Embryonic Growth of American Kestrels¹

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Descriptions of growth and criteria for aging embryos have been recorded for precocial avian species such as chickens (Hamburger and Hamilton 1951, Patten 1951, Hamilton 1952), Ring-necked Pheasant (*Phasianus colchicus*; Fant 1957, Labisky and Opsahl 1958), Northern Bobwhite (*Colinus virginianus*; Hanson 1954), and various waterfowl species (Hanson 1954, Weller 1956, Koecke 1958, Cooper and Batt 1972, Caldwell and Snart 1975, Burke et al. 1978), but such information exists for only one altricial species, the Pariah Kite (*Milvus migrans govinda*; Desai and Malhotra 1980).

Access to over 100 pairs of American Kestrels (*Falco sparverius*) breeding in captivity at McGill University, Montreal (Bird 1982, Bird and Laguë 1982a) allowed us to measure the growth of embryos at selected stages of development in this semi-altricial species. Such information provides us with criteria for aging embryos, a guideline for recognizing abnormalities and deformities, and an opportunity to compare embryonic growth and development of precocial species with that of altricial species.

A total of 27 eggs containing live embryos of known age were removed from 8 clutches at 3-day intervals beginning at day 3 and continuing to day 27, just before hatching. Three embryos were examined at each interval macroscopically with the aid of a dissecting microscope with an optical scale.

The total length of the uncurled embryo was measured at all stages, but other measurements were recorded at 12 days of age and older. The lengths of middle toe, tarsus, and culmen were measured according to Bird and Laguë (1982b). The eyeball was measured at its widest point and the wing in two sections: the antebrachium and the manus. Means and ranges in millimeters are given for all measurements.

The selected stages of embryo development are presented in Fig. 1 and are described below.

Day 3.—Blastodisc ca. 5 to 6 mm in diameter; concentric outer rings in the yolk around the blastodisc, indicating beginning of yolk digestion; blood islands are visible, but not the blood itself; brain differentiating into three vesicles; about 10 somites are recognizable; embryo length 3.5 mm (3-4.4). Day 6.—Area vasculosa about 25 mm; two cardiac vesicles visible in the rhythmically beating heart; blood and vitelline vessels are visible; pigmentation of the iris has begun; eye 0.87 mm (0.6–1.0) in diameter; allantoid vesicle is tiny, but visible; wing and leg buds appear without digitation; the head is turning toward the side and the tail is curving to give the embryo the appearance of the letter "C"; embryo length 11.7 mm (10.5–13.0).

Day 9.—Midbrain very prominent and cerebral hemispheres less so; heart still visible; pigmented eye 3.07 mm (2.8–3.2) in diameter; allantoid vesicle much larger, and the amnion is well developed; leg (approx. 2.0 mm) and wing (approx. 2.5 mm) buds show digitation, but digits still not distinct; embryo length 16.7 mm (15.8–17.2).

Day 12.—Cerebral hemispheres and diencephalon less evident, but mesencephalon very prominent; eye 5.17 mm (4.8-5.5) in diameter; allantoid vesicle still very large; otic vescicle visible; embryo making muscular movements; middle toe measurable in two embryos (2.1 mm); antebrachium 2.9 mm (2.7-3.0) and manus 1.4 mm (1.2-1.5); culmen without egg tooth 1.37 mm (1.2-1.5); tarsus 2.3 mm (2.2-2.5); embryo length 25.4 mm (24.0-26.2).

Day 15.—Mesencephalon still prominent; allantoid vesicle and amnion still well developed; nostrils, egg tooth, and feather papillae all visible; yolk volume decreasing to approximately 4.2 ml; diameter of eye 5.17 mm (4.8–5.5); middle toe 3.6 mm (3.3–3.9); antebrachium 5.7 mm (5.3–6.0) and manus 3.47 mm (3.0–3.8); culmen 1.57 mm (1.5–1.9); tarsus 5.33 mm (4.7–6.0); embryo length 31.13 mm (30.4–32.0).

