# Trumpeter Swan (*Cygnus buccinator*) Behaviour, Interactions with Snapping Turtles (*Chelydra serpentina*), and Their Pleistocene History

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Snapping Turtles (*Chelydra serpentina*) prey on and injure Trumpeter Swan (*Cygnus buccinator*) cygnets. Adult Trumpeter Swans stamp on and attack turtles, and this sometimes saves the lives of cygnets. Stamping behaviour, duetting, clamouring, and mobbing are directed at predators. The stamping behaviour may be derived from the water treading display. During the Pleistocene ice sheet maxima, all Trumpeter Swans east of the Rockies nested within the range of the Snapping Turtle. Snapping Turtle predation may have selected for the stamping behaviour.

Key Words: Snapping Turtle; *Chelydra serpentina*; predation; Trumpeter Swan; *Cygnus buccinator*; injuries, stamping attack; duetting; clamouring; mobbing behaviour; water treading display; Pleistocene distribution; Wisconsin glaciation; Yellowstone glacier; Ontario

There are two Trumpeter Swan (*Cygnus buccinator*) populations in North America. Studies of mitochondrial DNA by Oyler-McCance et al. (2007) showed that the Pacific coast population breeding in Alaska and west of the Rocky Mountains differ significantly from the remnant population breeding in a small area in and east of the Rocky Mountains and those centred in the Grand Prairie region of Alberta. This paper deals mostly with the Rocky Mountain population.

Snapping Turtle (*Chelydra serpentina*) predation on waterfowl and shorebirds was recorded long ago (Alexander 1943; Lagler 1943; Coulter 1957; Pryor 1996). Willey and Halla (1972) thought that Snapping Turtles were the primary source of mortality of Mute Swan (*Cygnus olor*) cygnets in Rhode Island. Lumsden (1986) reported on the loss to a Snapping Turtle of Trumpeter Swan cygnets cross-fostered by Mute Swan parents. Abel (1992) attributed the deaths of Trumpeter Swan cygnets cross-fostered by Mute Swans in Wisconsin to Snapping Turtles. At close range, Abel (1992) also witnessed the circumstances surrounding Snapping Turtle attacks on Trumpeter Swan cygnets imprinted on life-sized swan decoys. Despite its large size, a full-grown Trumpeter Swan has also fallen victim to a Snapping Turtle: Moriarty (1990) described how a Snapping Turtle drowned a yearling Trumpeter Swan weighing 14.5 kg in Minnesota.

On a 0.25 ha private pond in Aurora, Ontario (44°00'N, 79°28'W), a wild pair of Trumpeter Swans has been breeding since 2006. Each year between 2006 and 2012, one to three cygnets disappeared, probably killed by Snapping Turtles. Beginning in 2007, I watched the reaction and behaviour of full-grown Trumpeter Swans to the presence of Snapping Turtles.

The purpose of this paper is to describe aggression of Trumpeter Swans toward Snapping Turtles and injuries to Trumpeter Swan cygnets caused by Snapping Turtles. Other injuries to Trumpeter Swans are described. The Pleistocene history and distributions of both Trumpeter Swans and Snapping Turtles are discussed.

## Methods

Wild Trumpeter Swans were marked with alphanumeric wing tags at Aurora and elsewhere to distinguish individuals. Photographs were used to record injuries to cygnets and the postures and responses of Trumpeter Swans to various stimuli. A live Snapping Turtle tethered at the water's edge and a dummy Snapping Turtle moved with a cord in shallow water were used to simulate the movements of a live Snapping Turtle.

## Observations

### *Encounters between Trumpeter Swans and Snapping Turtles: stamping behaviour*

When a Trumpeter Swan sees a Snapping Turtle moving in shallow water, it moves onto the top of the Snapping Turtle's carapace and attacks by stamping. Disturbance of any kind makes a Snapping Turtle withdraw its head and legs within the overhang of the plastron and remain passive. Presumably, withdrawal is the Snapping Turtle's response to the attack. The Trumpeter Swan continues to stamp, splash, trumpet, and reach down into the water, as if pecking at the Snapping Turtle. The Trumpeter Swan may open its wings and flap, perhaps to maintain balance.

