

# Eggshell Taphonomy at Modern Gull Colonies and a Dinosaur Clutch Site

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*Eggshell taphonomy often is acknowledged to be worthy of investigation, but few studies have examined factors influencing eggshell preservation. In this study eggshell weathering, fragmentation, dispersal, orientation, and predation were characterized in field and laboratory studies. Modern gull eggshell fragment dispersal and orientation patterns were compared with analogous patterns at a non-avian dinosaur egg clutch site. Among other findings: (1) hatched and depredated gull eggshells protected by an enclosure, but exposed to two years of colony weathering, fragmented relatively slowly, suggesting that colony resident activity is responsible for the relatively rapid disappearance of eggshell on the colony surface; (2) depredated eggshells could be distinguished from hatched eggshells due, in part, to differences in fracture patterns; (3) both gull and non-avian dinosaur eggshell fragments were most abundant close to nest centers, whereas this was not true for bones and mollusc shells in gull territories; (4) both gull and non-avian dinosaur eggshell fragments within nest areas were oriented concave up more commonly than concave down, in contrast to transported eggshell fragments; (5) chicken eggs experimentally placed in a gull colony were more likely to be taken by egg predators in areas of short or sparse vegetation than in areas of tall vegetation; and (6) the extent of fracturing was greater in fresh than in hollow chicken eggshells following compression beneath simulated sediment loads. Eggshell weathering, fragmentation, orientation, and dispersion patterns should be characterized during the excavation of fossilized eggs and nest sites.*

## INTRODUCTION

What happens to eggshell once it has served the function of enclosing the developing embryo or once its developmental function has been interrupted prematurely by breakage, transport, and/or burial? Until recently this question would have been a trivial one, except to ethologists interested in nesting behavior (Tinbergen et al., 1962, 1963) and to scientists studying soils beneath the nesting colonies of birds (Ugolini, 1972). But considering efforts underway to understand the structure and ecologi-

cal relationships of dinosaur nests and nesting colonies (e.g., Horner 1982, 1984, 1987; Coombs, 1989; Norell et al., 1995; Varricchio et al., 1997), knowing what happens to eggshell may be crucial to our ability to attempt colony reconstructions. The presence of fossil eggshell fragments in sediments often leads to the reasonable inference that fossil nests may be nearby. Beyond that, patterns of eggshell chemistry, weathering, fragmentation, orientation, and dispersion all contain information useful to the paleoecologist.

Although papers describing fossil eggs (e.g., Sabath, 1991; Mikhailov et al., 1994; Sahni et al., 1994) often acknowledge eggshell taphonomy as worthy of investigation, until recently this topic has received only passing attention (Carpenter et al., 1994a). Growing interest in fossil eggs, however, is encouraging a closer examination of eggshell for the environmental information it contains and investigations into the degree to which eggshell elucidates past climates, diets, and histories of transport, burial, and preservation. For example, Sarkar et al. (1991) used oxygen and carbon isotope analyses of sauropod eggshells to assess ancient diets and water sources. Miller et al. (1997) examined amino-acid racemization in emu eggshells as a means to calibrate low-latitude glacial cooling during the Late Pleistocene. Tokaryk and Storer (1991) found that eggshell can be carried for great distances in simulated fluvial systems without significant damage. Hayward et al. (1997) examined the behavior of eggs in marine habitats and suggested that amniote eggs may be preserved commonly in marine sediments. Hayward et al. (1989) found that habitat variation, as well as inter- and intra-specific behavioral differences, biased the preservation of gull eggs buried by Mount St. Helens' 1980 ashfall. Hayward et al. (1991) demonstrated that ash-buried gull eggshell underwent considerable deterioration within the volcanic sediment over a seven-year period. Clayburn (1996) quantified the effects of acidity, heat, and moisture on eggshell dissolution, and Smith (1998) did the same for bacterial activity.

No previous study at the macroscopic level has characterized eggshell weathering, fragmentation, orientation, and dispersion patterns which are of potential interest to paleontologists attempting to reconstruct ancient nesting environments. Here modern eggshell weathering is described and five hypotheses are tested regarding the ta-

phonomy of eggshells in modern and fossil nesting colonies:

Hypothesis 1: Hatched and depredated gull eggshells are distinguishable on the basis of fracture patterns.

Hypothesis 2: Dispersion patterns of eggshell fragments differ from those of bones and mollusc shells.

Hypothesis 3: The ratio of concave-up to concave-down eggshell fragments provides a colony-typical taphonomic signature.

Hypothesis 4: Habitat type influences the chance of egg predation.

Hypothesis 5: Fracture patterns of crushed eggshells provide information on the internal state of eggs before crushing.

#### USE OF AVIAN EGGS AND NESTING COLONIES AS MODELS FOR ANCIENT EGGS AND NESTING COLONIES

Before describing our observations and experiments, the appropriateness and limitations of using avian eggs and nesting colonies as models with which to test hypotheses about dinosaur eggs and nesting colonies are described briefly.

Striking similarities between modern birds and extinct theropods led T.H. Huxley over a century ago to suggest that birds evolved from dinosaurs (Padian and Chiappe, 1997). Recent discoveries of feathered theropods from Cretaceous deposits in China provide substantial support for this hypothesis (Padian, 1998; Qiang et al., 1998; Swisher et al., 1999). Anatomical similarities, however, extend beyond feathers and bones to eggshell: For example, both non-avian theropods and birds have at least two structural layers in their eggshell (dinosaurid-prismatic and ornithoid-ratite morphotypes; Mikhailov, et al., 1996; Mikhailov, 1997). They also share(d) common behavioral and physiological traits. This has been demonstrated by the description of two adult specimens of *Oviraptor* on top of their clutches in China and Mongolia (Dong and Currie, 1996; Norell et al., 1995). The more complete specimen clearly shows an avian-like brooding position of the adult over its eggs (Norell et al., 1995; Clark et al., 1999). Horner (1982) and Varricchio et al. (1997) found evidence that the small coelurosaur *Troodon* (Horner and Weishampel, 1996) not only brooded its eggs much like *Oviraptor*, but also constructed rimmed nests and nested in colonies—behavioral features common among ground-nesting birds (Hayward et al., 1989). Varricchio et al. (1997), moreover, posited that *Troodon* exhibited several reproductive features found in birds, including asymmetric eggs, one egg produced per oviduct at a time, loss of egg retention, open nests, and brooding behavior.

Despite their similarities, birds and non-avian theropods also differ(ed) in significant ways. Birds eggs are usually ovoid in shape, whereas non-avian theropod eggs are often more elongate or in some cases spherical (see figure 1 in Carpenter et al., 1994a). Coelurosaurs presumably had two functional ovaries and oviducts, lacked egg rotation and chalazae, and partially buried their eggs, all in contrast to birds (Varricchio et al., 1997). But given that both birds and non-avian dinosaurs produce(d) brittle, calcitic eggshells with concave and convex surfaces, we believe the eggs of both types of animals respond(ed) similar-



FIGURE 1—Locations of study sites: Protection Island, Strait of Juan de Fuca, Washington, Harper Island, Sprague Lake, Washington, and Devil's Coulee, west of Warner, Alberta. Open squares on enlarged maps indicate specific data collection localities.

ly to hatching, trampling, transport, weathering, and burial on nest colony surfaces. Nonetheless, taphonomic comparisons and paleoecological reconstructions based on these comparisons should be made with caution and with reference to the taxonomic similarities and differences involved. They should also be made with an understanding that specific actualistic evidence from modern environments, such as is provided here, is strictly applicable only for cases in which specific conditions are met. These conditions may or may not have been met within a given ancient environment.

