three to five 10-ha sites (in parklands surrounded by residential areas) around Anchorage and the Matanuska-Susitna Valley. Ten traps at each site were baited with unhulled black oil sunflower seeds and peanut butter 10–14 days before each trapping session. We captured birds using mist nets around temporary feeders twice on the Kenai National Wildlife Refuge, 75 km south of our main study area and at least 15 km away from any residential areas, to determine whether birds with beak deformities occurred in areas normally devoid of bird feeders.

At each site, we trapped birds for 6 h per day beginning at sunrise, checking traps every 40–60 min and bringing birds back in individual laundered and bleached cloth bags to a central banding station. Each bird was examined for abnormalities, weighed, measured, bled, banded, and released. For each trapping period, we calculated the prevalence of beak abnormalities by sex and age cohort and we tracked the history of beak growth for all recaptured individuals. We also used mist nets and traps at targeted residences to capture additional affected birds for examination. These captures were not used in estimates of prevalence.

Measurements, aging, and sexing.—We recorded mass and other standard body measurements for each bird banded or collected (Pyle 1997). We used beak morphometrics to characterize normal and abnormal beaks and to monitor the development of beak deformities in individual birds through time. The standard measurement of the beak taken for all individuals was the distance from the anterior end of the right or left nare to the tip of the upper beak (with digital calipers to 0.1 mm). For birds with beak abnormalities, we also measured the exposed culmen (chord from base of the anterior-most feathers on the forehead to tip of the upper beak); the gonys (chord between anterior end of the notch along the centerline of lower beak to tip); and any overbite (chord of upper beak beyond where it meets lower beak) or underbite (chord of lower beak beyond upper). For individuals with an extremely curved beak, we used a piece of thread to measure (to 1 mm) the curved distances along the culmen and gonys. The direction and extent of lateral crossing of upper and lower beaks were noted and measured in extreme cases. Our terminology and measurements of the beak follow Lucas and Stettenheim (1972) and Pyle (1997).

We distinguished hatching-year Black-capped Chickadees from older ones during autumn by incomplete pneumaticizition of the skull and, later in the season, by narrowness of the outermost rectrices and absence of white on the tips (Meigs et al. 1983, Pyle 1997). All Black-capped Chickadees captured between January and June were classified as adults. Breeding adults were sexed by brood patch (female) or cloacal protuberance (male); nonbreeding adults and nestlings were sexed by genetic analysis of buccal samples or blood samples collected by ulnar venipuncture (Handel et al. 2006).

Pathology.—We collected a sample of birds from Anchorage and the Matanuska-Susitna Valley in south-central Alaska between 1999 and 2006 for pathologic examination. We used a GE Senographe DMR with Kodak MIN-R mammography film to obtain high-resolution radiographs of 4 Black-capped Chickadees with and 3 without gross beak abnormalities to look for evidence of skeletal lesions in the abnormal birds. Six adult Black-capped Chickadees with and two without beak abnormalities were examined at the U.S. Geological Survey's National Wildlife Health Center (NWHC; Madison, Wisconsin) for necropsy, histopathology, and microbiology (cases nos. 16169, 18458, and 19729). We also examined one nestling with a slightly elongated upper beak and two with abnormal legs (case no. 18224). One of the adults exhibited raspy breathing upon capture and died while being held for observation. All other birds were euthanized by cervical dislocation, exposure to CO_2 in a chamber, or open-drop exposure to isoflurane inhalant anesthesia. We air-shipped fresh carcasses in insulated coolers to NWHC, where they were examined for gross pathology and osteologic lesions. Histopathology included examination of beak, head, heart, lungs, liver, spleen, ventriculus, proventriculus, kidney, leg bone, and pectoral muscle. Tissues were fixed in 10% neutral buffered formalin, embedded in paraffin, sectioned at 5 μm, and stained with hematoxylin and eosin. Spleen and liver tissues were cultured for salmonella and other bacteria. Tissues from beak, kidney, spleen, liver, and skin were cultured for viruses; cloacal swabs were submitted to another laboratory for polymerase chain reaction (PCR) tests for viruses.

Estimates of prevalence.—The first step in estimating the prevalence of beak abnormalities in Black-capped Chickadees was discriminating abnormal from normal beaks. Gross elongation and crossing of the upper and lower beaks were obvious, but we were uncertain how to distinguish slight, normal overbites from incipient deformities. We had no historical data on normal beak measurements for our study population, so we were not certain at what point beak length should be classified as abnormal among individuals in which the tips of the beak did not cross or overgrow each other.

We reasoned that the average amount of overbite should be small and relatively constant across the range of normal beak lengths but for deformed beaks the overbite should increase abruptly with increasing length of the beak. Therefore, we employed a piecewise regression analysis to identify the length of the upper beak (as measured from nares to tip) at which a significant change in the amount of overbite in relation to the nares-to-tip measurement (i.e., slope of regression line) occurred. We used this change-point to determine what the maximum length of overbite should be for an upper beak of "normal" length (i.e., less than the change-point). Because measurements of individuals could vary seasonally and interannually, we included all measurements obtained from adults captured during our study. We used the SAS 9.1 Interactive Matrix Language program provided by Dunnigan et al. (1997), which uses an iterative grid-search process to identify the change-point in slope and fits a two-phase regression model (based on minimizing residual sum of squares). We used an F-test to compare the fit of the piecewise regression model with that of a simple linear regression model.

For individuals with a bill length less than the change-point and with no evidence of crossing, we ran a bootstrap analysis to estimate an upper tolerance level of overbite that would include 99% of the population with 99% confidence. Using MINITAB, version 14.20, we randomly resampled all individuals, with replacement, 1,000 times. From each of these bootstrap samples, we selected the measurement of the 99th percentile; the upper tolerance level for a normal overbite was the 99th percentile among these. Exceeding this amount of overbite (or the rarer underbite) was used as a criterion for classifying the beak as abnormal.

The final criterion we sought to determine was the length at which the upper beak should be considered abnormal in individuals in which both the upper and lower beaks were long but met at the tips (no overbite, not crossed). We first used SPSS, version 14.0, to construct a receiving operating characteristic (ROC) curve that used just the nares-to-tip measurement to identify individuals with known deformities (i.e., a crossed bill or an overbite that exceeded the normal length determined from the piecewise regression and bootstrap analysis). We then used the ROC curve to examine the tradeoff between sensitivity (probability of correctly identifying individuals with abnormal beak growth) and 1 – specificity (probability of falsely identifying individuals with "normal" beak growth as abnormal) at different lengths of nares-to-tip. To minimize false classifications of normal birds as abnormal, we selected a cutoff length that was greater than the change-point determined above and that was likely to be exceeded by only 2% of individuals without an excessive overbite or crossed bill. Exceeding this length in nares-to-tip was used as a third criterion for classifying a beak as abnormal.

Given the above criteria, we estimated prevalence of beak abnormalities as the proportion of birds affected in the following age cohorts: (1) nestlings from 0–12 days of age; (2) postfledging juveniles captured between September and December (about 3–6 months of age); and (3) adults (>6 months). For the first two age cohorts, prevalence was estimated across all years of the study combined. For adults, prevalence was estimated for each field season (1 July–30 June) in relation to timing of reproduction. Individuals captured during November and December with completely ossified skulls and indeterminate tail characteristics were excluded from these estimates because we could not distinguish whether they were juveniles or adults. Birds captured multiple times were included in estimates once for each field season in which they were captured and were characterized as affected if a deformity was recorded on any capture occasion within that season. The standard error of the proportion affected was calculated using the formula for a binomial proportion (Zar 1996). We used a chi-square test of independence to compare the sex ratio of postfledging Black-capped Chickadees with and without beak deformities and used a Student's *t*-test to compare beak measurements of males and females (Zar 1996). We also used chi-square tests of independence to compare the frequencies of other abnormal conditions in individuals with and those without beak deformities. Statistics are presented as means ± SE unless otherwise noted.

Results

Numbers and distribution of birds with beak abnormalities.—We documented 2,160 Black-capped Chickadees in Alaska and 31 elsewhere in North America with crossed or elongated beaks between 1986 and 2009 (Fig. 1). The earliest cases in Alaska included single individuals at King Salmon in western Alaska in November 1991 and at Nancy Lakes in south-central Alaska in April 1992. Since then, reports have been concentrated in Anchorage and the Matanuska-Susitna Valley in south-central Alaska but now extend

