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Avian Premaxilla and Tarsometatarsus from the Uppermost Cretaceous of Montana

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Despite a variety of fragmentary, apparently neognathous avian fossils known from the uppermost Cretaceous deposits (Brodkorb 1963, Olson 1985, Olson and Parris 1987), we still lack even an approximate idea of how many neognathous lineages survived beyond the Cretaceous/Tertiary boundary. Most of the Maastrichtian avian bones reveal a charadriiform or transitional charadriiform-gruiform morphology, which may be plesiomorphic for most (Olson 1985) but probably not all of the neognaths (Elzanowski 1995). Other than that, there is some fossil evidence for the existence of loons in the Cretaceous (Olson 1992) and mostly indirect evidence for the pre-Tertiary origins of the relict pelecaniforms (Phaethontidae and Fregatidae) and procellariiforms (Elzanowski and Galton 1991). The last of these are possibly represented in the basal portion of the Early Paleocene Hornerstown Formation in New Jersey (Olson and Parris 1987).

In this paper, we describe two fragmentary Late Cretaceous avian fossils: a premaxilla that fits in the charadriiform-gruiform assemblage and may possibly represent one of the already established genera; and a distal fragment of the right tarsometatarsus that may represent the earliest record of the anseriform lineage.

Both specimens come from the locality known as Bug Creek West, Montana, Hell Creek Formation, which is of Late Cretaceous (Maastrichtian) age; the specimens are part of the collections of the Museum of Paleontology of the University of California at Berkeley (UCMP). The premaxilla UCMP 117598 was collected in 1974 by J. D. Archibald and the tarsometatarsus UCMP 117599 in 1975 by D. Lawler.

Premaxilla.—We have made detailed comparisons of this specimen with the charadriiforms, gruiforms, podicipediforms, and *Gavia* (i.e. with those extant taxa having a premaxilla that shows an overall similarity to the fossil irrespective of size). The survey covered all genera of these groups represented in the avian osteological collection (Wood and Schnell 1986) of the National Museum of Natural History (USNM).

The fragment includes the premaxillary symphysis and the rostral fragment of the dorsal bar (Fig. 1). The symphysis is 17 mm long, slightly decurved and approximately as high (4.3 mm) as it is wide at its midpoint; it is slightly broader caudally (4.8 mm). The rostral end is somewhat squared, which may or may not be due to postmortem damage. The dorsal surface is rounded and smooth, and the sides are very steep. The largest among the neurovascular foramina scattered on each side are two elongate dorsal foramina: the vessel from the rostral one coursed rostrad, whereas the vessel from the caudal one apparently bifurcated into a smaller rostral and a larger caudal branch. In addition, a number of smaller openings perforates each side of the symphysis.

The ventral surface of the premaxillary symphysis is strongly concave (Fig. 1c, d). There are no distinct neurovascular foramina on the ventral (palatal) surface, with the possible exception of one small opening on the left side. The palatal shelves of the premaxilla begin from the symphysial tip and gradually broaden caudally where each of them occupies one-third of the symphysial width. They are flat and slightly sloped dorsad. The tomial edges are blunt. Between the palatal shelves is a deep, 1.1-mm-wide median groove whose bottom merges with the roof of the symphysis. The groove is imperceptibly expanded in the midlength of the symphysis. A pair of neurovascular canals is enclosed by the shelves ventrally.

The preserved fragment of the dorsal bar is composed exclusively of the frontal process of the premaxilla. It cannot be determined whether the premaxillary process of the nasal had extended to the symphysis and then fell off (which would be likely in a juvenile bird) or terminated more caudally. The frontal process is 3.4 mm wide and 1.8 mm thick, including a strong median ridge on the ventral surface behind the symphysis (Fig. 1d, e).