Such attacks are very noisy and may last as long as 30 seconds before the Trumpeter Swan moves aside. While on the water, the Trumpeter Swan may duet (see below) with another bird or with its mate. When the Snapping Turtle moves again, the Trumpeter Swan resumes the attack. Episodes of stamping and pausing may last for many minutes and continue until the Snapping Turtle reaches deeper water and is no longer visible.

On 11 June 2007 at 1520 EST, I was attracted by trumpeting and splashing. A yearling male Trumpeter Swan (wing tag no. 090) was attacking a Snapping Turtle. The water was shallow and the top of the Snapping Turtle's carapace was barely covered and was visible. This sequence of attack and pause lasted about 2.5 minutes.

On 13 June 2008 at 2050 EST, an eight-year-old male (wing tag no. 812) was attacking a Snapping Turtle. His mate, a seven-year-old female (wing tag no. 839) with four cygnets clustered round her sat on the water some 4 m away and did not participate in the attack. The water was shallow (<20 cm deep), and when the Snapping Turtle moved, the top of its carapace disturbed the surface. The male Trumpeter Swan duetted (see below) with his mate in the intervals between attacks, which lasted for about 7 minutes.

On 15 June 2009 at 2010 EST, one three-day-old cygnet was missing. On 22 June at 0825 EST, I saw a second, now ten-day-old cygnet from this brood, floating dead on the water. The father (wing tag no. H24) was sitting on the water about 3 m away in about 30 cm of water. He moved forward and started a brief sequence of stamping, splashing, and trumpeting. I could not see the presumed Snapping Turtle. I intended to pick up the body of the cygnet when it drifted to shore, but when I returned about 30 minutes later it had disappeared; the Snapping Turtle may have retrieved its prey.

On 12 July 2010 at 2026 EST, an unmated now four-year-old male, 090, accompanied by a yearling female (wing tag no. C04), was looking down into the water. Male 090 moved forward and started stamping, presumably on a Snapping Turtle, which I could not see.

On 14 August 2010 at 1959 EST, the male H24 and his mate 839 in turn stamped in deep water, deep enough that I could not see the presumed Snapping Turtle. I saw two bouts of attack before they left. The eight-week-old cygnets were sitting on the water several metres away.

On 4 June 2011 at 1214 EST, a three-year-old male (wing tag no. H09) was startled by something in the water. He sidled forward with neck bent and extended in the forward posture (Figure 1). His head was tilted to one side. He was apparently watching something. He then moved quickly forward and stamped twice with his feet. This was not very vigorous and there was no splashing or calling. He was followed by the female C04, who did not participate, and they swam away together.

On 17 June 2011, three swans (male 090 followed by female C04 and the three-year-old male, H09) were moving together close to the far western shore. Trumpeter Swan 090 started to stamp, presumably on a Snapping Turtle, which I could not see. During pauses, he started a duet (see below) with female C04, with notes spaced less than 1 second apart. About 0.3 seconds after C04 had responded, male H09 joined and added to the

FIGURE 1. Forward posture of a Trumpeter Swan (*Cygnus buccinator*) at Aurora, directed at a Snapping Turtle (*Chelydra serpentina*), visible at the edge of the water in the lower right-hand corner. Photo: by H. Lumsden. 5 August 2011.

FIGURE 2A. Trumpeter Swan (*Cygnus buccinator*) cygnet from Newmarket, Ontario, showing injuries to its bill caused by a Snapping Turtle (*Chelydra serpentina*). Photo: At Aurora by H. Lumsden. 28 July 2011.

FIGURE 2B. Deformed bill of the Newmarket cygnet at six weeks of age. Photo: At Aurora by H. Lumsden. 2 Septermber 2011.

"duet". Thus these three companions participated in a pattern that often involves only two birds.

The Snapping Turtles which the swans attacked were later trapped. The larger weighed 9.3 kg and the smaller 3.4 kg.