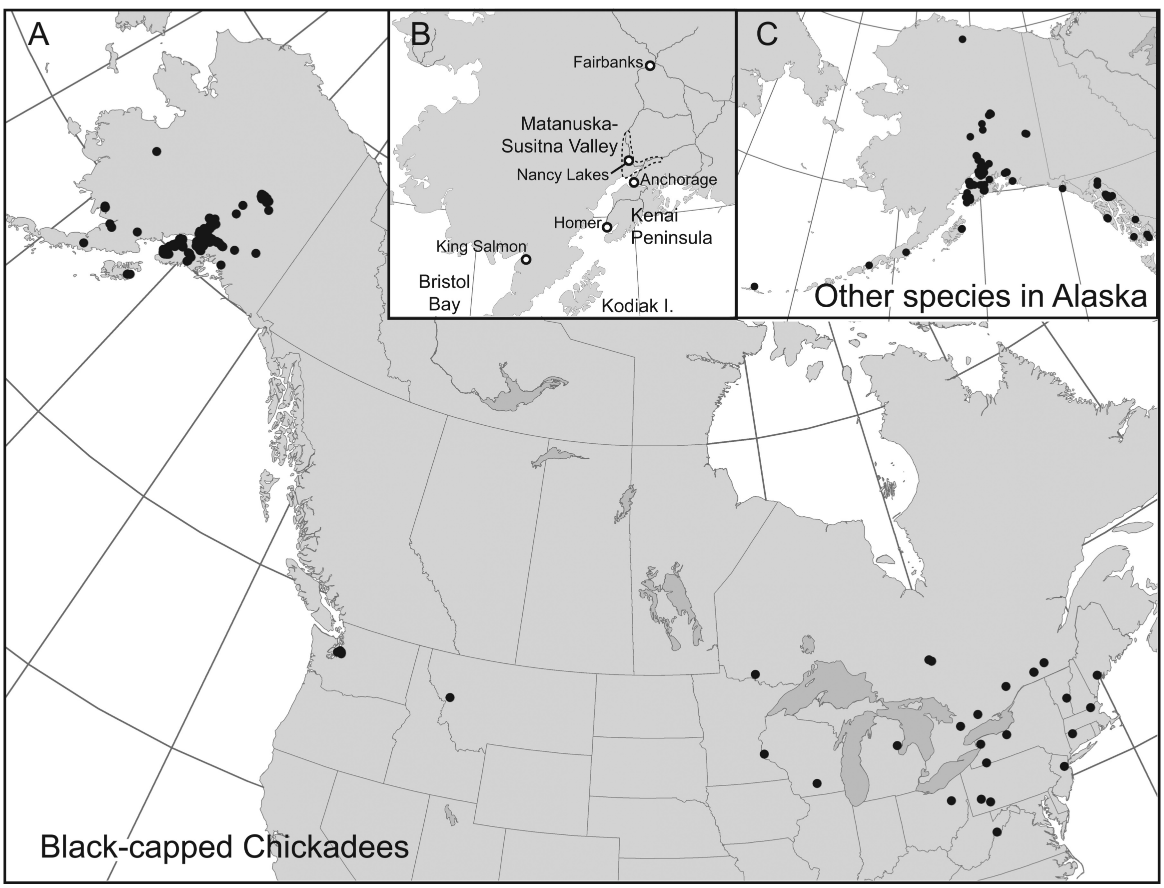

Fig. 1. (A) Locations of Black-capped Chickadees documented with crossed or elongated beaks from 1986 to 2009, including 2,160 in Alaska and 31 elsewhere in North America. (B) Places mentioned in the text and the major road systems along which potential observers and, therefore, observations were concentrated. Dashed line shows Matanuska-Susitna Valley. (C) Locations of 435 individuals of 29 other species of birds with beak deformities in Alaska documented ca. 1979–2009.

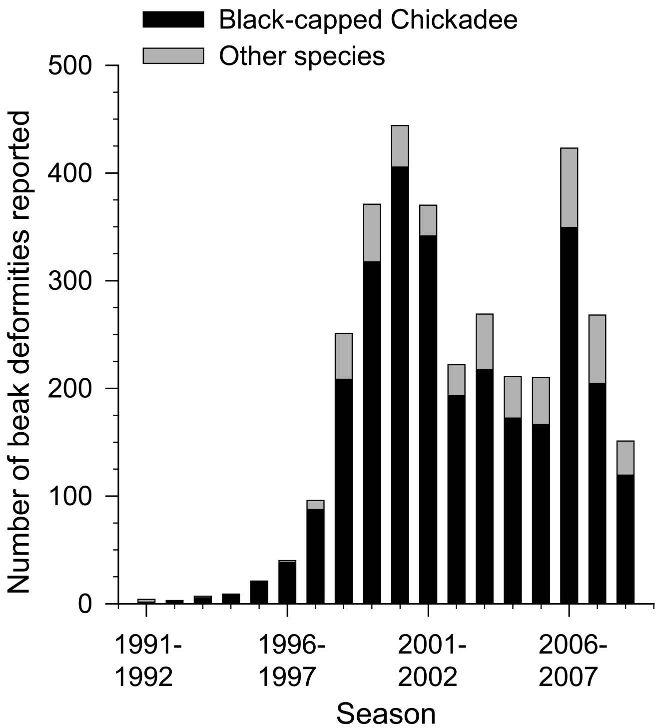

Fig. 2. Number of Black-capped Chickadees and individuals of other species with beak deformities documented during each field season (1 July–30 June) in Alaska, 1991–2009.

throughout much of the species' range in Alaska. Coincident with increased media coverage of the problem, numbers of reports increased exponentially until winter of 2000–2001, after which they fluctuated annually (Fig. 2). Outside of Alaska, the earliest documented cases we found were of single birds at two locations in Ontario during winter 1986–1987. Through June 2009, total reports included 7 Black-capped Chickadees from Ontario, 3 from Quebec, 5 from Washington, 3 from New York, 2 from Wisconsin and Pennsylvania, and 1 each in Montana, Michigan, Ohio, West Virginia, New Jersey, Connecticut, New Hampshire, Vermont, and Maine. All reports were of single individuals except in Lakefield, Ontario, where 2 Black-capped Chickadees with beak deformities were observed at one residence.

We also documented 435 individuals of 29 other species of birds in Alaska with grossly crossed or elongated beaks (Table 1). These belonged to 14 families and 6 orders, with corvids (Corvidae), woodpeckers (Picidae), and nuthatches (Sittidae) being most commonly reported. The earliest records were of a Downy Woodpecker collected in Homer on the Kenai Peninsula and of a Northwestern Crow observed on Kodiak Island, both during the late 1970s or early 1980s (specific dates unknown). Subsequent reports followed the same general temporal (Fig. 2) and geographic pattern as the Black-capped Chickadee reports, although many observations of crows were recorded from southeastern Alaska, where Black-capped Chickadees rarely occur (Fig. 1).

Gross morphology of beak deformities.—In a Black-capped Chickadee, normally the upper and lower beaks are straight and meet at the tips (Fig. 3A). In most individuals with gross beak abnormalities, the upper beak was elongated, often with a pronounced decurvature (Fig. 3B–D). In some cases, the lower beak was also elongated and often upcurved, resulting in crossed presentation (Fig. 3E–H). It was relatively rare to have only the lower beak overgrown (Fig. 3I), and we documented a single case in which the upper beak was curved in a lateral arc, almost from its base (Fig. 3J). In some cases both the upper and lower beaks were elongated but not laterally deviated; this generally resulted in a pronounced gap (Fig. 3K). In many cases the overgrowth, particularly of the upper beak, was thin and brittle (Fig. 3D). In a few cases, however, the beak exhibited severe thickening along its entire length (Fig. 3L). Abnormal beaks often had a series of semi-elliptical or longitudinal ridges along the upper beak surface anterior to the nares, which suggested patterns of irregular growth of the keratinized tissues. In many cases the tomia of the upper or lower beak or both were overgrown and had irregular, often thin edges.

We observed a few other abnormal characteristics more frequently among Black-capped Chickadees with beak deformities ($n = 246$) than among those with apparently normal beaks ($n = 2{,}545$): (1) patches of feathers missing, particularly in the loral or occipital regions, or contour feathers that appeared to be abnormally plumaceous (in 11.8% of birds with beak deformities vs. 1.30% of birds with normal beaks; $\chi^2 = 113.68$, df = 1, $P < 0.001$); (2) one to several white feathers instead of black in the loral region (2.4% vs. 0.55%; $\chi^2 = 11.25$, df = 1, $P = 0.001$); (3) brown feathers instead of black in the loral region (5.7% vs. 0.86%; $\chi^2 = 41.04$, df = 1, $P < 0.001$); (4) patches of dry, flaky, or reddened skin (Fig. 4A; 8.5% vs. 0.90%; $\chi^2 = 84.23$, df = 1, $P < 0.001$); and (5) dermatoses on the tarsometatarsi, conditions in which keratinized scales were sloughing off in layers without obvious inflammation (Fig. 4B; 4.5% vs. 0.16%; $\chi^2 = 78.11$, df = 1, $P < 0.001$). Two birds with overgrown beaks (0.8%) and 2 with apparently normal beaks (0.08%) had one or more claws that were abnormally long or malformed (Fig. 4C). One incubating female with a severe beak deformity had what appeared to be a large, subcutaneous lipoma on the abdomen along the brood patch.

Beak abnormalities reported among most other species in Alaska, particularly the corvids, were similar to those of Black-capped Chickadees, with varying amounts of elongation, lateral deviation, and crossing (Fig. 5 and Table 1). However, in Red-breasted Nuthatches, Downy Woodpeckers, and Hairy Woodpeckers, the upper and lower beaks generally grew long and straight, sometimes crossing at the tips (Fig. 5B–C). In species with a single or few individuals reported, the morphology of the deformities varied and may represent unrelated conditions or differences in expression of the same disorder. Most of the other small passerines had crossed beaks (Fig. 5F). Reports of adult Bald Eagles, a nestling Peregrine Falcon, and an immature Black-legged Kittiwake also indicated a crossed beak and little to no elongation of the upper beak; the Peregrine Falcon was also missing one eye (T. Swem pers. comm.). Photographs of what appeared to be an immature Glaucous-winged Gull × Herring Gull hybrid showed an elongated and irregularly shaped lower beak that was slightly offset laterally from the upper beak.

Pathology.—High-resolution radiographs of 4 adult Black-capped Chickadees with abnormal beaks showed no macroscopic evidence of skeletal lesions; lesions appeared to be restricted to the rhamphotheca, with elongation and thickening of the keratinized layers over anterior portions of the premaxillary and mandibular