#### STUDY SITES

Much of the research reported here was carried out between 1988 and 1996 at a glaucous-winged gull (*Larus glaucescens*) colony on Violet Point, Protection Island National Wildlife Refuge, Jefferson County, Washington (Fig. 1). Protection Island is located in the Strait of Juan de Fuca near Admiralty Inlet, 2 km north of the Olympic Peninsula. Violet Point is a spit about 200 m wide and extends for 1 km at the eastern end of Protection Island. The spit is relatively flat and composed of coarse gravel mostly covered with thin soil. No trees occur on the spit except at its west end, outside of the gull colony; non-beach areas are sparsely to densely covered with various grasses and other herbs. Approximately 5,100 pairs of gulls nested on the spit each year during this study. Soil pH on Violet Point was determined on July 29–30, 1991, using a LaMotte-Morgan Soil pH Test Set, at each of 10 randomly chosen points along each of two 50-m transects, one within a sparsely vegetated area ( $\text{pH} = 6.3 \pm 0.4$ ) and the other in a densely vegetated area ( $\text{pH} = 6.0 \pm 0.4$ ). Unless otherwise indicated, all procedures were carried out and all data were collected at this locality.

Two other study localities included a dinosaur egg and

TABLE 1—Summary of observations and experiments.

Focus of observation or experiment	Locality	Primary result
<i>Observation</i>		
Weathering of gull eggshell	Protection Is., WA	Initial shrinkage of eggshell membrane and subsequent falling away of smaller fragments followed by membrane and eggshell discoloration; little additional fragmentation after 1 year
<i>Hypothesis 1: Hatched and depredated gull eggshells are distinguishable on the basis of fracture patterns</i>		
Fracturing in hatched vs depredated eggs	Protection Is., WA	Distance from eggshell apex to midpoints of exit holes in hatched eggshells greater than for entry holes of depredated eggshells
<i>Hypothesis 2: Dispersion patterns of eggshell fragments differ from those of bones and mollusc shells</i>		
Dispersion of detritus around gull nests	Protection Is., WA	Eggshell fragment densities higher near (<1 m) than far (>1 m) from nests; no such difference for bones and mollusc shells
Dispersion of detritus around dinosaur nests	Devil's Coulee, AB	Eggshell fragment density higher near egg clutch than in more distant areas; 1 bone and 2 teeth found in plot
<i>Hypothesis 3: The ratio of concave-up to concave-down eggshell fragments provides a colony-typical taphonomic signature</i>		
Orientation of gull eggshell fragments	Protection Is., WA	63% of horizontal fragments oriented concave up, 37% oriented concave down
Orientation of dinosaur eggshell fragments	Devil's Coulee, AB	60% of horizontal fragments oriented concave up, 40% oriented concave down
<i>Hypothesis 4: Habitat structure influences the chance of egg predation</i>		
Habitat quality and egg predation	Sprague Lake, WA	Predation higher inside than outside colony; predation higher in sparsely vegetated areas than in areas with tall grass
<i>Hypothesis 5: Fracture patterns of crushed eggshells provide information on the internal state of eggs before crushing</i>		
Fracturing of eggs under sediment loads	Laboratory	Fracture patterns similar for fresh and hollow eggs; degree of fracturing higher in fresh than in hollow eggs

eggshell site at Devil's Coulee, 19 km west of Warner, southern Alberta (site 11 in Carpenter and Alf, 1994; described by Zelenitsky, 1995), which contains approximately 65 hectares of exposures of the Oldman Formation (Upper Cretaceous), Judith River Group; and a ring-billed and California gull (*L. delawarensis* and *L. californicus*, respectively) colony on Harper Island, Adams County, in the channelled scablands of eastern Washington (Fig. 1).

## OBSERVATIONS AND EXPERIMENTS

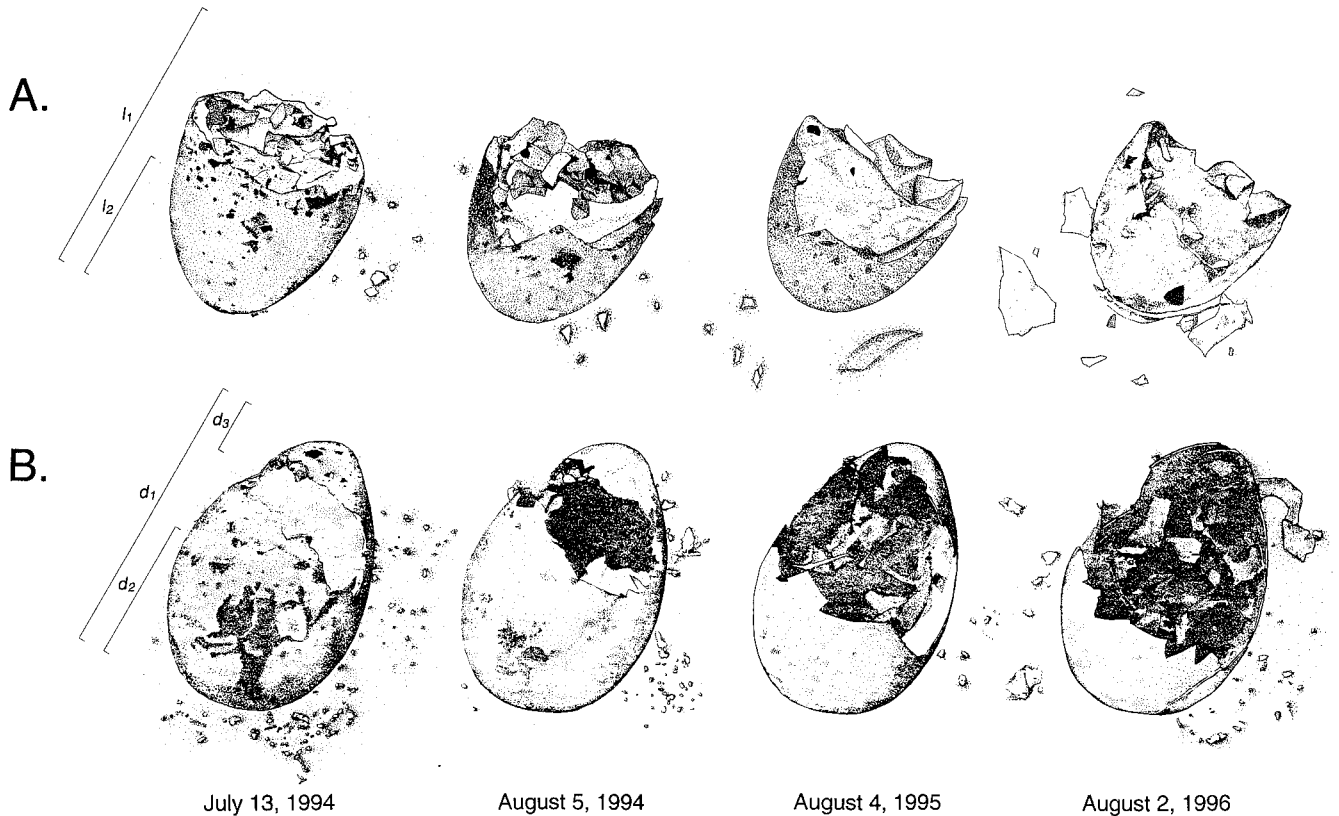
The results of the observations and experiments described below are summarized in Table 1. All hypotheses were tested at the .05 significance level.