In the primitive condition retained by most birds, the premaxillary symphysis is open ventrally (i.e. excavated up to its roof) at least along the midline. In the opposite, derived condition, the palatal shelves are fused in the midline, enclosing a median chamber. *Hesperornis* (Elzanowski 1991:figs. 1 and 3) and most of the neognathous birds with an open premaxillary symphysis have the palatal surface of the symphysis perforated by a pair of major neurovascular foramina at the rostral end, a condition possibly plesiomorphic for the Neornithes (Elzanowski 1995). The lack of these foramina seems, therefore, to be a derived condition that evolved in the Scolopacidae, Rallidae, Heliornithidae, Spheniscidae, and *Gavia.*

In *Hesperornis* (Elzanowski 1991:figs. 1 and 3) and the neognaths with an open premaxillary symphysis, the ventral (palatal) concavity of the symphysis shows a tripartite subdivision into two lateral elevations en-

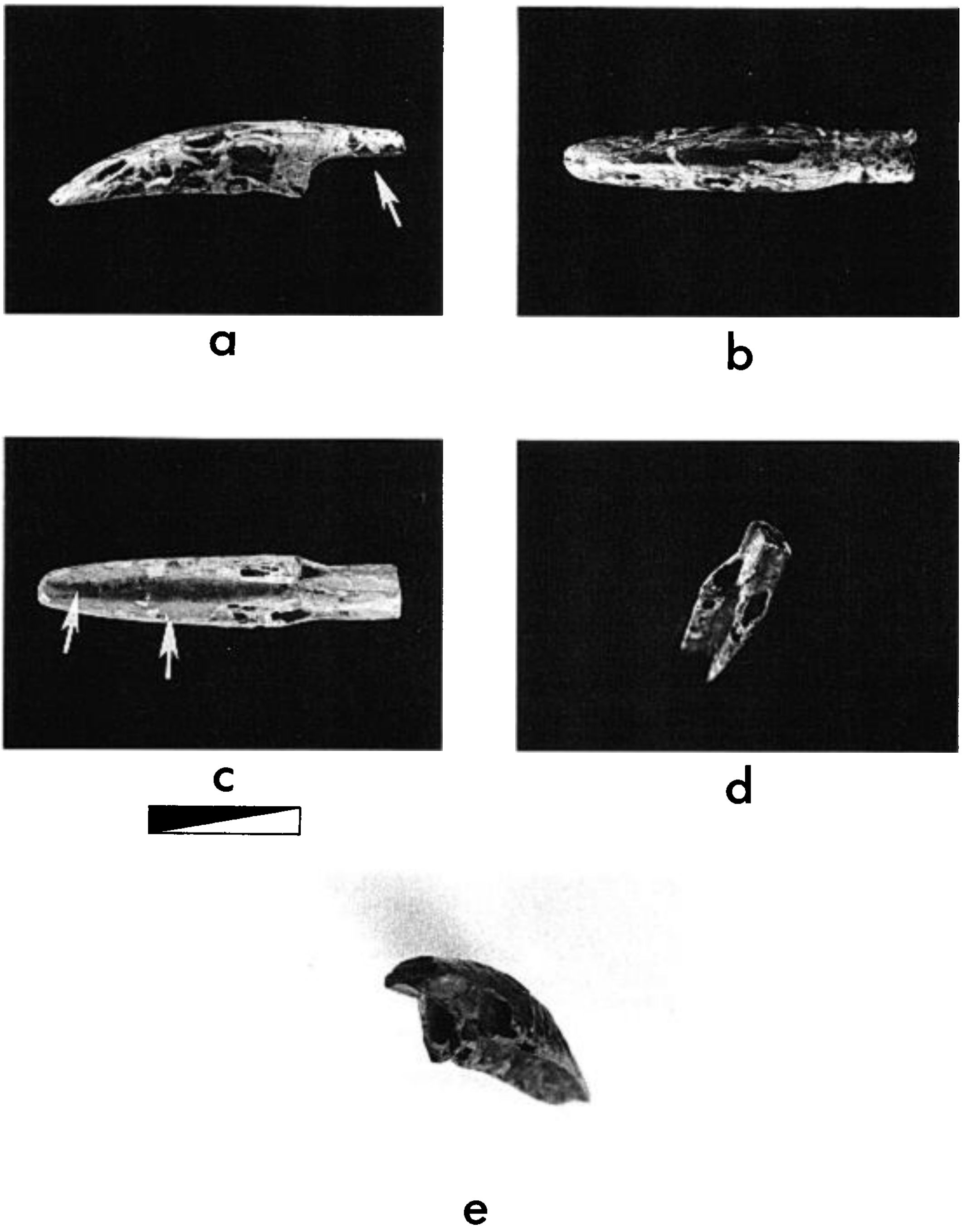

Fig. 1. Premaxilla UCMP 117598 in (a) left lateral, (b) dorsal, (c) ventral, (d) ventrocaudal oblique, and (e) right ventro-oblique views showing neurovascular canals. White arrows in panel a point to frontal process and in panel b to ventral groove in premaxillary symphysis and palatal shelf of premaxilla. Scale bar equals 10 mm.