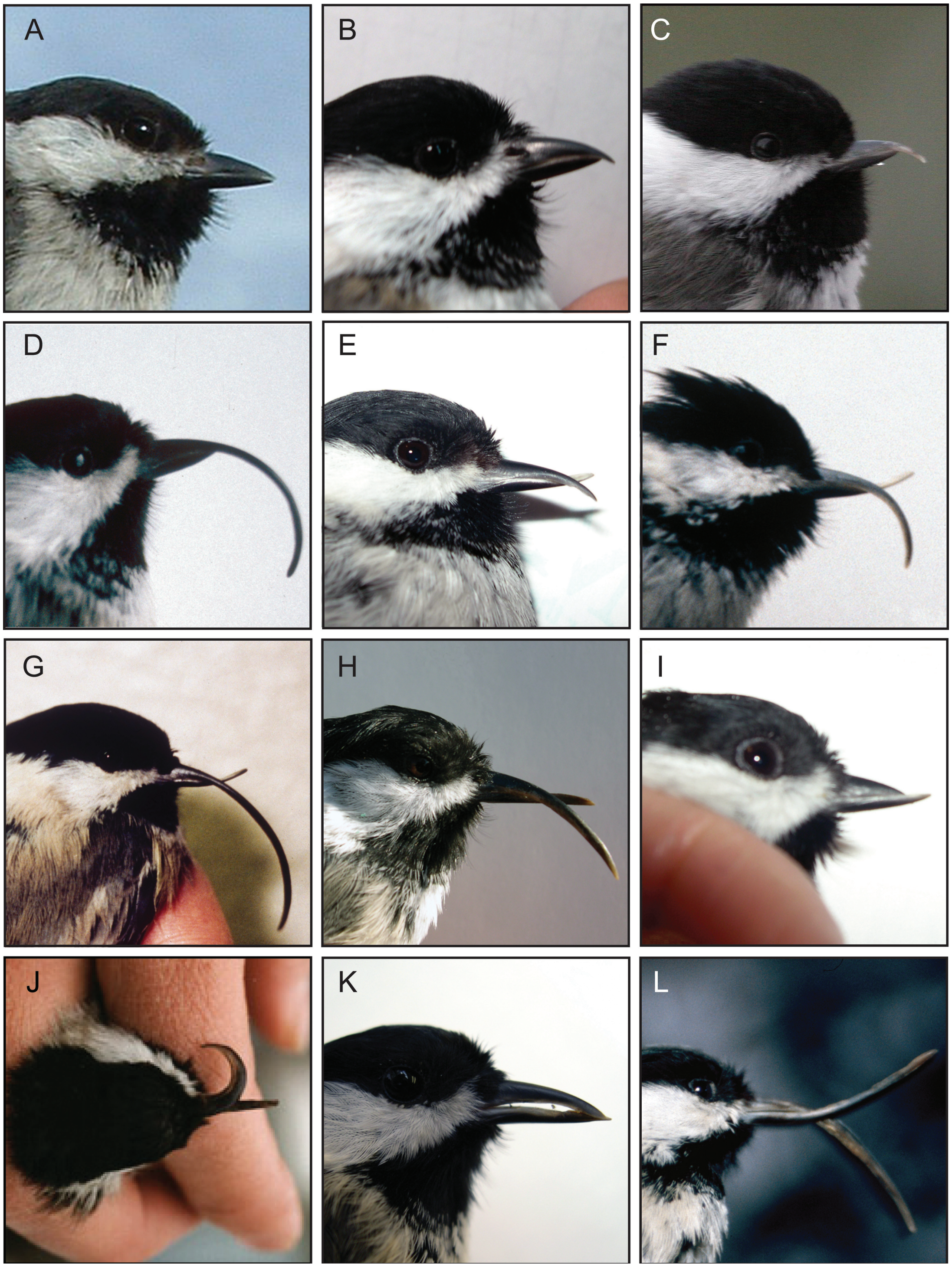

FIG. 3. Examples of Black-capped Chickadees in Alaska from 1999 to 2009 with (A) normal beak; (B–D) elongated upper beak; (E–H) elongated and crossed upper and lower beaks; (I) elongated lower beak; (J) laterally curved upper beak (showing malformed premaxilla); (K) elongated upper and lower beaks with pronounced gap; and (L) elongated, crossed, and thickened upper and lower beaks. Dirty, matted plumage (E–G) is typical of chickadees with impaired ability to preen. (Photograph C by E. VanderWerf; others by C. M. Handel.)

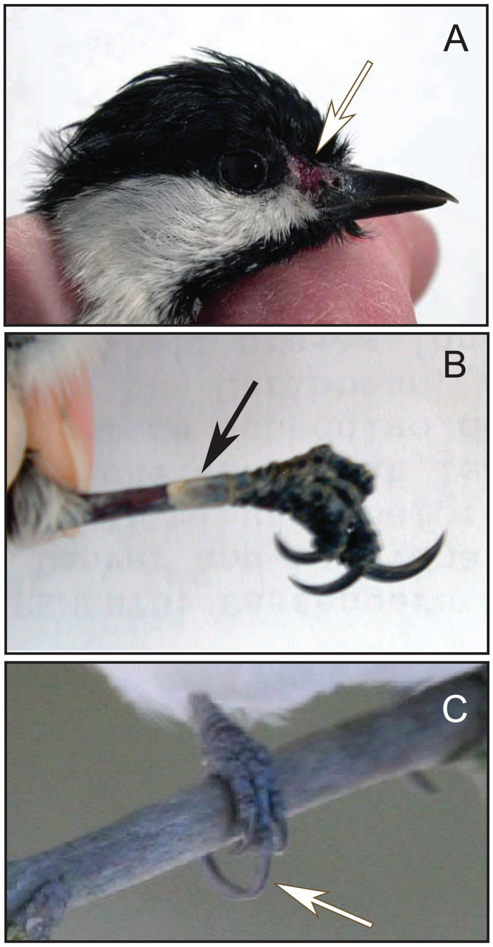

FIG. 4. Other lesions found in Black-capped Chickadees in Alaska from 1999 to 2009: (A) dry, reddened skin in loral region; (B) dry, sloughing scales on tarsometatarsus; (C) overgrown claw on middle toe. (Photograph C by D. Kuhle; others by C. M. Handel.)

bones (Fig. 6). Necropsy and histopathologic examination of 5 adults (3 females and 2 males) with crossed and elongated beaks revealed no significant osteological lesions of the cranium. Bacterial cultures for tissues of all 5 birds were negative. Three had unidentified feather lice (Mallophaga) and 2 had unidentified feather mites (Acari), but there was no evidence of infection by mites (*Knemidocoptes* spp.). No other gross or microscopic lesions were noted. No viruses were cultured from the beaks or from the pooled spleen–kidney or pooled spleen–liver of any of these adults. There was no radiographic evidence of reduced bone density in affected adults.

Necropsy of the fourth adult female, which exhibited a severely crossed and overgrown beak and labored breathing, determined the cause of death to be fractured ribs and massive thoracic hemorrhage. The bird's plumage was dirty and matted, and the head and breast were covered with egg cases of feather mites. The epithelium of the head and breast was dry, and the keratinized scutes on the tarsometatarsae were prominent and sloughing. Histopathologic examination revealed a mass of fungal hyphae in the cavity of an unidentified bone at the base of the brain and roof of the mouth, resulting in a clinical diagnosis of mycotic osteomyelitis. The hyphal mass was in the general area of the quadrate, pterygoid, and palatine bones; distortion of any of these could have affected the orientation of the quadratojugal and of the nasal and premaxillary bones that form the upper beak (L. Sileo pers. comm.). Bacterial and viral isolation attempts from the spleen were negative. Cloacal swabs submitted to Washington State University for PCR tests were negative for psittacine beak and feather disease, avian psittacine polyoma virus, and pigeon circovirus.

Necropsy and pathologic examination revealed no obvious cause of fatal illness in the two 12-day-old brood mates that had each exhibited labored breathing, extreme lethargy, and a twisted, dangling leg. One had a folding fracture of the right femur, and the other had a folding fracture in the right midshaft tibiofibula. There was no evidence of trauma in the surrounding tissues and no other gross lesions. A slight overbite was evident in both nestlings under magnification. Pathology revealed no gross lesions in the

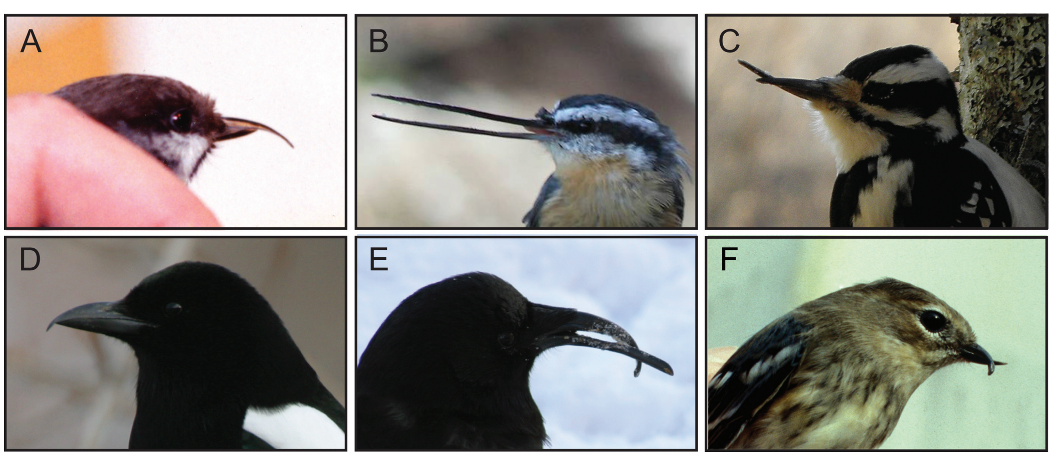

FIG. 5. Examples of other species in Alaska with beak deformities that ranged in the extent of crossing and elongation: (A) Boreal Chickadee (L. Quakenbush, Fairbanks, 1994); (B) Red-breasted Nuthatch (D. Henderson, Anchorage, 2007); (C) Hairy Woodpecker (R. Van Dusseldorp, Kenai, 2009); (D) Black-billed Magpie (J. Tileston, Anchorage, 2004); (E) Northwestern Crow (H. Cline, Seward, 2007); and (F) Yellow-rumped Warbler (C. Erwin, Kantishna, 1998).

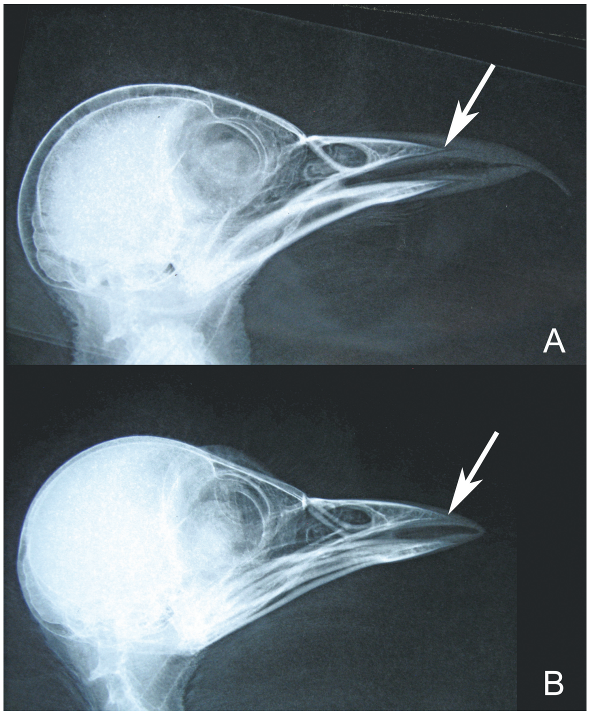

Fig. 6. Radiographs of (A) adult Black-capped Chickadee with overgrown rhamphotheca and (B) juvenile Black-capped Chickadee with normal beak collected in south-central Alaska in 1999. Arrows point to tip of premaxilla underlying rhamphotheca. Original image of juvenile was reversed for more direct comparison of beaks.