### Eggshell Weathering

Ten hatched eggshells and one depredated eggshell were collected between June 26 and July 15, 1994. During July 12–15, 1994, these eggshells were photographed and individually placed in 9.5 × 9.5-cm cells of a 4-cm-deep wooden grid on the surface of the Violet Point gull colony. The eggshells were in contact with the colony surface from below and completely exposed from above; the grid served only to keep the eggshells from blowing around. The entire grid was covered by an enclosure cage made from 2.5-cm-mesh poultry wire. Eggshells were examined for alterations and photographed on August 5, 1994, August 4, 1995, and August 2, 1996. During this two-year period, rainfall averaged 48 cm/year and temperature averaged 9.1°C/year; temperatures of 0°C or below occurred an average of 93 days/year and lasted for 24 hours on less than

three of these days (National Weather Service data from Station 457544, Sequim 2E).

Figure 2 shows the types of changes that occurred in eggshells placed on the colony for two years. The outer surface of fresh eggshell was light olive-gray, with dark olive pigment blotches (Smithe, 1975); the inner surface was cream-colored. Initial fragmentation of the eggshell was accelerated by drying and consequent shrinkage of the shell membranes. Within one week, shrinking membranes detached from the inner surface of the shell, thus removing significant structural support. Where fracture lines were present (and they always were present on hatched eggshells, especially along the borders of the exit holes), the eggshell fragmented. Fragments fell to the ground or to the inside of what remained of the eggshell. After one year, three of the 11 eggshells were missing (fate unknown), and four remained at least one-fourth intact; one of these, the depredated eggshell, was about two-thirds intact. Membranes of seven of the 11 eggshells were still present; these had changed in coloration from white to tan, and showed more wrinkling than one year earlier. Eggshell outer surfaces were somewhat bleached, although pigmentation patterns were still evident; inner surfaces were still white as in fresh eggshell. After two years, eggshells had undergone only a small amount of fragmentation since the previous year. The depredated eggshell was still about two-thirds intact. Membranes of seven eggshells were still present, but now showed extensive wrinkling; they also exhibited a dark greenish coloration, due to the growth of unicellular algae. Eggshell outer surfaces were considerably more discolored than one year earlier, and pigmentation patterns had largely disappeared. Inner surfaces were dark greenish, like the membranes.



**FIGURE 2**—Physical changes in a hatched gull eggshell (A) and a depredated eggshell (B) on a glaucous-winged gull colony over a two-year period. Eggshells were exposed to natural weathering on the gull colony surface during the experiment and were held in place within shallow wooden partitions protected by a poultry wire cage enclosure. The hatched eggshell on August 2, 1996, consists mostly of shell membrane with little outer shell remaining. Statistical comparisons between hatched and depredated eggs were based on the dimensions indicated at the left. Note that the hatched egg (A) is shown apex down, whereas the depredated egg (B) is shown apex up. Drawings by Shanna Marie Hayward.

Except where they were already fractured, the enclosure-protected eggshells experienced relatively little break-down over the two-year period. By contrast, hatched eggshells on the colony were difficult to find within a few days after the completion of hatching. Gulls of some species remove hatched eggshells from their nest sites, presumably so as not to attract the attention of predators (Tinbergen et al., 1962, 1963). Eggshells, however, commonly were found nearby newly-hatched glaucous-winged gull chicks. It appears that, at least in this species, trampling by territory residents and breakage due to wind action may have been responsible for eggshell fracturing beyond that caused by predation and hatching processes. In the long-term weathering experiment, these processes were prevented by the enclosure cage. Presumably if left undisturbed, eggshell, like other calcium carbonate structures, can survive intact for relatively long periods of time before burial. Even mildly acidic soil, however, such as found on Violet Point, would be expected to eventually dissolve eggshell in direct contact with it (Hayward et al., 1991; Clayburn, 1996). Soil bacteria also play a role in the eggshell dissolution process (Smith, 1998).

#### Hypothesis 1: Hatched and Depredated Gull Eggshells Are Distinguishable on the Basis of Fracture Patterns

During July, 1988, 17 unhatched glaucous-winged gull eggs ( $\bar{x}_{\text{length}} = 71.2 \pm 2.5$  mm,  $\bar{x}_{\text{width}} = 49.3 \pm 1.3$  mm) were

measured, numbered, then returned to their nests. After hatching, the minimum distance ( $l_2$ ) from the apex (most pointed end) of the eggshell to the hole exited by the hatching chick was determined for each eggshell. From these measurements the maximum length ( $l_1 - l_2$ ) of the exit hole, and the ratio of the distance between the apex and entry hole midpoint to the egg length ( $[0.5(l_1 - l_2) + l_2]/l_1$ ) were calculated (Fig. 2A). During June and July, 1989 and 1991, 16 depredated eggshells ( $\bar{x}_{\text{length}} = 70.4 \pm 4.2$  mm,  $\bar{x}_{\text{width}} = 47.9 \pm 2.2$  mm) taken by glaucous-winged gulls, northwestern crows (*Corvus caurinus*), and/or bald eagles (*Haliaeetus leucocephalus*), and having predator entry holes in their sides, were collected. Egg predators commonly leave eggshells highly fragmented, but crushed or halved depredated eggshells were excluded from the sample. This was because we wanted to devise a means to distinguish hatched eggshells, which usually remain mostly intact, from similar looking, mostly intact, depredated eggshells. Three measurements were taken of each depredated eggshell: (1) maximum length ( $d_1$ ); (2) minimum distance from the large end to the entry hole ( $d_2$ ); and (3) minimum distance from the apex to the entry hole ( $d_3$ ) (Fig. 2B). From these measurements the maximum length of the predator entry hole ( $d_1 - [d_2 + d_3]$ ) and the ratio of the distance between the apex and the midpoint of the entry hole to the egg length ( $[0.5([d_1 - d_2] - [d_1 - d_3]) + d_3]/d_1$ ) were determined.

In all hatched eggshells except one, the large end of the shell was missing, whereas all but two of the depredated eggshells sampled had intact large ends (Fig. 2). Lengths of the exit holes in hatched eggshells did not differ significantly from lengths of the entry holes in depredated eggshells ( $\bar{x}_{\text{hatched}} = 31.5 \pm 9.2$  mm,  $\bar{x}_{\text{depredated}} = 26.2 \pm 11.5$  mm; pooled  $t = 1.47$ ,  $p > 0.05$ ). The ratio of the distance of the midpoint of the hole from the eggshell apex, however, was significantly greater for hatched eggshells than for depredated eggshells ( $\bar{x}_{\text{hatched}} = 0.78 \pm 0.06$  mm,  $\bar{x}_{\text{depredated}} = 0.58 \pm 0.14$  mm; pooled  $t = 5.516$ ,  $p < 0.0001$ ), as was the minimum distance from the edge of the hole to the apex ( $\bar{x}_{\text{hatched}} = 39.73 \pm 7.99$ ,  $\bar{x}_{\text{depredated}} = 26.98 \pm 9.58$ ; pooled  $t = 4.163$ ,  $p < 0.001$ ). Thus, our hypothesis is supported: Hatched eggshells are readily distinguishable from relatively intact depredated eggshells in this species and population.

Biologists have described eggshell fracture patterns associated with specific types of predators. For example, Sooter (1946) found that coyotes (*Canis latrans*) opened eggs from the side in much the same fashion as the bird predators in our study. Rearden (1951) found that raccoons (*Procyon lotor*) commonly broke into eggs from the end and, less frequently, from the side; that mink (*Mustela vison*) produced small holes in the sides or ends of eggs; and that skunks (*Mephitis mephitis*) completely crushed eggs in their mouths, after which they ate the contents and left the eggshell fragments clinging to one another in "a shapeless mass." Marks and Hall (1992) reported that bristle-thighed curlews (*Numenius tahitiensis*) used stones to break holes in the sides of black-footed and Laysan albatross (*Diomedea nigripes* and *D. immutabilis*, respectively) eggs before feeding on the contents. It is important to realize, however, that depredation by the same organism can result in numerous fracture patterns. Glaucous-winged gulls on Protection Island sometimes simply punctured eggs before feeding on the contents. At other times they broke eggshells through the middle, leaving two half shells. At yet other times they broke eggshells into small fragments (see Rearden, 1951, for other examples). In short, one must use caution when attempting to identify specific predators on the basis of eggshell fracture patterns alone.