*Injuries to Trumpeter Swans caused by Snapping Turtles*

On 10 July 2011, P. Calverley was attracted by stamping behaviour on a Snapping Turtle by a breeding male Trumpeter Swan on his pond near Newmarket, Ontario (44°03'N, 079°28'W). The attack forced the turtle to release a cygnet, which was immediately rescued by Calverley. The cygnet's injuries were severe. Part of the left side of the mandible had been bitten off and the edge of the adjacent part of the maxilla had been removed (Figure 2a). By six weeks of age, the cygnet had developed a very deformed bill (Figure 2b).

On 7 February 2011, I caught a cygnet for banding at La Salle Park, Burlington, Ontario (44°18'N 079°51'W). It had a similar injury to its bill. The terminal half of the left side of the mandible had been severed and ripped away to its tip (Figure 3a). The remainder of the lower mandible was sharply deflected to the left. The edge of the maxilla had also been removed, and the cygnet's tongue protruded from the injured side of the bill (Figure 3b). These deformities prevented full occlusion of the bill, and this limited the cygnet's ability to feed (e.g., the cygnet was unable to pick up single grains of corn spilled on the ice). However, the cygnet was able to engulf and swallow corn from a bucket. The injury had completely healed.

The cygnet was just over 7 months old and did not appear to differ in size or the development of the body molt from its siblings. The injury probably occurred some time just before freeze-up, after the cygnet had achieved its current stature. It was not weighed but was noticeably light. The cause of deformity was not witnessed, but the strong similarity of the injury to that of the Newmarket cygnet suggests a Snapping Turtle attack.

In August 2010, E. Kaiser photographed a cygnet near Little's Corners, Ontario (43°21'N, 80°16'W), with

FIGURE 3A. Trumpeter Swan (*Cygnus buccinator*) cygnet from La Salle Park, Burlington, Ontario, showing injuries to its bill, presumably caused by a Snapping Turtle (*Chelydra serpentina*). The cygnet's age was about seven months. Photo: At La Salle Park by J. Kee. 7 February 2011.

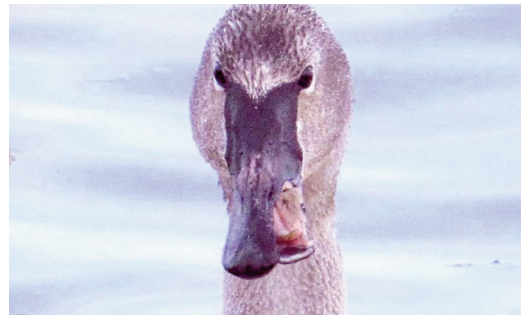

FIGURE 3B. Frontal view of the cygnet from La Salle Park showing bill deformities that prevented full occlusion of the bill. Photo: At La Salle Park by J. Kee. 7 February 2011.

a scarred bill and forehead (Figure 4a). The cause of these injuries was not witnessed, but one can only note that they are compatible with a Snapping Turtle attack.

The wild Trumpeter Swans wintering at La Salle Park, where they concentrate and are fed, provide an opportunity to examine the bills of many of the birds present. K. Intini (personal communication) found that 4 of the 200 Trumpeter Swans present in the winter of 2010-2011 had sections of the tip of the maxilla removed in a highly stereotypical manner. One side of the maxilla was affected. Three of these birds had been banded and carried wing tags numbers 508, 029, and E97. When they were marked as cygnets, there was no record of bill injury.

An unmarked Trumpeter Swan wintering on Lake Ontario at Bluffer's Park in Toronto, Ontario (43°42'N, 79°14'W) in 2009 was similarly affected. A five-year-old male (wing tag no. C24) photographed on 9 June 2011 by D. Bell at Colonel Sam Smith Park on Lake Ontario in Etobicoke (43°25'N, 79°32'W) had a section removed from the right side of his bill (Figure 4b). A captive breeding female (wing tag no. 122), held on an artificial pond at King City, Ontario (43°56'N, 79°32'W), was attacked, presumably by a Snapping Turtle, and lost nearly 1 cm from the end of the maxilla. She survived the attack.