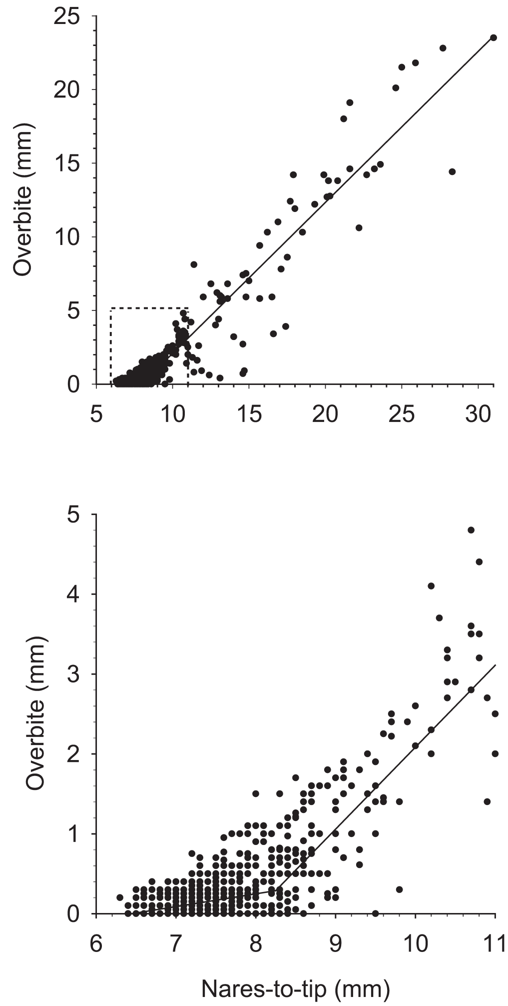

Fig. 7. Two-phase regression of overbite of upper beak in relation to length of beak measured from nares to tip in adult Black-capped Chickadees with normal and abnormal beaks captured in south-central Alaska, 1999–2008. Lower graph is enlargement of area inside dashed box in upper graph and illustrates change in slope at 8.25 mm.

15-day-old nestling with a slightly overgrown upper beak (0.5 mm overbite, and whose attending male parent had 0.8 mm overbite), but cross sections of the beaks of all 3 nestlings showed occasional areas of epithelial disorganization. A similar finding was noted in the beak epithelium of the 3 cross-beaked adults upon reexamination. Slides were submitted to Kansas State University for electron microscopy, and no viral inclusion bodies were found.

Characterization of beak abnormalities based on measurements.—We classified any beak as abnormal if the upper and lower beaks were laterally offset from each other (i.e., crossed). For individuals in which the upper beak was longer than the lower (overbite), we determined statistically what amount of overbite should be considered abnormal. A two-phase regression with a change-point for the nares-to-tip measurement at 8.25 mm (Fig. 7) explained more of the variation in overbite than a single linear regression ($F = 243$, df = 3 and 2,096, $P < 0.0001$). Adults with nares-to-tip <8.25 mm had a mean overbite of only 0.127 ± 0.004 mm ($n = 1{,}894$); 50% had an overbite of ≤0.1 mm, 99.5% were ≤1.0 mm, and the maximum recorded was 1.5 mm. There was a very slight increase in overbite for each 1.0-mm increase in the length of the upper beak ($\beta_1 = 0.16 \pm 0.01$, adj. $R^2 = 0.13$, $P < 0.0001$).

For adults with nares-to-tip >8.25 mm ($n = 206$), the overbite increased an average of 1.03 ± 0.03 mm for each 1 mm of increase in nares-to-tip (β_1, adj. $R^2 = 0.89$, $P < 0.0001$). This suggested that each unit of increase in overbite reflected an equivalent increase in beak length. Fewer than 5% of these birds had an overbite ≤0.1 mm, 50% exceeded 1.5 mm, and the overbite averaged 3.6 ± 0.3 mm. Bootstrap resampling suggested that, with a confidence level of 99%, the overbite did not exceed 1.0 mm for 99% of the adults with uncrossed bills and nares-to-tip <8.25 mm ($n = 1{,}821$). Thus, we classified any beak as abnormal if the overbite or (much rarer) underbite exceeded 1.0 mm.

We next determined what constituted an abnormal beak in birds in which the upper and lower beak met at the tips but were both long and did not cross. The ROC curve analysis of all adult Black-capped Chickadees ($n = 2{,}100$) suggested that 95.8% of birds with a crossed beak or an overbite of >1.0 mm would have a nares-to-tip measurement ≥8.25 mm and thus be correctly classified as abnormal on the basis of beak length alone. However, 3.5% of birds without crossed beaks or overbites would have been classified (perhaps incorrectly) as abnormal above that cut-point. Using a cut-point of 8.5 mm provided a true positive rate (sensitivity) of 89.6% and a false positive rate (1 – specificity) of 2.0%. We thus

Table 2. Beak measurements of Black-capped Chickadees with normal and deformed beaks when first captured in south-central Alaska from 1999 to 2008.

		Normal					Deformed				
Measurement[a]	Sex[b]	Mean	SE	Minimum	Maximum	*n*	Mean	SD	Minimum	Maximum	*n*
Nares to tip	M	7.28	0.01	6.0	8.5	1248	11.15	0.42	6.6	31.6	111
	F	7.15	0.01	6.1	8.4	1331	12.40	0.48	7.3	40.3	147
Culmen	M	9.76	0.03	7.2	11.6	437	14.00	0.55	9.2	34.0	80
	F	9.59	0.02	8.0	11.1	440	15.02	0.56	8.9	34.4	101
Gonys	M	6.58	0.10	6.0	7.3	17	9.37	0.41	5.4	28.3	86
	F	6.65	0.10	5.8	7.5	24	9.13	0.35	5.7	28.4	121

[a]Nares to tip = chord measurement from anterior end of nare to tip of upper beak; exposed culmen = chord measurement from base of most anterior feathers on forehead to tip of upper beak; gonys = chord measurement between anterior end of notch along center line of lower beak to tip.
[b]M = male, F = female.

selected 8.5 mm as a generous upper cut-point for a "normal" nares-to-tip measurement, given that we were likely to incorrectly classify at most 2% of normal birds as abnormal on the basis of this measurement alone and that we might misclassify ~10% of abnormal birds as normal.

In normal adult Black-capped Chickadees, the upper beak ranged from 6.0 to 8.5 mm from nares to tip and averaged slightly longer in males (7.28 ± 0.01 mm, $n = 1{,}248$) than in females (7.15 ± 0.01 mm, $n = 1{,}331$, $P < 0.001$); the gonys of the lower beak ranged from 6.0 to 7.5 mm and did not differ by sex ($P = 0.61$; Table 2). Among 258 Black-capped Chickadees of known sex that we classified as having abnormal beaks, the upper beak ranged from 6.6 to 40.3 mm from nares to tip, averaging about 4–5 mm longer than that of normal birds (Table 2). The gonyl measurement of abnormal lower beaks ranged from 5.4 to 28.4 mm, averaging ~3 mm longer than normal. Measurement along the curvature of the upper beak ranged from 6.5 to 43.0 mm and averaged 17.7 ± 1.0 mm ($n = 62$). Among 14 birds with an upcurved lower beak, the length along the curvature ranged from 7.4 to 21.5 mm, averaging 14.3 ± 1.1 mm. Abnormal beaks did not differ between males and females in any measurements (all $P > 0.05$).

Prevalence of deformities by age and sex.—The percentage of adult (>6 months of age) Black-capped Chickadees captured each year with beak abnormalities varied from 3.6% to 9.7% between 1999 and 2008 during systematic trapping efforts at nest boxes and winter feeding stations in the greater Anchorage area and Matanuska-Susitna Valley (Fig. 8). We recorded 161 cases of beak deformities among the 2,479 bird-years sampled (average annual prevalence of 6.5 ± 0.5%); these cases represented 150 different individuals among 2,054 birds examined one or more times across this entire period. Two of 641 juveniles captured during systematic banding efforts in the same areas between September and December 2001–2007 had beak abnormalities (0.3 ± 0.2%), one with a crossed beak and one with the upper beak 1.3 mm longer than the lower. We found one 12-day-old nestling Black-capped Chickadee with an apparent beak abnormality among 1,896 nestlings from 266 broods examined from hatch until 12 days of age between 2000 and 2008 in this area (0.05 ± 0.05%). The upper beak was 0.5 mm longer than the lower beak, and the tips were slightly crossed. When we trapped postfledging birds on the Kenai Peninsula in areas ≥15 km away from any residential feeders, 1 (8%) of 13 Black-capped Chickadees captured in October had a severely overgrown and crossed beak; none of 9 adults captured in April had any gross abnormalities. Including all juvenile and adult Black-capped Chickadees of known sex examined during all trapping efforts, the proportion of birds that were females was slightly higher among birds with abnormal beaks (57.9% of 261) than among birds with normal beaks (51.2% of 2,547; $\chi^2 = 4.20$, df = 1, $P = 0.04$).

We documented 80 cases in which individuals were first captured with apparently normal beaks and were subsequently recaptured with abnormal beaks. The most rapid beak growth recorded within a 12-month period ($n = 24$ birds) was that of an adult male captured at a nest box on 3 June 2003 with an apparently normal beak (7.9 mm nares-to-tip) and recaptured in a nearby winter trap on 11 September 2003 with a severely elongated upper beak (21.1 mm nares-to-tip). This individual had a minimum rate of net increase in length of the upper beak of 0.13 mm day^{-1}.