Fossil eggs that match, at least in a general way, our characterization of hatched and depredated eggs have been found. Horner (1982; 1984; 1987), Faccio (1994), and Zelenitsky and Hills (1996) all described what possibly were hatched dinosaur eggs with intact lower portions but with missing tops. Williams (1981) described eggs of the Late Pleistocene bird *Genyornis* from Australia that appeared to have been punctured from the outside by a predator, and Hirsch et al. (1997) reported a similar example for a lower Eocene bird egg.

#### Hypothesis 2: Dispersion Patterns of Eggshell Fragments Differ from Those of Bones and Mollusc Shells

##### *Gull Colony*

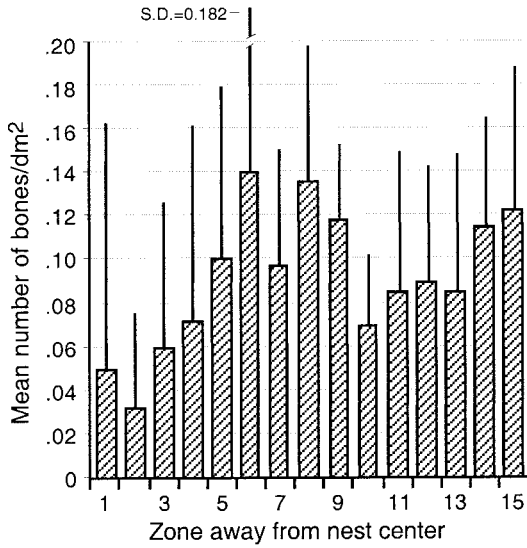
To examine debris dispersion around isolated nests, five glaucous-winged gull nests, each containing three eggs and each no closer than 3 m to any other nest, were chosen in a relatively nonvegetated area in the western part of

the colony. A 3 × 3-m grid was patterned over each nest with the nest at the exact center of the grid. The corners of each of nine 1 × 1-m quadrats within the grid were marked with steel spikes driven flush with the colony surface. Twice each week, from June 25 to August 5, 1993, a lightweight 1 × 1-m grid, partitioned into 1 × 1-dm subquadrats, was placed over each quadrat around each sample nest. A photograph was taken of the quadrat from above. Care was taken to avoid disturbing area debris during photographic sessions. Color photographic prints of each quadrat from each photographic session were cut out and mounted so that a time series of composite pictures of each 3 × 3-m nest area was obtained. Between July 26 and August 5, 1993, numbers of eggshell fragments were counted in each of the 900 subquadrats within each nest area. All bones and bone fragments (hereafter called bones) and mollusc shells and shell fragments (hereafter called mollusc shells) present on August 5, 1993, were collected and identified. Locations of all items were plotted on a map of each area. Each mapped area was viewed as consisting of 15 concentrically arranged, progressively larger, square zones, each 1 dm wide, surrounding each nest. Thus, zone 1, at the nest center, had an area of 4 dm<sup>2</sup>; zone 2, which surrounded zone 1, had an area of 12 dm<sup>2</sup>; etc. Eggshell fragment, bone, and mollusc shell densities were calculated and plotted by zone and averaged for the five sample nest areas. The gains, losses, and changes in location of bones visible in the composite photographs were recorded for each of the five isolated nest areas.

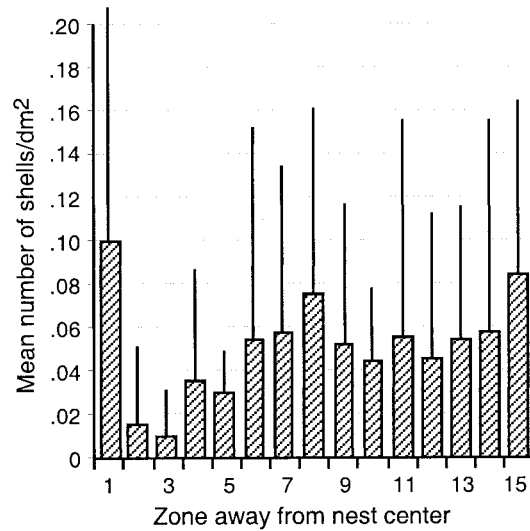
Table 2 summarizes the numbers of items found around each nest. Of the three items counted, eggshell fragments were the most abundant, followed by bones, and then mollusc shells. Most bones were from adult and juvenile glaucous-winged gulls (minimum number of individuals summed for five nest areas = 10) and adult chickens (*Gallus gallus*; presumably brought to the colony from landfills; minimum number of individuals = 7) and were most commonly long bones—femora, ulnae, coracoids, tibiotarsi, humeri, radii, furculae, and tarsometatarsi (in decreasing order of frequency). Bird and fish vertebrae were also common. Forty-nine percent of the bone specimens were fragmentary, and most showed evidence of extensive weathering, including desiccation fractures and worn epiphyses. Eighty-six percent of the mollusc shells were fragmentary. Less frequent and uncounted items included regurgitated gull pellets, beetle exoskeletons, crustacean parts, and fish scales. Bone density was highest about 0.8 m from nest centers and increased again toward the edges of the sampled areas (1.5 m from nest centers; Fig. 3A). Mollusc shell distribution patterns seemed to parallel bone patterns (Fig. 3B). Fifty-nine bones were counted on the June 25 composite photographs of all five isolated nest areas, whereas 65 bones were counted on the August 5 composite photographs. During the 41-day interval, 66 bones were newly sighted, while 60 bones were lost from sight. Bones visible on the composite photographs taken on August 5 ( $n = 65$ ) represented 15% of the bones actually present on the plots ( $n = 435$ ) as determined by collection on that date. Eggshell fragment density was highest close to the nests and decreased sharply as distance increased from nest centers (Fig. 3C).

To examine debris dispersion within a larger area of the colony, a relatively non-vegetated, 8 × 12-m plot contain-

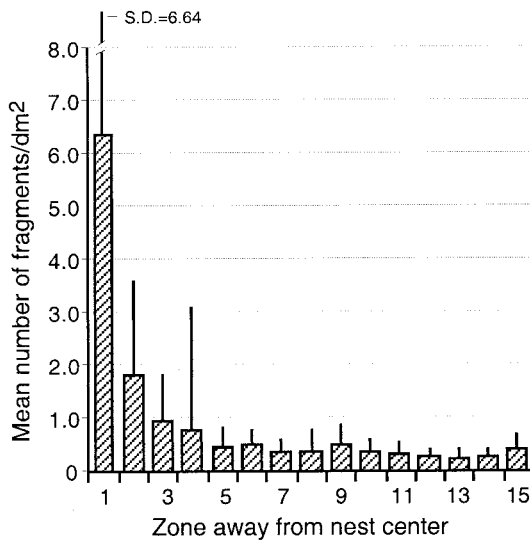
A. Bone dispersion, gull nest sites



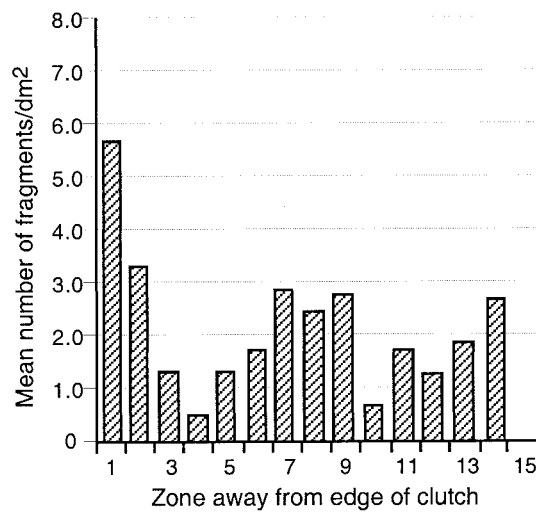
B. Mollusc shell dispersion, gull nest sites