The fact that Snapping Turtles sometimes prey on adult Trumpeter Swans is confirmed by Moriarty (1990). The bill damage is consistent with what one would expect from the bite of a Snapping Turtle. There were no witnesses to the events that led to most of the injuries described above. One cannot eliminate other causes, such as encounters with traps set for Muskrats (*Ondatra zibethicus*) or outboard motor propellers. Caution must be used when using indirect evidence as inference of predation on waterbirds by Snapping Turtles (Igl and Peterson 2010).

FIGURE 4A. Trumpeter Swan (*Cygnus buccinator*) cygnet at Little's Corners, Ontario, showing injuries to its bill and forehead that may have been caused by a Snapping Turtle (*Chelydra serpentina*). Photo: by E. Kaiser. August 2011.

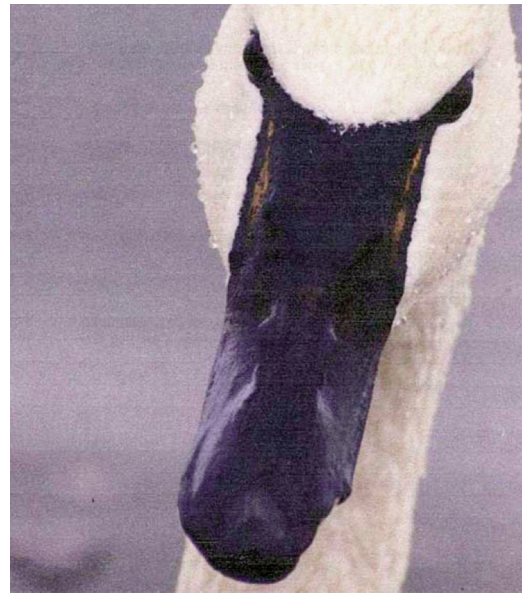

FIGURE 4B. Adult Trumpeter Swan (wing tag no. C24) at Col. Sam Smith Park, Etobicoke showing a notch missing from the bill that may have been caused by a Snapping Turtle. Photo: D. Bell. 5 June 2011.

## Behaviour of Trumpeter Swans

*Duetting*

The triumph ceremony of the Whooper Swan (*Cygnus cygnus*) was described as a duet (Ferguson-Lees et al. 1977). Johnsgard (1968) also described duetting displays of other species of the tribe Anserini. Trumpeter Swans perform a duet of a different and distinctive kind in response to potential predators. A duetting pair stands in the upright posture (see below) with the neck sleeked. The male utters a short, sharp trumpet-like note, which is immediately answered by the female, usually less than 1 second later, at a slightly higher pitch. These duets are usually repeated at 3–4 second intervals. They may be performed by mated pairs or by two companion Trumpeter Swans when disturbed by a variety of predators. Duets are sometimes performed during pauses between stamping attacks on a Snapping Turtle.

When Trumpeter Swan cygnets are caught for banding in fall and winter at La Salle Park and elsewhere (Lumsden, personal observations), the male parent, the primary defender of the brood, typically backed by the female, advances aggressively and stands 5 to 10 m from the bander, displaying in the upward posture (Figure 5), and starts the duet. The parents continue to call until the cygnet is released.

Two cygnets from an isolated brood at Leaskdale, Ontario (44°12'N, 79°10'W), were caught in a drop-door trap placed on top of a bank. The parents were in the water below the bank and could not see the cygnets

or the banding process. They duetted repeatedly, with the notes spaced about 3 seconds apart. When a cygnet was caught for banding at Claremont, Ontario (43°58'N, 79°07'W), on 13 February 2012, the parents duetted as usual. Immediately 14 other Trumpeter Swans that had gathered there for food clamoured (see below) using the same duetting calls. When a male (wing tag no. 140) and his mate were frightened by a domestic dog at La Salle Park, they adopted the upward posture (Figure 5) and duetted. The Trumpeter Swan pair H24 and 839 at Aurora responded to a dog in a similar manner.