We also documented 8 cases in which individuals originally captured with beak abnormalities were subsequently recaptured

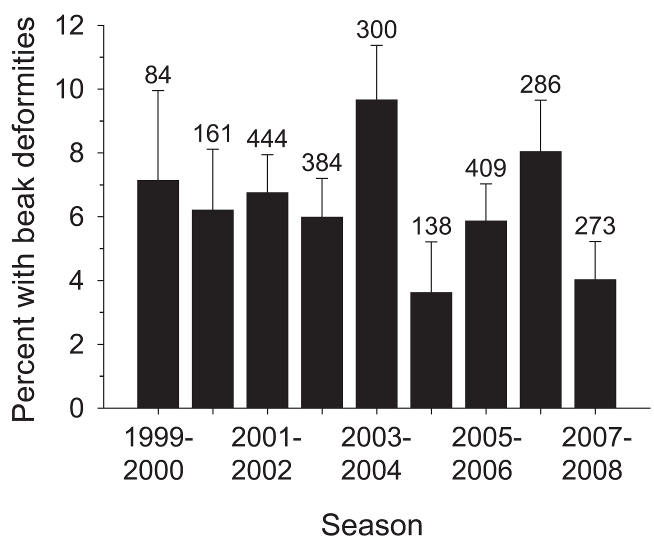

Fig. 8. Prevalence (± SE) of beak deformities in adult Black-capped Chickadees captured during systematic banding efforts in south-central Alaska, 1999–2008. Field seasons span from 1 July to 30 June. Sample sizes are above bars.

with apparently normal beaks. The most extreme case was that of an adult female captured in February 2002 whose upper and lower beaks were elongated and crossed (21.6 mm nares-to-tip; 28.4 mm gonys). When this bird was recaptured in April 2004, both parts of the beak were normal in length (7.6 mm nares-to-tip) but the rhamphotheca was thicker than normal. We brought the bird into captivity, where both the upper and lower beaks grew abnormally long until the bird died 2 months later of an undetermined cause. In the remaining 7 cases the upper beak was moderately or slightly overgrown or the upper and lower beaks were slightly crossed. We recaptured these individuals from 1 to 16 times; 3 of them vacillated between an obviously abnormal state and an apparently normal state, whereas the other 4 became indiscernible from normal individuals. We also noted several cases of individuals with severely overgrown beaks whose brittle tips had obviously broken off. This may have been the mechanism through which evidence of abnormalities was largely erased.

Prevalence of beak abnormalities in other species.—During our nest-box studies, no nestlings of either Boreal Chickadees (n = 337 from 49 broods) or Red-breasted Nuthatches (n = 208 from 39 broods) showed any evidence of crossed or overgrown beaks. Among 234 postfledging Boreal Chickadees captured one or more times during our banding efforts (23 juveniles, 188 adults, and 23 unknown age), none had a crossed or grossly elongated beak; the maximum overbite was 0.7 mm, and the maximum underbite was 0.2 mm. None of the juvenile Red-breasted Nuthatches (n = 55) or those of unknown age (n = 10) captured during autumn had any evidence of beak abnormalities. However, one (1.0%) of 98 adult Red-breasted Nuthatches captured one or more times during systematic banding efforts had a severe beak deformity. This adult female had been captured 10 times between September 2002 and November 2004 with an apparently normal beak (10.6–11.1 mm) before being captured with a grossly abnormal beak in April 2005. Its upper and lower beaks were slightly crossed, and both were elongated; the nares-to-tip measurement (18.3 mm) was 7.8 mm longer than the mean measurement of all normal adult Red-breasted Nuthatch beaks when first captured (10.46 ± 0.05 mm, n = 98). Among 109 Common Redpolls captured once or more during winter banding efforts, only one (0.9%) had a gross beak deformity; the upper and lower beaks were crossed, with slight underbite (0.4 mm) and a pronounced gap (0.8 mm) along the commissure of the upper and lower beaks.

DISCUSSION

Prevalence.—The occurrence of beak deformities in more than 2,500 individuals of 30 species in Alaska constitutes the largest epizootic of gross abnormalities ever recorded among wild bird populations. Abnormal beaks are relatively rare, with most published reports being of single aberrant individuals (for a review, see Craves 1994). The prevalence among adult Black-capped Chickadees (3.6–9.7% per year) was 2–5 times higher than the maximum rate documented previously for any passerine (1.8% of 271 Blue Tits [*Cyanistes caeruleus*]; Pomeroy 1962) and as much as 25× higher than the frequency of abnormal beaks (0.38%) found in a sample of ~10,000 European Starlings (Hicks 1934). The prevalence of beak deformities in Black-capped Chickadees also exceeded rates found among wild bird populations exposed to high concentrations of contaminants. Beak defects occurred in only 1.0–3.3% of eggs or chicks examined with regard to selenium exposure (Gilbertson et al. 1991) and rarely occurred in more than 1% of eggs or young produced in areas with high organochlorine concentrations (Gilbertson et al. 1976, Fox et al. 1991, Yamashita et al. 1993, Bowerman et al. 1994, Ludwig et al. 1996, Ryckman et al. 1998). The high prevalence of beak abnormalities in Black-capped Chickadees clearly represents a recent increase, because we found no beak deformities in 491 Black-capped Chickadees captured in mist nets during the breeding season at three study sites in the Anchorage area from 1992 to 1999 (nor in 5,147 individuals of 38 other species captured then; C. M. Handel unpubl. data).

It is possible that our estimates of prevalence in Black-capped Chickadees were positively biased if the probability of capture in nest boxes or winter traps was higher for birds with beak deformities than that for birds with normal beaks. Because both members of a breeding pair normally excavate the nest cavity (Odum 1941, Smith 1991), affected Black-capped Chickadees may be more likely to breed in nest boxes because of the difficulty of excavating a natural cavity. During winter, affected birds may be more attracted to baited traps because of difficulty in procuring natural foods. Black-capped Chickadees, however, are adept at finding supplemental food sources and will regularly forage on them when available (Brittingham and Temple 1988, Desrochers et al. 1988), so we expect winter capture bias to be slight.

Prior to our study, there was one published record of a Black-capped Chickadee with a grossly overgrown beak (Kinch 1998), that of a single bird observed at a winter feeder in 1997 at Mountain Chutes Camp, Ontario. A few other published reports exist of individuals with similar beak deformities in closely related parids in Europe, including the Blue Tit (King and Collenette 1951, Sage 1956, Pomeroy 1962, Newton 1988, Jebbett 1991), Great Tit (*Parus major*; Howard 1951, Pomeroy 1962), and Willow Tit (*Poecile montanus*; Magnusson 1978). An overgrown rhamphotheca had previously been reported in only two species of birds in Alaska: the American Tree Sparrow (West 1959) and the White-winged Crossbill (*Loxia leucoptera*; West 1974).

Although we documented crossed or elongated beaks in 30 species in Alaska, many of these were represented by only one or a few individuals and the etiology of these deformities may have been unrelated. Our parallel study confirmed an even higher prevalence (17 ± 5%) of similar beak deformities in adult Northwestern Crows in Alaska, with some indication of geographic clusters (Van Hemert and Handel 2010). As judged from descriptions, photographs, and numbers of reports from the public, the other species that seemed to be most commonly affected by this disorder were other corvids and cavity-nesting birds (nuthatches and woodpeckers).

Annual variability in prevalence among Black-capped Chickadees was likely influenced by differential mortality rates. Birds with severely crossed and elongated beaks had difficulty foraging and often spent prolonged periods at feeders manipulating foods. They often foraged on the snow beneath feeders, picking up scraps dropped by other birds. Because of their increased time away from protective cover, they were likely more susceptible to predation. Affected Black-capped Chickadees also had difficulty preening, and many had parasitic feather mites and dirty, matted plumage, which likely compromised their ability to thermoregulate during winter. Birds with beak deformities that had been regularly observed at winter feeders often disappeared suddenly after periods of pronounced cold.

Distribution.—The first beak abnormalities in Black-capped Chickadees were observed in two broadly separated areas in Alaska: the Matanuska-Susitna Valley in south-central Alaska and Bristol Bay in southwestern Alaska. It is difficult to determine how much of the apparent temporal change in distribution was due to variation in observer effort, which was strongly affected by media coverage. Regardless of this potential bias, the initial reports during winter 1991–1992 were separated by more than 500 km and a large mountain range, and adult Black-capped Chickadees are unlikely to have moved such long distances or across such a barrier. Elsewhere in their range they are highly faithful to breeding and wintering territories (6–39 ha; Odum 1942, Glase 1973, Brewer 1978), and few adults move long distances once established (Weise and Meyer 1979, Desrochers et al. 1988, Smith 1991). The greatest distance we recorded was for a juvenile that dispersed 28 km from its natal site (C. M. Handel unpubl. data), similar to the maximum recorded in an Alberta study (39 km; Desrochers et al. 1988). Thus, the records at the apparent onset of this phenomenon for Black-capped Chickadees suggest that the causative agent was widely spread across the region, rather than that affected Black-capped Chickadees transported the agent. There is some indication, however, that the occurrence of beak deformities has spread northward more recently, based on the increasing number of reports from observers in Fairbanks (C. M. Handel unpubl. data). Geographic patterns are obscured by the patchy distribution of human settlements throughout the state.

Beak abnormalities in other species in Alaska occurred in the same general geographic pattern as those of Black-capped Chickadees, with the earliest records along the coast of south-central Alaska. Recent reports of Northwestern Crows and possibly American Crows (*Corvus brachyrhynchos*) suggest that this beak disorder now extends south along the Pacific Coast at least to Puget Sound (Van Hemert and Handel 2010), where we also had a small cluster of abnormal Black-capped Chickadees. Since 1997, large numbers of raptors (mainly Red-tailed Hawks [*Buteo jamaicensis*]) with similar beak abnormalities of unknown etiology have been documented between Vancouver, British Columbia, and Los Angeles, California (C. M. Anderson pers. comm.). Our finding of an affected Black-capped Chickadee in a remote area of Alaska, well beyond normal distances traveled by adults from any feeders, suggests that the geographic distribution is not restricted to areas with human settlements, although access to anthropogenic food sources is likely to increase survival of affected birds.

Developmental onset.—We found little evidence that the beak deformities in Black-capped Chickadees were congenital, which differs from findings in birds exposed to contaminants. In a study of aquatic birds exposed to selenium, 61% of nests had at least one dead embryo or at least one embryo or chick with an obvious malformation (Ohlendorf et al. 1986a). The prevalence of beak malformations in Double-crested Cormorant (*Phalacrocorax auritus*) chicks from colonies in the Great Lakes affected by polychlorinated biphenyls (PCBs) and other chlorinated compounds was 0.52% (Fox et al. 1991), 10× higher than that recorded in nestling Black-capped Chickadees (0.05%). We may have had difficulty detecting developmental malformations in Black-capped Chickadees because of their short nestling period (14–21 days), especially given that the beak is not fully grown by the time young leave the nest (Olsen 2003, C. M. Handel unpubl. data). If the prevalence of congenital malformations were indeed high, however, we would have expected increased embryonic mortality, which we did not see (C. M. Handel unpubl. data), or a higher prevalence of beak deformities than we found in juveniles after fledging.