closing the neurovascular canals and a median trough. In most of these neognaths, the two lateral elevations take the form of well-defined palatal shelves and the median trough is represented by a well-defined median groove. In the majority of cases, the shelves taper rostrally, whereby the tripartite shelf-and-groove configuration does not extend to the symphysial tip. In contrast, the groove extends to the symphysial tip in the Bug Creek fossil. Among extant birds, the groove extends to the symphysial tip in one of the two species of the Rostratulidae (the American Painted Snipe; *Nycticryphes semicollaris*), and the majority of Scolopacidae, the exceptions being the Broad-billed Sandpiper (*Limicola falcinellus*), the Jack Snipe (*Lymnocryptes minimus*), the Red Phalarope (*Phalaropus fulicarius*), and the turnstones (*Arenaria*). In the Red-necked Phalarope (*P. lobatus*) the rounded tomial margins could be regarded as vestigial shelves.

What makes the fossil premaxilla dramatically different from all rhynchokinetic charadriiforms is the presence of a prominent ventral ridge or bulge on the ventral side of the frontal process next to the premaxillary symphysis (Fig. 1d, e). Such a structure makes the dorsal bar rigid at the rostral end. The significance of this morphology for cranial kinesis is well illustrated by its diversity among the Rallidae. In those rails (e.g. *Rallus, Capellirallus*) that are amphikinetic (Zusi 1984:table 1) and, thus, have a distal bending zone (see Olson 1975:fig. 3), the ventral surface of the dorsal bar is flat, concave, or at most slightly convex. By contrast, all prokinetic rails—including *Atlantisia, Diaphorapteryx, Fulica, Gallinula, Porzana* (see Olson 1977), *Tribonyx* (see Olson 1975:fig. 1), *Himantornis, Porphyrula, Porphyriops, Poliolimnas*, and *Pardirallus*—have the ventral surface of the dorsal bar markedly convex and/or with a distinct median ridge. This evidence suggests that the Bug Creek bird had a prokinetic rather than rhynchokinetic or amphikinetic skull.

A combination of a shelf-and-groove structure of the symphysial tip (known only in the probing charadriiforms) with a thick, ridged, and rigid rostral end of the dorsal bar (not found in the probing charadriiforms) is unique to the Bug Creek fossil and precludes its assignment to any extant family of birds.

Tarsometatarsus.—This fossil was compared in detail with tarsometatarsi of charadriiforms, gruiforms, anseriforms, galliforms, and fossil genera of the charadriiform-gruiform assemblage (Brodkorb 1963, Olson 1985, Olson and Parris 1987). Body-mass values are from Dunning (1993).

As far as preserved, the distal end of the tarsometatarsus is intact except for a break between trochlea II and trochlea III. The arrangement of the trochleae is compact, with narrow intertrochlear spaces (Fig. 2). Trochlea III protrudes far beyond the trochleae II and IV, trochlea IV protrudes far beyond trochlea II, trochlea II is in a ventral position, and the entire medial surface of trochlea III exposed in the medial view. Trochlea II has a tongue-shaped wing and no distinct ligamental pit. Trochlea III has the lateral margin slightly sigmoid and the ventral part of the articular surface pointed and strongly asymmetrical at the end, which is embayed medially. Trochlea IV has the lateral lip descending gradually onto the shaft and bears a distinct ligamental pit. The attachment scar of the sesamoid ligament is distinct and slightly elevated distally. The distal foramen is large, elongate, and separated by a very narrow bridge (which itself is much shorter than the foramen) from the lateral intertrochlear incisure.