Day 18.—Mesencephalon still more prominent than metencephalon; talons becoming visible; eye slit developing normal shape; yolk decreasing in volume to 3.1 ml (3.0–3.2); diameter of eye 10.4 mm (10.2– 10.5); middle toe 4.3 mm (4.0–4.7); antebrachium 7.77 mm (7.5–8.3) and manus 5.17 mm (5.0–5.3); culmen 2.83 mm (2.6–3.2); tarsus 7.7 mm (7.5–8.0); embryo length 40.4 mm (39.2–42.0).

Day 21.—Down feathers well grown; yolk volume decreasing to 2.43 ml (2.3–2.7); diameter of eye 10.17 mm (10.0–10.5); middle toe 5.33 mm (5.2–5.5); antebrachium 9.17 mm (9.0–9.5) and manus 5.7 mm (5.5–6.0); culmen 3.57 mm (3.3–4.0); tarsus 8.87 mm (8.6–9.3); embryo 45.1 mm (44.0–46.2).

Day 24.—Metencephalon now more prominent than mesencephalon; digits on feet in normal position; yolk volume decreasing to half that at 15 days old, 2.06 ml (1.5–2.5); eye diameter 11.1 mm (10.2–12.0); middle toe 5.8 mm (5.0–6.7); antebrachium 9.91 mm (8.7– 11.0) and carpus 6.3 mm (5.8–7.0); culmen 3.7 mm

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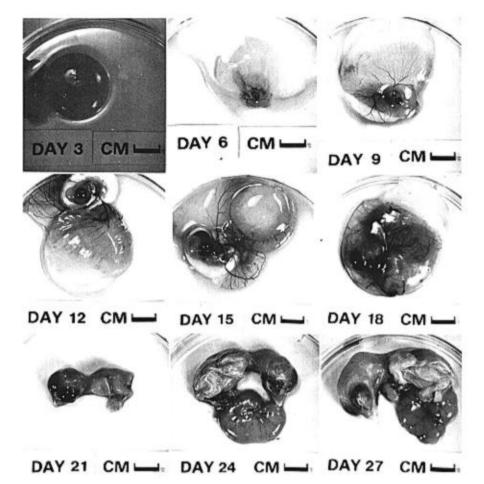


Fig. 1. Development of American Kestrel embryos by 3-day intervals.

(3.0-4.4); tarsus 10.2 mm (9.0-10.7); embryo 50.8 (44.0-53.5).

Day 27.—Yolk volume decreased to 1.5 ml (0.0-2.2); eye diameter 12.3 mm (10.9-13.1); middle toe 6.4 mm (5.5-7.7); antebrachium 11.2 mm (9.5-12.0) and manus 7.6 mm (7.1-8.0); culmen 4.1 mm (3.4-4.6); tarsus 12.0 mm (9.9-14.0); embryo 56.35 mm (51.0-62.0).

All body parts measured in the kestrel embryo grew in a steady linear fashion from day 12 to 27.

Cooper and Batt (1972) described the growth of the precocial Giant Canada Goose (*Branta canadensis maxima*) and Desai and Malhorta (1980) described that of the Pariah Kite at stages identical to those selected for our study. Data on adult goose are taken from Palmer (1976) and on kites from Weick (1980).

The pigmentation of the iris and formation of the hind limb occurred at approximately the same time (day 6) in all three species. The onset of the development of digits, talons, and down did not differ in the kite and kestrel. The development of the circulatory system and the appearance of the feather papillae began roughly 3 days earlier in the goose.

The embryos of the semi-altricial kestrel increased their size in length 6 times (9–56 mm) and the precocial goose 16 times (9–144 mm) (Fig. 2a). The growth of the kite embryo was only slightly greater than that of the kestrel. Expressing embryo length as a percentage of adult body length, the American Kestrel showed more rapid development than both the Canada Goose and Pariah Kite. The former achieved approximately 23% of the adult length, whereas the goose gained only 15% and the kite 14% (Fig. 2b).