We were surprised to recapture so many birds with beak deformities that previously had been captured with what appeared to be normal beaks. This finding, coupled with the low prevalence of abnormalities in juvenile birds, suggests that either this is an acquired condition or there is a delayed expression of a congenital condition. A similar case was recorded in Europe: a Great Tit that had been observed for 4 years with a normal beak developed, within 4 months, an upper beak that was twice the normal length (Pomeroy 1962). Most beak deformities for which we monitored development were fairly subtle in form at the onset, with a slight overbite or asymmetry of the upper and lower beaks. Thus, the incipient condition could have been congenital and latent, only becoming obvious as the bird aged. In only one case did we document an adult with an apparent malformation of the bone, which involved a pronounced lateral curvature of the premaxilla.

Clinical signs and possible etiology.—In all affected Black-capped Chickadees except the single case mentioned above, beak lesions did not appear to involve bone tissue but instead were restricted to the keratinized layers of the rhamphotheca and possibly the underlying epidermis and dermis. Epithelial disorganization, irregular ridges, scaly plates, brittleness, and thickening of the keratinized layers all suggested abnormal growth of the rhamphotheca, including what appeared to be very rapid growth in some individuals. In most birds, beak growth generally compensates for normal mechanical wear but may be slightly mismatched seasonally, largely as an effect of change in diet and concomitant foraging behavior (e.g., Davis 1954, Hulscher 1985, Morton and Morton 1987, Matthysen 1989). The greatest rate of net growth (absolute growth minus wear) in length of the upper beak that we recorded in a wild Black-capped Chickadee (0.13 mm day^{-1}) was almost twice the normal rate of absolute growth (measured using marks on the beak) in other passerines: 0.076 mm day^{-1} for a Common Canary (*Serinus canaria*) in captivity (Lüdicke 1933) and 0.085 mm day^{-1} for 45 Eurasian Nuthatches (*Sitta europaea*) in the wild (Matthysen 1989). It also exceeded the growth rates of abnormal gnathothecal projections that developed on the beaks of 6 American Tree Sparrows caged at high temperatures (0.08–0.09 mm day^{-1}; West 1959, 1974). Thus, excessive elongation of the beaks of affected Black-capped Chickadees was likely initiated by an accelerated growth rate rather than a reduced rate of abrasion. The occurrence of extremely thickened beaks in some individuals corroborates this assertion. Deformities may have been exacerbated by subsequent reduction in the wear process due to offset of the beak tips and changes in patterns of beak use.

The etiology of this keratin disorder remains unknown. We detected a fungal infection that may have disrupted normal beak growth in the most recent Black-capped Chickadee examined histologically; however, abnormal bone growth was not found in any other specimens and we could not determine whether this fungal infection caused the lesion of the rhamphotheca or was a secondary condition. Keratinophilic fungi have been associated with many species of birds worldwide, commonly growing on feathers or nails (Pugh 1972, Abdel-Gawad and Moharram 1989, Hubálek 2000, Efuntoye and Fashanu 2001, Czeczuga et al. 2004). Some of these dermatophytes have been documented to cause feather loss on the head and lesions of unfeathered regions of the body, including the beak, although overgrowth of the rhamphotheca has rarely been reported (Bradley et al. 1993, Ramis et al. 1998, Mans and Guzman 2007, Chermette et al. 2008, Keymer 2008).

We found no evidence for infection by bacteria, viruses (polyomavirus, poxvirus, or circovirus), or mites in the genus *Knemidocoptes*, all of which have caused beak lesions in other species (e.g., Raidal 1995, Tully et al. 2000, Gartrell et al. 2003, Galligan and Kleindorfer 2009). We found no necrosis of the beak typical of exposure to selenium (Ohlendorf 1996, 2002), nor the suite of internal and external clinical signs found in birds with crossed beaks around the Great Lakes and indicative of PCB-induced pathology (Gilbertson et al. 1991, O'Hara and Rice 1996), with the possible exception of the nestling Peregrine Falcon with a crossed beak and missing eye. Excessive growth of the beak can be a symptom of liver disease (Harrison 1986), but necropsy and histopathology of a small sample of affected Black-capped Chickadees did not reveal any abnormal pathology of internal organs, including liver, spleen, and thyroid.

Abnormalities of the beak have also been attributed to malnutrition, including deficiencies of vitamins A and D, pantothenic acid, biotin, and folic acid, but supporting experimental evidence has often been lacking (Keymer and Samour 2008). Seed-based diets are usually deficient in vitamin A and calcium; the high fat content of seeds can also interfere with calcium uptake (Harper and Skinner 1998). Thus, if Black-capped Chickadees are overly reliant on sunflower seeds at feeders, nutritional deficiencies could develop. A high frequency of lipomas, such as that found in one adult female with a severely overgrown beak, is often found in domestic birds maintained on a high-fat diet (Harrison and Harrison 1986). Hyperkeratosis of beak tissue is sometimes associated with hypovitaminosis A, particularly in captive Psittaciformes on a restricted seed diet (Macwhirter 1994, Keymer and Samour 2008); however, we never found abscesses in the oral cavity or respiratory tract, or discharges from the nares, which are diagnostic signs of this condition (Tully et al. 2000, Garland and Pritchard 2008).

Vitamin D_3 is synthesized in birds through exposure of the skin to sunlight (Klasing 1998) and helps regulate the balance of calcium and phosphorus (Macwhirter 1994). The folding leg fractures that we observed in a few nestling Black-capped Chickadees may have resulted from vitamin D_3 or calcium deficiency, as has been reported in domestic and wild birds (Austic and Scott 1984, Tangredi and Krook 1999, Phalen et al. 2005, Tangredi 2007). The types of beak abnormalities associated with calcium-related deficiencies, such as shortening (Sunde et al. 1978, Stevens et al. 1984), softening (Garland and Pritchard 2008), and ventral curvature of the beak (Tangredi 2007), however, are consistent with disturbances of mineralization of the bone and are quite different from the hard and brittle keratin overgrowth in the affected Black-capped Chickadees. This discrepancy, along with the absence of osteomalacia in adult Black-capped Chickadees, suggests that deficiencies of calcium or vitamin D_3 did not cause the beak deformities.

Recent studies of the genetic control of beak development have found that two signaling molecules (bone morphogenic protein 4 and calmodulin) play key roles in determining the depth, width, and length of the beak (Wu et al. 2004, Abzhanov et al. 2006, Grant et al. 2006). These proteins are active during embryonic craniofacial development and control the outgrowth of the beak primordia. Computed tomography (CT) scans have shown that the dimensional scaling of the keratin layers of the beak in various species matches that of the underlying bone (Campàs et al. 2010). Thus, it is unlikely that these proteins are involved with the abnormal beak-keratin growth we have documented in adult birds. However, it is possible that some unknown agent has affected other genes that may control the keratinization process.

Dermatoses on the head, neck, and legs found on 15% of the birds with beak deformities suggest that this disorder may not be restricted to beak tissue but instead may be a systemic keratin problem. The presence of overgrown claws in some of the affected chickadees corroborates this idea, but the low proportion (0.8%) is perplexing. The abnormal appearance of feathers in many of the affected birds could reflect a structural change in the feather keratin or a secondary condition associated with ectoparasites and the impaired ability to preen. We are now focusing on detailed histopathology and other studies of affected tissues to identify diagnostic signs, discern mechanisms controlling abnormal tissue growth, and determine the etiology of what we are terming "avian keratin disorder." We are also investigating the potential effects of beak deformities on survival and reproductive fitness of chickadees in Alaska. Systematic studies in other regions and examination of museum collections could help elucidate the geographic and taxonomic extent of this puzzling and troubling epizootic.

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Literature Cited

Abdel-Gawad, K. M., and A. M. Moharram. 1989. Keratinophilic fungi from the duck nails in Egypt. Journal of Basic Microbiology 29:259–263.

Abzhanov, A., W. P. Kuo, C. Hartmann, B. R. Grant, P. R. Grant, and C. J. Tabin. 2006. The calmodulin pathway and evolution of elongated beak morphology in Darwin's finches. Nature 442:563–567.

Abzhanov, A., M. Protas, B. R. Grant, P. R. Grant, and C. J. Tabin. 2004. *Bmp4* and morphological variation of beaks in Darwin's finches. Science 305:1462–1465.

Amadon, D. 1947. Ecology and the evolution of some Hawaiian birds. Evolution 1:63–68.

Austic, R. E., and M. L. Scott. 1984. Nutritional deficiency diseases. Pages 38–64 *in* Diseases of Poultry, 8th ed. (M. S. Hofstad, H. J. Barnes, B. W. Calnek, W. M. Reid, and H. W. Yoder, Jr., Eds.). Iowa State University Press, Ames.

Badyaev, A. V. 2010. The beak of the other finch: Coevolution of genetic covariance structure and developmental modularity during adaptive evolution. Philosophical Transactions of the Royal Society of London, Series B 365:1111–1126.

Badyaev, A. V., R. L. Young, K. P. Oh, and C. Addison. 2008. Evolution on a local scale: Developmental, functional, and genetic bases of divergence in bill form and associated changes in song structure between adjacent habitats. Evolution 62:1951–1964.

Bassir, O., and A. Adenkunle. 1970. Teratogenic action of aflatoxin B_1, palmotoxin B_0 and palmotoxin G_0 on the chick embryo. Journal of Pathology 102:49–51.

Benkman, C. W., and A. K. Lindholm. 1991. The advantages and evolution of a morphological novelty. Nature 349:519–520.

Boag, P. T., and P. R. Grant. 1981. Intense natural selection in a population of Darwin's finches (Geospizinae) in the Galápagos. Science 214:82–85.