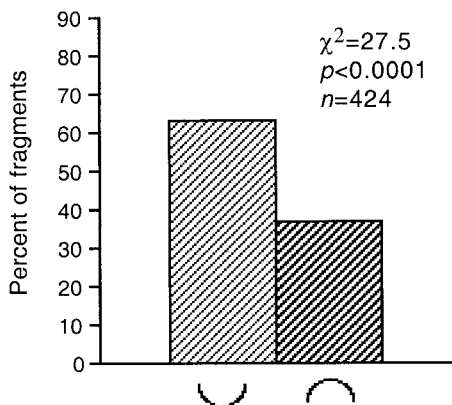
C. Eggshell dispersion, gull nest sites



D. Eggshell dispersion, dinosaur clutch site



E. Eggshell orientation, gull nest sites



F. Eggshell orientation, dinosaur clutch site

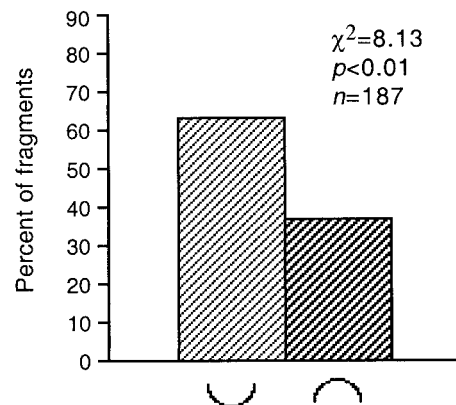


TABLE 2—Debris around sample gull nests.

	Nest area					Total
	1	2	3	4	5	
Eggshell fragments	331	363	232	314	682	1,922
Bones						
Unbroken	26	56	51	47	41	221
Broken	36	71	49	37	19	212
Mollusc shells						
Unbroken	6	4	2	3	19	34
Broken	25	31	2	21	138	217

ing five active gull nests was marked near the western end of the Violet Point. During July 22–29, 1994, a baseline was stretched between grid line endpoints. A  $1 \times 1$ -m grid with  $1 \times 1$  dm-subquadrats was placed at the edge of the baseline at successive 1-m intervals. During each such placement all visible eggshell fragments, bones, and mollusc shells were counted in each subquadrat and plotted in relation to nest locations. The total number of each of the three categories of items was determined for each of the 96  $1\text{-m}^2$  subplots. The 27 subplots intersecting an area defined by a 1-m radius surrounding each of the five nest centers formed what was designated as the “near” area, whereas the 69 other subplots were designated as the “far” area. Expected numbers of eggshell fragments, bones, and mollusc shells were determined for both near and far areas by dividing the number of each item in each area by 96 and multiplying the resultant quotient by 27 and 69, respectively. Eggshell fragments were about three times as common as bones, whereas bones were about twice as abundant as mollusc shells (Fig. 4). Eggshell fragment numbers were significantly higher in near than in far areas ( $\chi^2 = 45.9$ ,  $p < .0001$ ), whereas similar comparisons showed no significant differences for numbers of bones ( $\chi^2 = 3.26$ ,  $p > .05$ ) and numbers of mollusc shells ( $\chi^2 = .70$ ,  $p > .05$ ) between the two areas.

These results suggest that eggshell fragment density is a better indicator of nest proximity than bone or mollusc shell distributions. The high degree of breakage and weathering of bones and mollusc shells, however, implies that these items remain on the colony surface for considerably longer periods of time than eggshell fragments. This may be because eggshell is often thinner than bones and mollusc shells; also, bone is composed largely of calcium phosphate, a less soluble mineral than the calcium carbonate of eggshell (Weast, 1974). Thus, eggshell fragments would be expected to degrade more rapidly than bone or mollusc shell, especially on acidic substrates (Retallack, 1984). This may account for the fact that eggshell fragments from previous nesting seasons were relatively sparse on the acidic soils of the Violet Point gull colony (Clayburn, 1996).

Although the total number of bones visible around nest sites remained fairly constant during the nesting season, the results show that there was considerable movement of bones within, into, and out of the sample areas. This movement probably occurred as a result of resident gull activity including trampling, beak transport, and deposition during feeding. It is doubtful that many newly-visible bones were deposited during feeding. Most were adult and juvenile gull bones generated by the death and decomposition of colony residents. Conversely, fish bones, generally not visible on the composite photographs but common in the end-of-season collections, were usually imported by feeding.

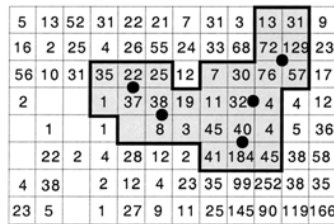
In contrast to bone and mollusc shell densities, eggshell fragment densities around isolated gull nests showed rapid decline with increasing nest distance. This pattern was less apparent when nests were close together, although even under such circumstances eggshell was significantly more dense closer to nest sites than farther away. Thus, the hypothesis that dispersion patterns of eggshell fragments differ from those of bones and mollusc shells was supported on this colony.

On August 3, 1994, eggshell fragments were counted within a  $1 \times 1$ -m quadrat in the area of greatest eggshell density in each of two territories of egg robbers, gulls that specialize in eating the eggs of conspecifics (Tinbergen, 1962). Egg robber territories accounted for less than 1% of the territories on Violet Point (unpublished data, JLH), but were easily identified by the presence of more fresh eggshell fragments than could be produced by eggs from one parental pair. Highest eggshell-fragment densities in two egg-rober territories were 2,894 and 8,231 fragments/ $\text{m}^2$ , respectively. By contrast, the two highest fragment densities we observed in any non-egg robber territories studied were 252 and 273 fragments/ $\text{m}^2$ . Thus, highest fragment densities in egg-rober territories sampled ranged from 10 to 30 times higher than the highest fragment densities in non-egg-rober territories sampled. High concentrations of eggshell fragments in fossil deposits may sometimes indicate the presence of egg predator middens.

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**FIGURE 3**—Mean zonal densities of (A) bones and bone fragments, (B) mollusc shell and shell fragments, and (C) eggshell fragments centered around five glaucous-winged gull nests on the Protection Island colony. Error bars denote standard deviations. (D) Zonal densities of dinosaur eggshell fragments around a single Devil's Coulee clutch site. In A–D, higher numbered zones were those more distant from nest centers. (E) Eggshell fragment orientations at the Protection Island gull colony. (F) Eggshell fragment orientations at the Devil's Coulee clutch site. Statistical tests on eggshell fragment orientation are based on an expectation of equal numbers of concave-up and concave-down shells. Shells with unclassified orientations (including upright and indeterminable) were not included in the orientation analyses.