From day 15, the culmen increased in magnitude about 4 times in the kite, 2.5 times in the kestrel, and 1.5 times in the goose (Fig. 3a). At day 15, the kestrel and goose had achieved about 15% of the adult culmen, whereas the kite had only reached about 11%.

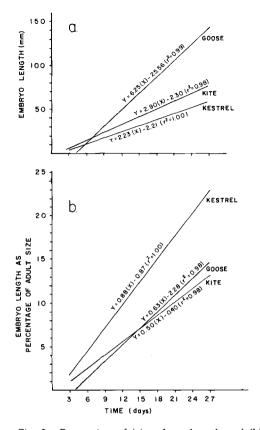


Fig. 2. Regression of (a) embryo length and (b) embryo length as a percentage of adult size over the 27-day incubatory period in the American Kestrel, Pariah Kite (from Desai and Malhotra 1980), and Giant Canada Goose (from Cooper and Batt 1972).

By day 27, however, the kite had gained an additional 35% towards its final size, whereas the kestrel gained only 20% and the goose 8% (Fig. 3b).

At day 15, the kestrel tarsus was slightly more than 1 mm longer than that of the kite, and by day 27 the tarsal lengths of the kestrel had doubled and those of the kite had tripled, so that they were equivalent in size (Fig. 4a). Expressed as a percentage of adult tarsus length (Fig. 4b), the kestrel achieved 14% by day 15 and 32% by day 27, and the kite had achieved 7% by day 15 and 22% by day 27.

Conversely, the middle toe grew faster in the kite (Fig. 5). Between day 15 and 27, it tripled in length in the kite and only doubled in the kestrel.

In summary, the semi-altricial American Kestrel is more advanced in development at hatching than the precocial Canada Goose in terms of lengths of body and culmen. This is surprising, because the egg of a precocial species contains between 35 and 50% yolk

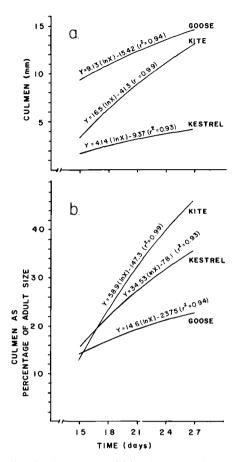


Fig. 3. Regression of (a) culmen and (b) culmen as a percentage of adult size over the 27-day incubatory period in the American Kestrel, Pariah Kite (from Desai and Malhotra 1980), and Giant Canada Goose (from Cooper and Batt 1972).

by volume, compared with only 20% for altricial species such as eagles (Heinroth 1938). Simply put, more energy is available for embryonic development in the precocial goose. Perhaps the smaller yolk supply available to the kestrel is more efficiently used. A better explanation, however, is that the goose's energy supply is diverted to more immediate needs such as the development of strong legs for swimming and of the nervous system and sense organs for alertness (Portmann 1950). Furthermore, Stresemann (1927– 1934) showed that precocial chicks generally have up to one third of their yolk supply left after hatching to sustain them through the first 2 or 3 days.

The fast embryonic growth of the kestrel bill fulfills an immediate need for feeding during the remaining 29-30 days of nest life. The even faster de-

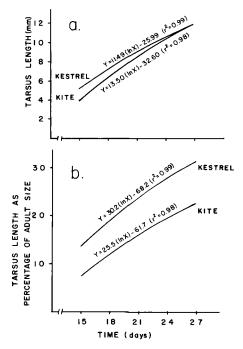


Fig. 4. Regression of (a) tarsus length and (b) tarsus length as a percentage of adult size over the 27day incubatory period in the American Kestrel and Pariah Kite (from Desai and Malhotra 1980).

velopment of the kite's bill is not explainable at this time but may reflect differences in feeding habits between the two raptor species.