Bowerman, W. W., IV, T. J. Kubiak, J. B. Holt, Jr., D. L. Evans, R. G. Eckstein, C. R. Sindelar, D. A. Best, and K. D. Kozie. 1994. Observed abnormalities in mandibles of nestling Bald Eagles *Haliaeetus leucocephalus*. Bulletin of Environmental Contaminants and Toxicology 53:450–457.

Bradley, F. A., A. A. Bickford, and R. L. Walker. 1993. Diagnosis of favus (avian dermatophytosis) in Oriental breed chickens. Avian Diseases 37:1147–1150.

Brewer, R. 1978. Winter home ranges of Black-capped Chickadees in southern Michigan oak forest. Jack-Pine Warbler 56:96–98.

Brittingham, M. C., and S. A. Temple. 1988. Impacts of supplemental feeding on survival rates of Black-capped Chickadees. Ecology 69:581–589.

Campàs, O., R. Mallarino, A. Herrel, A. Abzhanov, and M. P. Brenner. 2010. Scaling and shear transformations capture beak shape variation in Darwin's finches. Proceedings of the National Academy of Sciences USA 107:3356–3360.

Chermette, R., L. Ferreiro, and J. Guillot. 2008. Dermatophytoses in animals. Mycopathologia 166:385–405.

Clancey, P. A. 1948. Seasonal bill variation in Tree-Sparrow. British Birds 41:115–116.

Clayton, D. H., B. R. Moyer, S. E. Bush, T. G. Jones, D. W. Gardiner, B. B. Rhodes, and F. Goller. 2005. Adaptive significance of avian beak morphology for ectoparasite control. Proceedings of the Royal Society of London, Series B 272:811–817.

Cooper, J. E., and G. J. Harrison. 1994. Dermatology. Pages 607–639 *in* Avian Medicine: Principles and Application (B. W. Ritchie, G. J. Harrison, and L. R. Harrison, Eds.). Wingers Publishing, Lake Worth, Florida.

Cory, C. B. 1886. The birds of the West Indies, including the Bahama Islands, the Greater and Lesser Antilles, excepting the islands of Tobago and Trinidad. Auk 3:337–381.

Craves, J. A. 1994. Passerines with deformed bills. North American Bird Bander 19:14–18.

Custer, T. W., C. M. Custer, R. K. Hines, S. Gutreuter, K. L. Stromborg, P. D. Allen, and M. J. Melancon. 1999. Organochlorine contaminants and reproductive success of Double-crested Cormorants from Green Bay, Wisconsin, USA. Environmental Toxicology and Chemistry 18:1209–1217.

Czeczuga, B., A. Godlewska, and B. Kiziewicz. 2004. Aquatic fungi growing on feathers of wild and domestic bird species in limnologically different water bodies. Polish Journal of Environmental Studies 13:21–31.

Darwin, C. 1859. On the Origin of Species by Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life. John Murray, London. [Reprinted in 1964 *in* On the Origin of Species by Means of Natural Selection. A Facsimile of the First Edition (E. Mayr, Ed.). Harvard University Press, Cambridge, Massachusetts.]

Davis, J. 1954. Seasonal changes in bill length of certain passerine birds. Condor 56:142–149.

Davis, J. 1961. Some seasonal changes in morphology of the Rufous-sided Towhee. Condor 63:313–321.

Desrochers, A., S. J. Hannon, and K. E. Nordin. 1988. Winter survival and territory acquisition in a northern population of Black-capped Chickadees. Auk 105:727–736.

Dunnigan, G. M., J. L. Hammen, and T. R. Harris. 1997. A SAS-IML program for implementing two-phase regression analysis of geophysical time series data. Computers & Geosciences 23:763–770.

Efuntoye, M. O., and S. O. Fashanu. 2001. Occurrence of keratinophilic fungi and dermatophytes on domestic birds in Nigeria. Mycopathologia 153:87–89.

Fox, G. A., B. Collins, E. Hayakawa, D. V. Weseloh, J. P. Ludwig, T. J. Kubiak, and T. C. Erdman. 1991. Reproductive outcomes in colonial fish-eating birds: A biomarker for developmental toxicants in Great Lakes food chains. II. Spatial variation in the occurrence and prevalence of bill defects in young Double-crested Cormorants in the Great Lakes, 1979–1987. Journal of Great Lakes Research 17:158–167.

Galligan, T. H., and S. Kleindorfer. 2009. Naris and beak malformation caused by the parasitic fly, *Philornis downsi* (Diptera: Muscidae), in Darwin's small ground finch, *Geospiza fuliginosa*

(Passeriformes: Emberizidae). Biological Journal of the Linnean Society 98:577–585.

Garland, P. W., and S. Pritchard. 2008. Nutritional disorders. Pages 510–535 *in* Poultry Diseases, 6th ed. (M. Pattison, P. McMullin, J. M. Bradbury, and D. Alexander, Eds.). Elsevier, New York.

Gartrell, B. D., M. R. Alley, and T. Kelly. 2003. Bacterial sinusitis as a cause of beak deformity in an Antipodes Island Parakeet (*Cyanoramphus unicolor*). New Zealand Veterinary Journal 51: 196–198.

Gilbertson, M., T. Kubiak, J. Ludwig, and G. Fox. 1991. Great Lakes embryo mortality, edema, and deformities syndrome (GLEMEDS) in colonial fish-eating birds: Similarity to chick-edema disease. Journal of Toxicology and Environmental Health 33:455–520.

Gilbertson, M., R. D. Morris, and R. A. Hunter. 1976. Abnormal chicks and PCB residue levels in eggs of colonial birds on the lower Great Lakes (1971–1973). Auk 93:434–442.

Glase, J. C. 1973. Ecology of social organization in the Black-capped Chickadee. Living Bird 12:235–267.

Gosler, A. G. 1987. Pattern and process in the bill morphology of the Great Tit *Parus major*. Ibis 129:451–476.

Grant, P. R. 1986. Ecology and Evolution of Darwin's Finches. Princeton University Press, Princeton, New Jersey.

Grant, P. R., and B. R. Grant. 2006. Evolution of character displacement in Darwin's finches. Science 313:224–226.

Grant, P. R., B. R. Grant, and A. Abzhanov. 2006. A developing paradigm for the development of bird beaks. Biological Journal of the Linnean Society 88:17–22.

Handel, C. M., L. M. Pajot, S. L. Talbot, and G. K. Sage. 2006. Use of buccal swabs for sampling DNA from nestling and adult birds. Wildlife Society Bulletin 34:1094–1100.

Harper, E. J., and N. D. Skinner. 1998. Clinical nutrition of small psittacines and passerines. Seminars in Avian Exotic Pet Medicine 7:116–127.

Harrison, G. J. 1986. Disorders of the integument. Pages 509–524 *in* Clinical Avian Medicine and Surgery (G. J. Harrison and L. R. Harrison, Eds.). W.B. Saunders, Philadelphia.

Harrison, G. J., and L. R. Harrison. 1986. Nutritional diseases. Pages 397–407 *in* Clinical Avian Medicine and Surgery (G. J. Harrison and L. R. Harrison, Eds.). W.B. Saunders, Philadelphia.

Hays, H., and R. W. Risebrough. 1972. Pollutant concentrations in abnormal young terns from Long Island Sound. Auk 89:19–35.

Hicks, L. E. 1934. Individual and sexual variations in the European Starling. Bird-Banding 5:103–118.

Hoffman, D. J., H. M. Ohlendorf, and T. W. Aldrich. 1988. Selenium teratogenesis in natural populations of aquatic birds in central California. Archives of Environmental Contaminants and Toxicology 17:519–525.

Howard, L. 1951. Abnormal bill of Great Tit. British Birds 44:350.

Hubálek, Z. 2000. Keratinophilic fungi associated with free-living mammals and birds. Pages 93–103 *in* Biology of Dermatophytes and Other Keratinophilic Fungi (R. K. S. Kushwaha and J. Guarro, Eds.). Revista Iberoamericana de Micologia, Bilbao, Spain.

Hulscher, J. B. 1985. Growth and abrasion of the Oystercatcher bill in relation to dietary switches. Netherlands Journal of Zoology 35:124–154.

Jackson, J. A. 2002. Ivory-billed Woodpecker (*Campephilus principalis*). *In* The Birds of North America, no. 711 (A. Poole and F. Gill, Eds.). Birds of North America, Philadelphia.

Jebbett, D. E. 1991. Blue Tits with deformed bills. British Birds 84:511–512.

Keymer, I. F. 2008. Fungal diseases—Dermatophytosis, favus or ringworm infection. Pages 390–392 *in* Avian Medicine, 2nd ed. (J. Samour, Ed.). Elsevier, New York.

Keymer, I. F., and J. Samour. 2008. Disorders of the digestive system. Pages 281–302 *in* Avian Medicine, 2nd ed. (J. Samour, Ed.). Elsevier, New York.

Kinch, B. 1998. Deformed chickadee. Ontario Birds 16:45–46.

King, J. M., and C. L. Collenette. 1951. Abnormal bill of Blue Tit. British Birds 44:350.

Klasing, K. C. 1998. Comparative Avian Nutrition. Cab International, New York.

Lucas, A. M., and P. R. Stettenheim. 1972. Avian Anatomy: Integument. Part I. U.S. Department of Agriculture Handbook, no. 362:1–340.

Lüdicke, M. 1933. Wachstum und Abnutzung des Vogelschnabels. Zoologische Jahrbücher, Abteilung für Anatomie und Ontogenie der Tiere 57:465–534.

Ludwig, J. P., H. Kurita-Matsuba, H. J. Auman, M. E. Ludwig, C. L. Summer, J. P. Giesy, D. E. Tillitt, and P. D. Jones. 1996. Deformities, PCBs, and TCDD-equivalents in Double-crested Cormorants (*Phalacrocorax auritus*) and Caspian Terns (*Hydroprogne caspia*) of the upper Great Lakes 1986–1991: Testing a cause-effect hypothesis. Journal of Great Lakes Research 22:172–197.

Lumeij, J. T. 1994. Gastro-enterology. Pages 482–521 *in* Avian Medicine: Principles and Application (B. W. Ritchie, G. J. Harrison, and L. R. Harrison, Eds.). Wingers Publishing, Lake Worth, Florida.