The overall configuration of the trochleae agrees with: Anseriformes, including *Presbyornis* (Wetmore 1926:figs. 10–12, Olson and Parris 1987:fig. 7); small Phasianidae, especially Odontophorinae; Gruidae, *Aramus*, and Rallidae, which are probably closely related within the gruiforms; and most of the Charadriiformes except for the Burhinidae, Jacanidae, Haematopodidae, Rhynchopidae, and *Telmatornis* (Olson and Parris 1987:fig. 7).

A prominent character that is shared exclusively with the anseriforms is the extremely distal position of the distal foramen in ventral view, with only a narrow bridge separating it from the lateral intertrochlear fissure (Fig. 2e). This character has not been found in any other terrestrial or aquatic nonpasserines. Although the distal foramen is relatively large in the grebes and loons, it is separated from the intertrochlear space by a broad bony bridge. In addition, the fossil agrees specifically with the anatids in the compact positioning of the trochleae, which is probably a swimming adaptation, and with *Presbyornis* in the extraordinary size of the distal foramen, which is even larger than in the anatids. Since the anatids have legs adapted for swimming and *Presbyornis* was a wader, the large size and extreme distal position of the distal foramen do not seem to be correlated with any particular locomotory function. The consistent similarities to *Presbyornis* and the anatids suggest that the new tarsometatarsus represents a close relative of the anseriforms.

However, the fossil differs from either the anatids or *Presbyornis* in having trochlea III distinctly embayed medially at its ventral end, a condition found elsewhere only in the sheathbills (*Chionis*; Fig. 2f, g), and in the tongue-shaped wing of its trochlea II, such as seen in cranes (Gruidae) and limpkins (*Aramus*). In *Presbyornis* this wing is more or less truncated at the end, whereas in anatids it takes the form of a flange descending onto the shaft. In addition, the fossil differs specifically from the anatids in lacking a distinct furrow in trochlea II, and from *Presbyornis* in lacking a distinct ligamental pit on the trochlea II and in having the lips of trochlea III barely set off from the shaft in side view.

Presbyornis is known since the Paleocene (Olson 1994) and unquestionable anatids only since the Oligocene (Olson 1985). Another possible early record