Finally, if embryo length can be correlated with

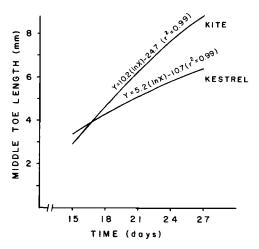


Fig. 5. Regression of middle toe length over the 27-day incubatory period in the American Kestrel and Pariah Kite (from Desai and Malhotra 1980).

embryo weight in the three species discussed, the much greater embryo length (expressed as a percentage of adult body length) in the kestrel supports Pettingill's (1970) statement that the weight of the precocial chick is less than that of the altricial young in proportion to the site of the adult female. The Pariah Kite, however, does not appear to support this. Further research in this area would be fruitful.

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Cayenne Tern New to North America, with Comments on Its Relationship to Sandwich Tern

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On 30 May 1983, at Cape Hatteras Point, Cape Hatteras National Seashore, Buxton, North Carolina (that portion of the Outer Banks closest to Gulf Stream waters and where the Banks abruptly turn 90° to the southwest), we watched an adult Cayenne Tern (*Sterna sandvicensis eurygnatha*) engage in courtship behavior for 20 min with three Sandwich Terns (*S. sandvicensis* cf. *acuflavidus*). This is the first known occurrence of an individual of this taxon in North America, and it is some 2,100 km across open ocean from the nearest (and very recent) previous occurrence in the Virgin Islands.

This individual, identified as a male from its role in courtship activities and as at least 3 yr old from plumage characters, was identical to the accompanying Sandwich Terns except for bill color. All had varying degrees of white feathers in their crowns, a condition typifying incubating or brooding Sandwich and Royal (S. maxima) terns in that area (Buckley and Buckley 1972). It was immediately distinguished from members of the sandvicensis group (American Ornithologists' Union 1983: 229) by its allyellow bill, in color somewhere between "lemon" and "banana" yellow. This feature, size, and the allblack forehead in alternative plumage distinguish eurygnatha from other crested terns, and, as we had previous familiarity with eurygnatha courting sandvicensis-like individuals in Puerto Rico (Buckley and Buckley 1970), we were able to identify this bird on sight. A suggestion of duskiness on both mandibular rami was apparent when the bird was viewed through a 30× spotting scope as close as 30 m, but, except for its bill color, it was not readily distinguishable from the accompanying Sandwich Terns in size, mantle color, vocalizations, or display postures. It performed Forward-erects, High-flights, and Pass-ceremonies [with accompanying vocalizations similar to those of both Sandwich and Royal terns (Buckley and Buckley

in press)], in this manner behaving as a local breeder. Unfortunately, conditions did not permit our close examination of the two nearby (< 30 km) Royal and Sandwich colonies for its possible nest site. The Outer Banks of North Carolina harbor the largest aggregation of breeding Sandwich Terns away from the Gulf Coast, and in winter they disperse southwest to the Pacific Coast from Oaxaca to Ecuador, into the western Caribbean, and occasionally into the normal winter range of *eurygnatha* in the southern Caribbean. The North Carolina individual may have returned north with Sandwich Terns.

The Cayenne Tern is generally poorly known, although a review of its distribution, affinities, and taxonomic status is in preparation by Ruud van Halewijn. In the West Indies, eurygnatha was completely unknown or overlooked until the first sight report in 1962, and the first colony of sandvicensis was not found there until 1965. Eurygnatha was believed to breed somewhere in northern South America, and it was not until 1952 that its nest and eggs were described from Curaçao by Junge and Voous (1955). Shortly thereafter, Ansingh et al. (1960) reported additional colonies of crested terns in the Netherlands Antilles, all of which contained apparently freely interbreeding individuals ranging from phenotypically "pure" sandvicensis to "pure" eurygnatha, with great variation between those extremes. [A good recent summary is in Voous (1983).] Based on those findings, most workers now treat both forms as races of a single species, sandvicensis. Thirty years later we know of no other breeding population so variable, and recent fieldwork has uncovered more apparently "pure" sandvicensis colonies in the West Indies (Bond 1956 et seq.). It was thus quite a surprise when in June 1982 a Cayenne Tern was found paired with a Sandwich near St. Thomas, Virgin Islands and another unpaired Cayenne Tern was seen at nearby Anegada