Macwhirter, P. 1994. Malnutrition. Pages 842–861 *in* Avian Medicine: Principles and Application (B. W. Ritchie, G. J. Harrison, and L. R. Harrison, Eds.). Wingers Publishing, Lake Worth, Florida.

Magnusson, A. 1978. Talltita med missbildad näbb [Willow Tit with deformed beak]. Ornis Fennica 55:83–84.

Mans, C., and D. S.-M. Guzman. 2007. What is your diagnosis? Journal of Avian Medicine and Surgery 21:235–238.

Matthysen, E. 1989. Season variation in bill morphology of Nuthatches *Sitta europaea*: Dietary adaptations or consequences? Ardea 77:117–125.

Meigs, J. B., D. C. Smith, and J. Van Buskirk. 1983. Age determination of Black-capped Chickadees. Journal of Field Ornithology 54:283–286.

Møller, A. P., T. A. Mousseau, F. de Lope, and N. Saino. 2007. Elevated frequency of abnormalities in Barn Swallows from Chernobyl. Biology Letters 3:414–417.

Morton, M. L., and G. A. Morton. 1987. Seasonal changes in bill length in summering Mountain White-crowned Sparrows. Condor 89:197–200.

Newton, G. T. 1988. Blue Tits with various bill deformities. British Birds 81:648–649.

Newton, I. 1967. The adaptive radiation and feeding ecology of some British finches. Ibis 109:33–96.

Nogales, M., A. Martin, and F. Zino. 1990. Bill malformation of juvenile Cory's Shearwaters (*Calonectris diomedea borealis*) on Selvagem Grande. Bocagiana 139:1–5.

Odum, E. P. 1941. Annual cycle of the Black-capped Chickadee—2. Auk 58:518–535.

Odum, E. P. 1942. Annual cycle of the Black-capped Chickadee—3. Auk 59:499–531.

O'Hara, T. M., and C. D. Rice. 1996. Polychlorinated biphenyls. Pages 71–86 *in* Noninfectious Diseases of Wildlife, 2nd ed. (A. Fairbrother, L. N. Locke, and G. L. Hoff, Eds.). Iowa State University Press, Ames.

Ohlendorf, H. M. 1996. Selenium. Pages 128–140 *in* Noninfectious Diseases of Wildlife, 2nd ed. (A. Fairbrother, L. N. Locke, and G. L. Hoff, Eds.). Iowa State University Press, Ames.

Ohlendorf, H. M. 2002. Ecotoxicology of selenium. Pages 465–500 *in* Handbook of Ecotoxicology, 2nd ed. (D. J. Hoffman, B. A. Rattner, G. A. Burton, Jr., and J. Cairns, Jr., Eds.). Lewis Publishers, New York.

Ohlendorf, H. M., D. J. Hoffman, M. K. Saiki, and T. W. Aldrich. 1986a. Embryonic mortality and abnormalities of aquatic birds: Apparent impacts of selenium from irrigation drainwater. Science of the Total Environment 52:49–63.

Ohlendorf, H. M., R. L. Hothem, C. M. Bunck, T. W. Aldrich, and J. F. Moore. 1986b. Relationships between selenium concentrations and avian reproduction. Transactions of the North American Wildlife and Natural Resources Conference 51:330–342.

Ohlendorf, H. M., A. W. Kilness, J. L. Simmons, R. K. Stroud, D. J. Hoffman, and J. F. Moore. 1988. Selenium toxicosis in wild aquatic birds. Journal of Toxicology and Environmental Health 24:67–92.

Olsen, G. H. 2003. Oral biology and beak disorders of birds. Veterinary Clinics of North America: Exotic Animal Practice 6:505–521.

Owen, H. C., R. J. T. Doneley, R. E. Schmidt, and J. C. Patterson-Kane. 2007. Keratoacanthoma causing beak deformity in a Budgerigar (*Melopsittacus undulatus*). Avian Pathology 36:499–502.

Phalen, D. N., M. L. Drew, C. Contreras, K. Roset, and M. Mora. 2005. Naturally occurring secondary nutritional hyperparathyroidism in Cattle Egrets (*Bubulcus ibis*) from central Texas. Journal of Wildlife Diseases 41:401–415.

Piersma, T., R. van Aelst, K. Kurk, H. Berkhoudt, and L. R. M. Maas. 1998. A new pressure sensory mechanism for prey detection in birds: The use of principles of seabed dynamics? Proceedings of the Royal Society of London, Series B 265:1377–1383.

Pomeroy, D. E. 1962. Birds with abnormal bills. British Birds 55: 48–72.

Pugh, G. J. F. 1972. The contamination of birds' feathers by fungi. Ibis 114:172–177.

Pyle, P. 1997. Identification Guide to North American Birds, part 1: Columbidae to Ploceidae. Slate Creek Press, Bolinas, California.

Raidal, S. R. 1995. Staphylococcal dermatitis in quail with a parakeratotic hyperkeratotic dermatosis suggestive of pantothenic acid deficiency. Avian Pathology 24:579–583.

Ramis, A., J. Fernandez-Moran, X. Gilbert, and H. Fernandez-Bellon. 1998. Dermatophytosis in a Hyacinth Macaw (*Anodorhynchus hyacinthinus*)—A case report. Proceedings of the International Virtual Conferences in Veterinary Medicine: Diseases of Psittacine Birds. [Online.] Available at www.vet.uga.edu/vpp/archives/ivcvm/1998/ramis/index.php.

Rockwell, R. F., B. M. Pezzanite, and P. Matulonis. 2003. Developmental abnormalities in wild populations of birds: Examples from Lesser Snow Geese (*Chen caerulescens caerulescens*). American Museum Novitates 3400:1–14.

Romanoff, A. L. 1972. Pathogenesis of the Avian Embryo. An Analysis of Causes of Malformations and Prenatal Death. Wiley-Interscience, New York.

Ryckman, D. P., D. V. Weseloh, P. Hamr, G. A. Fox, B. Collins, P. J. Ewins, and R. J. Norstrom. 1998. Spatial and temporal trends in organochlorine contamination and bill deformities in Double-crested Cormorants (*Phalacrocorax auritus*) from the Canadian Great Lakes. Environmental Monitoring and Assessment 53:169–195.

Sage, B. L. 1956. On some examples of melanism in the genus *Parus* Linnaeus. British Birds 76:130–132.

Schneider, R. A. 2005. Developmental mechanisms facilitating the evolution of bills and quills. Journal of Anatomy 207:563–573.

Schneider, R. A., and J. A. Helms. 2003. The cellular and molecular origins of beak morphology. Science 299:565–568.

Senar, J. C., J. Domènech, L. M. Carrascal, and E. Moreno. 1997. A funnel trap for the capture of tits. Butlletí del Grup Català d'Anellament 14:17–24.

Sharp, M. S., and R. L. Neill. 1979. Physical deformities in a population of wintering blackbirds. Condor 81:427–430.

Smith, S. M. 1991. The Black-capped Chickadee: Behavioral Ecology and Natural History. Cornell University Press, Ithaca, New York.

Stettenheim, P. 1972. The integument of birds. Pages 1–63 *in* Avian Biology, vol. 2 (D. S. Farner, J. R. King, and K. C. Parkes, Eds.). Academic Press, New York.

Stettenheim, P. R. 2000. The integumentary morphology of modern birds—An overview. American Zoologist 40:461–477.

Stevens, V. I., R. Blair, R. E. Salmon, and J. P. Stevens. 1984. Effect of varying levels of dietary vitamin D_3 on turkey hen egg production, fertility and hatchability, embryo mortality and incidence of embryo beak malformations. Poultry Science 63:760–764.

Storer, R. W. 1971. Adaptive radiation of birds. Pages 149–188 *in* Avian Biology, vol. 1 (D. S. Farner and J. R. King, Eds.). Academic Press, New York.

Sunde, M. L., C. M. Turk, and H. F. DeLuca. 1978. The essentiality of vitamin D metabolites for embryonic chick development. Science 200:1067–1069.

Tangredi, B. P. 2007. Environmental factors associated with nutritional secondary hyperparathyroidism in wild birds. Avian and Poultry Biology Reviews 18:47–56.

Tangredi, B. P., and L. P. Krook. 1999. Nutritional secondary hyperparathyroidism in free-living fledgling American Crows (*Corvus brachyrhynchos brachyrhynchos*). Journal of Zoo and Wildlife Medicine 30:94–99.

Temeles, E. J., and W. J. Kress. 2003. Adaptation in a plant-hummingbird association. Science 300:630–633.

Tully, T. N., Jr., M. P. C. Lawton, and G. M. Dorrestein, Eds. 2000. Avian Medicine. Butterworth-Heinemann, Oxford, United Kingdom.

Tweit, R. C., K. B. Burk, S. M. Russell, J. B. Truan II, and P. M. Walters. 1983. Incidence of crossed bills in Inca Doves. North American Bird Bander 8:12.

Van Hemert, C., and C. M. Handel. 2010. Beak deformities in Northwestern Crows: Evidence of a multispecies epizootic. Auk 127: 746–751.

Weise, C. M., and J. R. Meyer. 1979. Juvenile dispersal and development of site-fidelity in the Black-capped Chickadee. Auk 96:40–55.

West, G. C. 1959. Effects of high air temperature on the bill and claw keratin structures of the Tree Sparrow. Auk 76:534–537.

West, G. C. 1974. Abnormal bill of a White-winged Crossbill. Auk 91:624–626.

Wu, P., T.-X. Jiang, J.-Y. Shen, R. B. Widelitz, and C.-M. Chuong. 2006. Morphoregulation of avian beaks: Comparative mapping of growth zone activities and morphological evolution. Developmental Dynamics 235:1400–1412.

Wu, P., T.-X. Jiang, S. Suksaweang, R. B. Widelitz, and C.-M. Chuong. 2004. Molecular shaping of the beak. Science 305:1465–1466.

Yamashita, N., S. Tanabe, J. P. Ludwig, H. Kurita, M. E. Ludwig, and R. Tatsukawa. 1993. Embryonic abnormalities and organochlorine contamination in Double-crested Cormorants (*Phalacrocorax auritus*) and Caspian Terns (*Hydroprogne caspia*) from the upper Great Lakes in 1988. Environmental Pollution 79:163–173.

Zar, J. H. 1996. Biostatistical Analysis, 3rd ed. Prentice Hall, Upper Saddle River, New Jersey.

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