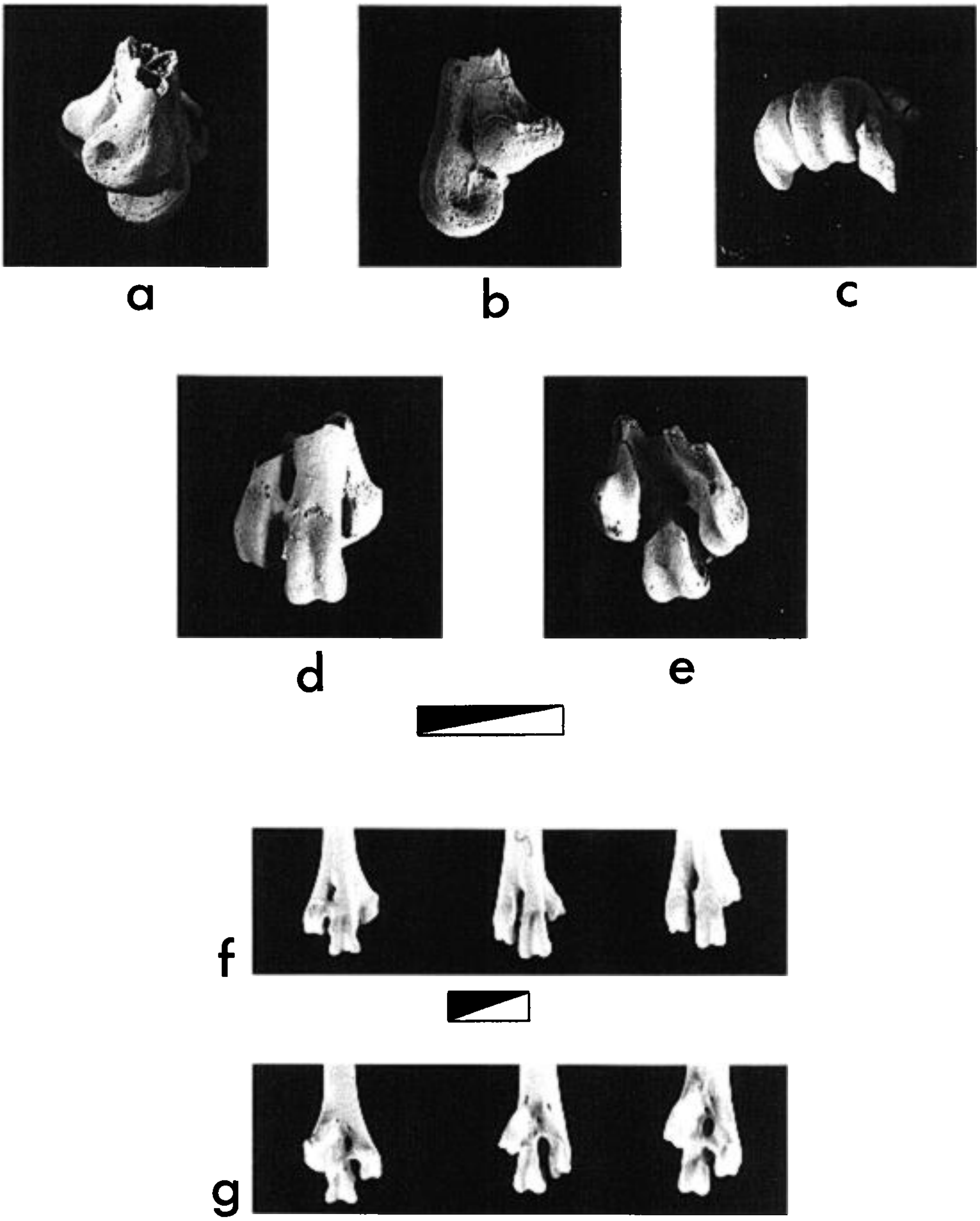

Fig. 2. Distal ends of right tarsometatarsi. UCMP 117599 in (a) lateral, (b) medial, (c) distal, (d) dorsal, and (e) ventral view. Panel f is dorsal view and panel g is ventral view of *Chionis alba* (maximum width 9.8 mm) on left, *Anas platyrhynchos* (maximum width 8.8 mm) in middle, and *Fulica atra* (maximum width 9.7 mm) on right. Note differences in position of distal foramen and strong asymmetry of ventral end of trochlea III in UCMP 117599 and *Chionis*. Scale bars equal 10 mm (upper scale for panels a–e and lower for panels f and g).

TABLE 1. Measurements (in millimeters) of the tarsometatarsus UCMP 117599.

Character	Measurement
Maximum distal width	10.2
Trochlea II	
Maximum depth	6.5
Maximum width	3.2
Trochlea III	
Medial depth	5.5
Lateral depth	5.7
Dorsal width	3.4
Distal width	4.1
Ventral width	3.2
Trochlea IV	
Medial (internal) depth	6.8
Lateral (external) depth	5.2
Ligamental pit	1.6 × 2.0

of the anseriform lineage is a humerus with a ducklike appearance that was described as *Anatalavis rex* (Olson and Parris 1987) from the Hornerstown Formation, which now proves to be of Paleocene age (Olson 1994). Thus, the tarsometatarsus UCMP 117599 may represent the oldest known bird with anseriform affinities.

Size comparisons.—The distal width of the fossil tarsometatarsus (Table 1) is close to that of the Red-knobbed Coot (*Fulica cristata*; 10.7 mm, body mass 826 g) and falls within the range of this measurement in the Double-striped Thick-knee (*Burhinus bistriatus*; body mass 787 g), being slightly below the figure for the largest subspecies *B. b. vocifer* (Table 2). The fossil tarsometatarsus comes from a bird of approximately the same size as two early Paleocene fossils from New Jersey (Olson and Parris 1987): a humerus described as *Anatalavis rex*; and a tibiotarsus described as *Palaeotringa littoralis* (Table 2). All three fossils, therefore, may represent the same genus if not the same species. In addition to size, the fossil tarsometatarsus UCMP 117599 and *A. rex* agree in showing anatid similarities.