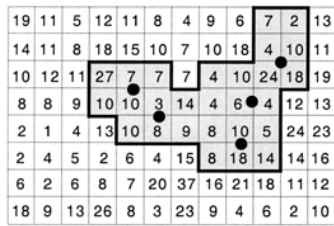
A. Eggshell fragments



Near density=37.4 fragments/m<sup>2</sup>  
Far density=28.8 fragments/m<sup>2</sup>

	Obs.	Exp.	$\chi^2$	p
Near	1,009	842	45.9	<.0001
Far	1,986	2,153		

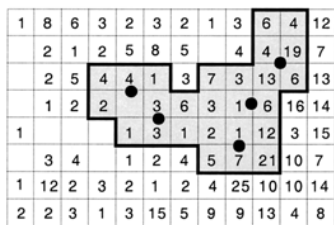
B. Bones



Near density=9.7 bones/m<sup>2</sup>  
Far density=11.0 bones/m<sup>2</sup>

	Obs.	Exp.	$\chi^2$	p
Near	261	287	3.26	>.05
Far	759	733		

C. Mollusc shells



Near density=5.4 mollusc shells/m<sup>2</sup>  
Far density=4.9 mollusc shells/m<sup>2</sup>

	Obs.	Exp.	$\chi^2$	p
Near	145	137	0.70	>.05
Far	341	349		

1 meter

FIGURE 4—Dispersion of items in a 96-m<sup>2</sup> plot containing five glaucous-winged gull nests. Nest locations are indicated by dark circles. (A) Eggshell fragment dispersion. (B) Bone and bone fragment dispersion. (C) Mollusc shell and shell fragment dispersion. Densities of these items for the near (shaded) and far (unshaded) areas are shown to the right. Expected values were determined for near and far areas by dividing the number of each type of item in each area by 96 (the total number of m<sup>2</sup> in the plot), then multiplying the resultant quotients by 27 (number of m<sup>2</sup> in near area) and 69 (number of m<sup>2</sup> in far area), respectively.

These results suggest the possibility that eggshell fragment dispersion patterns may contain important paleoenvironmental information useful to paleontologists.

*Non-Avian Dinosaur Egg Site*

The dispersion pattern of eggshell fragments, exposed by weathering but preserved in lithified sediment in 14 concentrically arranged, progressively larger, square zones, each 1 dm wide, was determined from a field map of a 1.69-m<sup>2</sup> area containing one dinosaur egg clutch (Fig. 5) at Devil's Coulee. Laboratory preparation revealed that the tops were missing on all 12 eggs within the clutch, only nine of which appear on the field map (Zelenitsky and Hills, 1996; the nest and associated eggshell fragments are now in the collections of the Royal Tyrrell Museum of Palaeontology, museum number TMP 94.179.1). Zone 1, unlike zone 1 for each of the sample gull nest areas, did not include the nest (or in this case, clutch) but enclosed it. Moreover, some of the outer zones were not complete

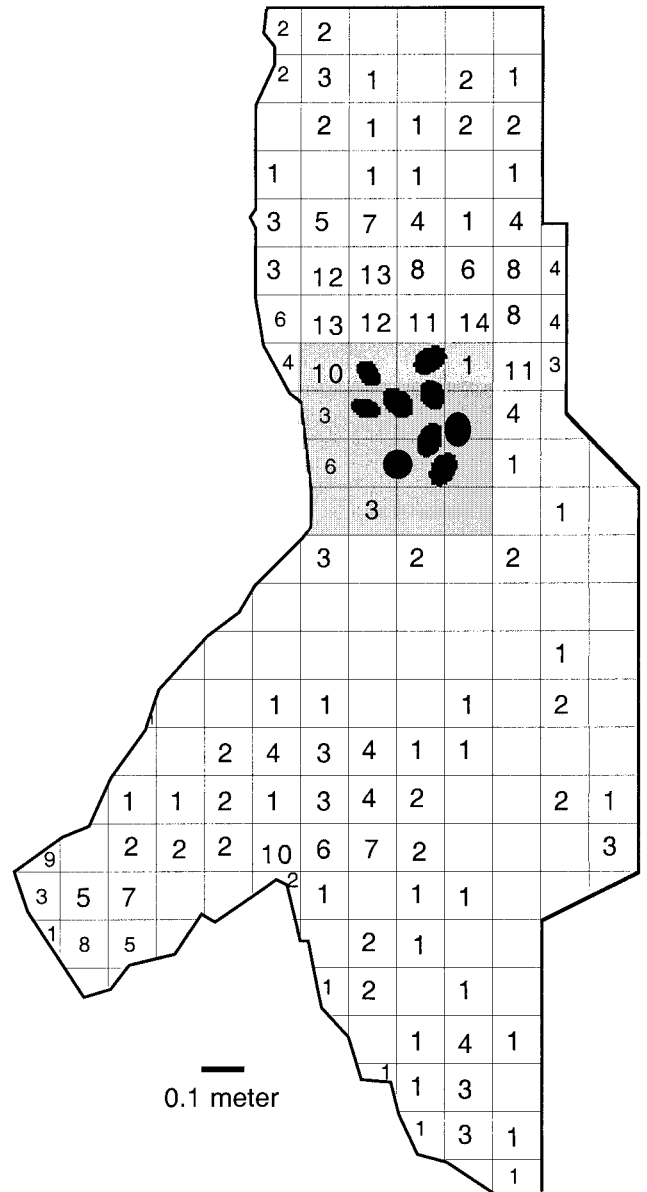


FIGURE 5—Field map showing the dispersion pattern of dinosaur eggshell fragments (*Prismatoolithus levis*) at the Devil's Coulee, Alberta, nest site, with the locations of nine of 12 partial eggs indicated. The three eggs not shown were exposed during preparation of the clutch after it was collected. The shading indicates the area designated as the clutch zone.

squares due to the irregular shape of the exposure that was excavated.

Figure 3D shows the dispersion pattern of dinosaur eggshell fragments (*Prismatoolithus levis*, Zelenitsky and Hills, 1996) from the Devil's Coulee clutch site (Fig. 5). From the map, 341 fragments were counted, not including the 12 partial eggshells that made up the clutch or the 23 fragments mapped inside the clutch zone. The overall fragment density for the 1.53-m<sup>2</sup> area mapped outside the clutch zone was thus 222.9 fragments/m<sup>2</sup>. Eggshell fragment density was highest in zone 1, which surrounded but did not include the egg clutch. In addition to eggs and egg-

shell fragments, a fossil lizard jaw bone, a *Troodon* tooth, and a *Saurornitholestes* tooth were found at this site.

Overall eggshell fragment densities around the Devil's Coulee dinosaur clutch were similar to the highest densities around non-egg robber gull nest sites examined. Moreover, the same general pattern of eggshell fragment densities around isolated gull nests seemed to hold for the dinosaur clutch site at Devil's Coulee, as well as for dinosaur nest sites in Montana illustrated by Horner (1994).

The small number of skeletal remains and absence of mollusc shells at Devil's Coulee clutch site did not allow us to test for differences between the dispersion patterns of eggshell fragments and those of bone and mollusc shells at a non-avian dinosaur colony locality.

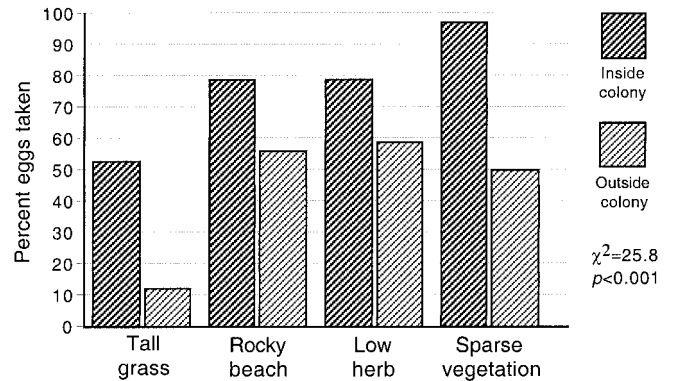
### Hypothesis 3: The Ratio of Concave-Up to Concave-Down Eggshell Fragments Provides a Colony-Typical Taphonomic Signature

Orientations of sample eggshell fragments, whether concave up, concave down, or unclassified (including upright and indeterminable), were tallied for 471 fragments in the 96-m<sup>2</sup> plot on Violet Point gull colony on July 28, 1994. Of these, 266 were oriented concave up, 158 were oriented concave down, and 47 undetermined. The 63:37 ratio of concave-up:concave-down represented a significant deviation from an expected 50:50 ratio ( $\chi^2 = 2705$ ,  $p < .0001$ ; Fig. 3E). Likewise, 424 fragments that previously had been collected from the 1.37-m<sup>2</sup> area of the Devil's Coulee clutch were examined for orientation; surface weathering of the surrounding lithified sediments allowed for determination of *in situ* orientations for 187 of these fragments. Of these, 113 had been oriented concave up and 74 had been oriented concave-down, a 60:40 ratio which represented a significant deviation from an expected 50:50 ratio ( $\chi^2 = 8.13$ ,  $p < .01$ ; Fig. 3F). Hayward et al. (1997), similarly, found a 67:33 ratio for gull eggshell fragments at an egg cannibal midden on Violet Point, and a 60:40 ratio for dinosaur eggshell fragments at a site near Augusta, Montana, both significant deviations from a 50:50 ratio. By contrast, they found that following transport within simulated turbidity currents, eggshell fragments exhibited orientations that did not vary significantly from a 50:50 ratio. Moreover, colony site orientations differed markedly from an approximately 20:80 ratio for eggshell fragments following transport in natural and experimental fluvial systems (Owen and Hayward, 1997; Dickson and Hayward, 1998).

The results reported herein support the hypothesis that an approximately 60:40 ratio of concave-up:concave-down may be typical for eggshell fragments at relatively undisturbed avian and non-avian dinosaur colony sites. The predominance of concave-up eggshell fragments at colony sites may be due to the mechanics of hatching and eggshell trampling.

### Hypothesis 4: Habitat Type Influences the Chance of Egg Predation

An egg-predation experiment was conducted at a ring-billed and California gull (*L. delawarensis* and *L. californicus*, respectively) colony on Harper Island, Sprague Lake, Washington, during May, 1981. That year, the



**FIGURE 6**—Percent of 34 chicken eggs taken by predators after 18 hours of experimental exposure in each of four habitat types inside and four habitat types outside a ring-billed gull colony, Harper Island, Sprague Lake, Washington. Total number of experimental eggs = 272. The chi-squared test compares each of the eight observed values with an expected value of 17, assuming equal numbers of eggs taken in all habitats, both inside and outside the colony.

Harper Island colony contained 975 ring-billed gull nests and 142 California gull nests. Nests were distributed non-randomly throughout four distinct habitat types: rocky beach, tall grass, dense herb, and sparse vegetation (Hayward, 1993). On May 5, 1981, 13 white infertile chicken eggs were set out at locations within 1 m of randomly chosen ring-billed gull nests in each of the four habitat types. In addition, 13 such eggs were set out in each of the same four habitats at locations adjacent to, but outside, the colony. Spots chosen for egg placement were similar to those chosen by gulls for nest sites. Each egg was placed so that it could be seen by gulls flying over or walking nearby. On May 6, 18 hr following placement, missing or broken eggs (collectively called depredated eggs) were counted in each of the eight areas. The experiment was repeated using 21 eggs per area on May 16–17, 1981, and the results were combined with those of the first experiment. A Chi-square test was used to compare the eight observed values with an expected value of 17 for each, assuming equal numbers of eggs taken in all habitats, both inside and outside the colony.

Figure 6 summarizes the results of the egg predation experiment in a ring-billed gull colony. Numbers of chicken eggs eaten and not eaten in four habitats, both inside and outside the colony, varied significantly. A greater proportion of eggs was eaten inside the colony than outside, although differences by habitat were apparent in both situations. The lowest proportion of eggs eaten, both inside (equal to number for rocky beach) and outside, was in tall grass. Almost all eggs set out in sparse vegetation within the colony were taken, whereas outside only half were eaten. More eggs placed on rocky beach and in low dense vegetation were taken than were not, both inside and outside the colony. Thus, eggs placed within tall grass were least likely to be taken, regardless of location.

The results of this experiment support the hypothesis that habitat features play an important role in determining the vulnerability of eggs to predation. Not only were the chicken eggs placed close to tall vegetation less likely to be taken by predators than other eggs both inside and outside the gull colony, but so were the naturally occur-

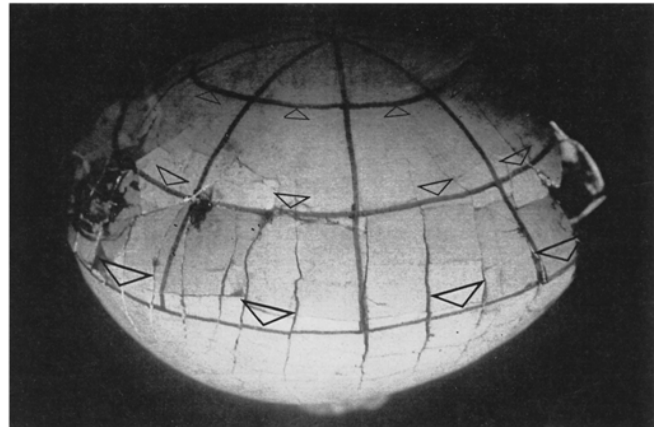
ring ring-billed gull eggs within nests occupying this habitat (Hayward, 1993). This latter difference also may have been influenced by parental behavior differences among nesting gulls (Hayward et al., 1982). Similarly, Littlefield (1995) found that predation frequency on sandhill crane (*Grus canadensis*) eggs by coyotes and common ravens (*Corvus corax*) varied by habitat. Whether such habitat features played a similar role in the predation frequencies of dinosaur eggs is currently unknown, but this possibility should be kept in mind by paleontologists studying dinosaur nesting colonies.

#### Hypothesis 5: Fracture Patterns of Crushed Eggshells Provide Information on the Presence or Absence of Egg Contents before Crushing