The premaxillary symphysis in UCMP 117598 is almost of the same length (17 mm) as that of the Double-striped Thick-knee (*B. b. vocifer*), whose tarsometatarsus is close in size to the tarsometatarsus UCMP 117599 (Table 2). It is therefore possible that the birds that yielded the premaxilla UCMP 117598 and tarsometatarsus UCMP 117599 were of equal size, which in turn opens up a possibility of their being conspecific. However, the length of the premaxillary symphysis may be only loosely correlated with body size even within a single family, such as the Rallidae (pers. obs.).

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TABLE 2. Size comparison of Bug Creek bird (as represented by tarsometatarsus UCMP 117599) with two Early Paleocene avian fossils, using an extant burhinid (*Burhinus bistriatus vocifer*; male, USNM 492371) as a reference (100%). All measurements (in millimeters) are of width of bones.

Species/fossil	Tarsometatarsus (distal)	Tibiotarsus (supracondylar)	Humerus (distal)
B. b. vocifer	11.0	7.4	14.1–14.2
UCMP 117599	10.2 (93%)	—	—
Palaeotringa littoralis	—	7.0[a] (95%)	—
Anatalavis rex	—	—	13.2–13.6[a] (94–96%)

[a] From Olson and Parris (1987).

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Forest Fragmentation and Nest Predation: Are Experiments with Japanese Quail Eggs Misleading?

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There is recent concern over the status of many Neotropical migrant bird populations. Reports of declining numbers and the continuing loss and degradation of breeding and overwintering habitats have prompted an upsurge of interest in the conservation biology of these birds (review papers in Hagan and Johnston 1992). Fragmentation of the breeding habitat in North America often is cited as one of the factors contributing to the decline of many species. Fragmentation is thought to act in two ways. First, brood-parasitic Brown-headed Cowbirds (*Molothrus ater*) thrive in fragmented landscapes, decreasing the productivity of many species (Brittingham and Temple 1983). Second, fragmentation is widely believed to increase rates of nest predation, further decreasing productivity (e.g. Wilcove 1985, Terborgh 1989, 1992).

The evidence that fragmentation of forests in eastern North America increases rates of nest predation is based on the results of experiments in which artificial nests baited with Japanese Quail (*Coturnix coturnix*) eggs are used to compare rates of predation in fragments of different sizes (Wilcove 1985, Small and Hunter 1988; see also Yahner and Scott [1988] who used chicken eggs). There is some evidence for the fragmentation effect based on studies of real nests in Europe (Møller 1988) and in grassland habitats in North America (Paton's [1994] reanalysis of Best 1978, Gates and Gysel 1978, Johnson and Temple 1990; Gates and Gysel's [1978] analysis included 10 nests of forest-dwelling birds). Despite the absence of data on the effects of fragmentation on the nesting success of real nests of forest-dwelling birds, the results of quail-egg studies have been widely accepted as reflecting relative trends for rates of predation on real bird nests (e.g. Sieving 1992, Terborgh 1992, Böhning-Gaese et al. 1993).

The lack of parental and nestling activity and the potentially unnatural positioning and appearance of artificial nests complicates the interpretation of artificial-nest experiments. Studies that have investigated these, and other, potential biases (Boag et al. 1984, Martin 1987, Storaas 1988, Yahner and Voytko 1989, Götmark et al. 1990, Reitsma et al. 1990, Roper 1992) have reached conflicting conclusions as to the utility of artificial-nest experiments. Based on the scratch marks found on many of the quail eggs in artificial nests, Reitsma et al. (1990) suggested that small mammals may have attempted to consume the eggs, but failed to break them because of the animals' small mouths. Roper (1992) used a similar line of reasoning to account for the difference between predation rates on his real and artificial nests in the tropics, and concluded that quail-egg experiments were inappropriate for making comparisons between rates of nest predation in tropical and temperate habitats.

In this paper, I report the results of an experiment testing the suggestions of Reitsma et al. (1990). I discuss whether quail-egg experiments are an appropriate tool for investigating among-fragment differences in the rate of predation on Neotropical migrant bird nests. The potential inappropriateness of using quail eggs to estimate differences in rates of predation on the nests of Neotropical migrant birds becomes evident when the egg sizes of forest-nesting Neotropical migrant birds are compared to the size of quail eggs (Fig. 1). All Neotropical migrant passerines nesting in forests or scrub in eastern North America have eggs that are much smaller than quail eggs. I tested