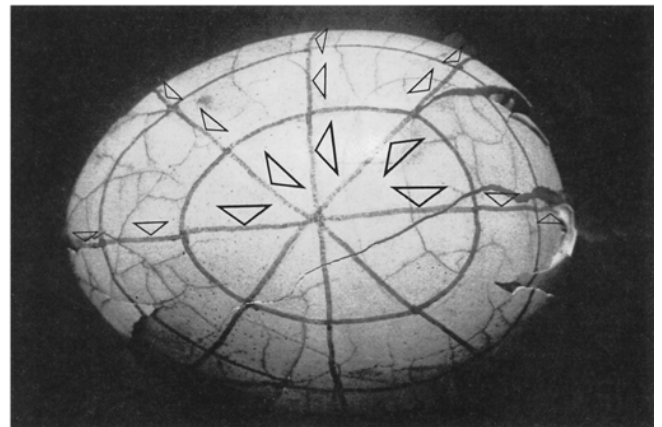
Ten medium-sized grade AA chicken eggs randomly were designated as "fresh" and another ten were designated as "hollow". A small hole was made at both ends of the long axis of each of these 20 eggs. The contents of eggs designated as hollow were blown out, while the contents of the fresh eggs were kept intact. A grid was drawn on one randomly determined, lengthwise half of each horizontally positioned egg, with all grid segments of a given type designated as a transect: transects I, II, or III for each of three circumferential grid lines; transects x, y, or z for ascending segments of each radial grid line (Fig. 7). Each egg was buried horizontally, grid pattern up, in a 23 × 23 cm sand-filled box beneath 3.5 cm of sand. A 1.9-cm thick plywood board was placed over the sand, and the box was placed in a hydraulic press (Universal Testing Machine, Model-60hv-60,000 lb. capacity). Approximately 700 kg pressure applied by the press was distributed evenly over the sand surface by the plywood board. Rubber sides of the box expanded outward in response to lateral displacement of sand during compression. This resulted in triaxial loading in which horizontal forces were less than the vertical force (Rieke and Chilingarian, 1978). Triaxial loading occurs as matrix material consolidates around a potential fossil (Rex and Chaloner, 1983). Fresh and hollow eggs were compressed to an average of  $85.0 \pm 9.6\%$  and  $82.1 \pm 14.0\%$ , respectively, of their original widths, a nonsignificant difference (pooled  $t = 0.63$ ; 18 d.f.;  $p > 0.05$ ). Crushed eggs were excavated from the box and immersed in a solution of methylene blue, then rinsed, after which fracture lines stood out in dark contrast to the white eggshell. The degree of fracturing for each egg was determined by counting the number of fractures that intersected each transect. The number of fractures per transect was then divided by the transect length to obtain a "fracture score." Mean fracture scores for transects were compared between fresh and hollow eggs using two-way analysis of variance (Sokal and Rohlf, 1987) and Tukey's multiple comparison tests (Zar, 1996).

Fracture patterns were similar for crushed fresh and hollow eggs (Fig. 7). All crushed eggs showed a horizontal crease-like fracture along transect I, between the upper and lower halves; vertical cracks, roughly equidistant from one another, intersected transect I. Along all transects, fresh eggs exhibited significantly higher fracture scores than hollow eggs; moreover, for both fresh and hollow eggs, transects I and II exhibited significantly higher fracture scores than transect III, and transects x and y

#### A. Side view



#### B. Top view



**FIGURE 7**—Chicken egg after crushing beneath a simulated sediment load. Arrows indicate transects. (A) side view: transect I—large arrows; transect II—medium arrows; transect III—small arrows. (B) top view: transect x—small arrows; transect y—medium arrows; transect z—large arrows.

were significantly more fractured than transect z (Table 3). Fracturing of lower eggshell halves was not quantified, but generally fracture lines did not extend into the center of the shell as far as fracturing along the top halves.

During crushing, physical properties of the eggshell itself and a complex interplay of undefined forces on both sides of the shell determine the pattern and degree of fracturing. These results suggest that such forces differ significantly between fresh and hollow eggs.

Gull eggs buried by Mount St. Helens' 1980 ashfall were hollow after one year beneath the ash, although they had not been crushed (Hayward et al., 1982, 1989). These results suggest that if a second and larger sedimentation event had partially crushed these hollow eggs before they experienced infilling and lithification, they may have been less fractured than fresh eggs similarly buried and crushed. Fracture patterns exhibited by compressed fossil eggs sometimes look quite similar to patterns produced experimentally (e.g., see Figures 7.15A and 7.16C in Mikhailov et al., 1994); in other cases they differ considerably

TABLE 3—Fracture score comparisons between crushed fresh and hollow chicken eggs.

Egg type	Transect			Row means	F	p
	I	II	III			
Hollow	.251	.235	.167	.218	4.71	<0.05
Fresh	.330	.351	.172	.284		
Column means	.291	.293	.169	.251		
	x	y	z			
Hollow	.151	.162	.053	.122	5.20	<0.05
Fresh	.233	.180	.085	.166		
Column means	.192	.171	.069	.144		

(e.g., see figures in Carpenter et al., 1994a, and in Currie, 1996). Nevertheless, the preliminary work presented herein supports the hypothesis that fracture patterns differ, depending on the presence or absence of egg contents.

Our experiment simulated sediment loading only during matrix consolidation; further experimentation should be carried out using uniaxial loading which would simulate compression within an already consolidated matrix (Rex and Chaloner, 1983). Experiments with eggs of different sizes, shell thicknesses, shapes, orientations, and infilling materials would provide an increasingly sophisticated understanding of eggshell mechanics and fracture patterns (e.g., see Zhao and Ma, 1997).

## DISCUSSION

Nesting colonies of egg-laying animals produce vast numbers of potentially fossilizable eggs. For example, the 5,100 gull pairs that nest on Violet Point produce an estimated 9,400 eggs each year which yield about 80 kg of eggshell (unpublished data; JLH). Non-avian dinosaur nesting colonies sometimes contained many nests and covered large areas (Horner and Gorman, 1988). Given the large clutch sizes of some of these animals (Moratalla and Powell, 1994), the number of eggs produced in large colonies would have been extremely high. Moreover, the large sizes of many non-avian dinosaur eggs (e.g., Mikhailov et al., 1994; Moratalla and Powell, 1994) resulted in high yields of eggshell. In low moisture, high pH, and high calcium substrates (as often indicated by the presence of caliche nodules at dinosaur sites in Montana and Alberta) this material would accumulate over time (Clayburn, 1996). This accumulation would explain the abundance of eggshell at many non-avian dinosaur nesting colonies (e.g., Hirsch and Quinn, 1990; Cousin et al., 1994; Sahni et al., 1994; Zhao, 1994; Sanz et al., 1995), as well as at ancient Adelie penguin (*Pygoscelis adeliae*) colonies in Antarctica (Ugolini, 1972; Baroni and Orombelli, 1994), and at Pleistocene nesting grounds of the flightless goose, *Chendytes lawi*, on San Miguel Island, California (Guthrie, 1992).

Fractured eggshells, like fractured bones (Behrensmeier, 1984), provide different taphonomic information than their relatively unaltered counterparts. The results of these experiments demonstrate that eggshell weathering, fracture, dispersion, and orientation patterns contain information about the history of an egg from the time it was laid to the time of its discovery as a fossil. This information

is useful to paleontologists attempting to reconstruct nesting paleoenvironments and post-burial events that crush and otherwise deform eggs. In view of this usefulness, the results of our observations and experiments lead us to suggest that the following data be collected when fossil nests and eggs are excavated:

(1) Eggshell surfaces should be examined for signs of weathering and/or dissolution, including pitting, cratering, and honeycombing (see also Hayward et al., 1991). These signs may provide information pertinent to paleoenvironment reconstruction and on the timing of egg-laying in relation to burial.

(2) Fracture patterns on significantly intact eggshells should be quantified and described. These fracture patterns may contain information regarding hatching, depredation, and/or presence or absence of egg contents at the time of compression.

(3) All eggshell fragments and other debris associated with nests, clutches, and individual eggs should be mapped. Debris patterns, particularly of eggshell fragments, may contain information about nest locations and colony geographies. Unusually high eggshell fragment densities may indicate the presence of predator middens.

(4) Proportions of concave-up to concave-down eggshell fragment orientations should be determined. These proportions differ, depending on whether the fragments are part of the debris that surrounds a nest or whether they have been transported away from the nest vicinity.

Our understanding of eggshell taphonomy remains tentative and fragmentary, but the potential it offers paleontologists interested in reconstructing ancient nesting patterns and environments is significant (Carpenter et al., 1994a, 1994b). It is hoped that this preliminary study will encourage greater care in the collection of data when ancient nest sites are excavated, and will stimulate further research into how modern eggshells of various sizes, shapes, thicknesses, and contents respond to a multitude of environmental variables.

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