On 2 February 2012 at Bluffer's Park in Toronto, the Trumpeter Swan pair (wind tag no. J42 and wing tag no. A70) duetted as I approached. I have never seen Trumpeter Swans in Ontario respond in this way to the approach of a human. In this case, this pair probably recognized me as a predator because I had caught and tagged both of them and between 2004 and 2010 I had caught and banded their cygnets. Their duetting attracted the other 18 Trumpeter Swans in Bluffer's Park. They gathered nearby, and their collective duetting calls amounted to clamouring.

*Clamouring*

A pair of Trumpeter Swans duetting in the presence of a predator stimulates other Trumpeter Swans that may be nearby to concentrate and clamour. They join the duetting pair with a chorus of "duet calls". With many Trumpeter Swans present, the noise can be very loud and sustained. This clamouring is a form of mobbing (McFarland 1987), which informs the entire wetland community that a predator is present.

*Forward posture*

On 5 August 2011, I tethered a live Snapping Turtle near the shore of the pond at Aurora. This released the forward posture in male H24 (Figure 1). The bird stood motionless, silent, on the alert with the neck sleeked and extended forward and with bill pointing at the Snapping Turtle. He watched intently for more than half a minute. On 24 May 2011, a dummy Snapping Turtle moved by pulling a cord released the forward posture in male H24, 18 days before his cygnets hatched.

*Upward posture*

The Trumpeter Swan stands motionless and alert, with the neck sleeked and extended upward, the fore part of the body slightly raised (Figure 5). This posture is usually adopted when duetting in response to predators.

*Similarity between the stamping behaviour and the water treading display*

The stamping behaviour may have evolved from a very similar Trumpeter Swan behaviour that de Vos (1964) described as the water treading display. This threat display is usually directed at an intruder at the boundary of a territory. For example, in the Aurora study area, injured Trumpeter Swans were occasionally confined in a small pen at the corner of the main pond. The resident breeding male frequently performed the water treading display at the boundary fence adjacent to the "intruding" injured bird.


FIGURE 5. Upward posture of Trumpeter Swans (*Cygnus buccinator*) at La Salle Park, adopted when duetting or when startled by a domestic dog. Photo: H. Lumsden. 22 March 2011.

During the water treading display, the aggressor does not trumpet while it stamps vigorously and with loud splashing, raising the forepart of its body, shaking its wings, and extending its neck forward (Figure 6) (photo by de Vos by permission). There is broad similarity between the water treading display and the stamping behaviour.

FIGURE 6. Water treading display by a male Trumpeter Swan (*Cygnus buccinator*). Photo: A. de Vos. Reproduced *from* de Vos. 1964. Observations on the behaviour of captive Trumpeter Swans during the breeding season. Ardea 52: 166–148. Used with permission.

## Discussion

The stamping behaviour on Snapping Turtles described above was performed by both yearling and adult and by both female and male Trumpeter Swans. The stamping behaviour appears to be a fixed action pattern (Lorenz 1970), which is an instinctive rather than a learned behaviour. This behaviour appears to be released by a Snapping Turtle swimming below the surface of the water. I tried to release the stamping behaviour using a dummy Snapping Turtle moved by pulling a cord. I subsequently used a live Snapping Turtle tethered near the shore, but it would not swim. Both failed to release the stamping behaviour.

The stamping attack at Newmarket by the parent forced the Snapping Turtle to release the cygnet it had seized, thereby saving it's life. Similarly, stamping attacks may have been involved in the survival of other cygnets showing evidence of possible turtle attack (e.g., Figures 3a and b, and 4a and b).

Although Snapping Turtles are omnivores and opportunistic foragers, they are also ambush predators (Earnst et al. 1994). They likely choose an ambush site which provides the best opportunities for seizing prey. The stamping behaviour may disrupt a predation opportunity, cause the Snapping Turtle to abandon an optimal site, and move to one that is less favourable.

Lamprecht et al. (1985) described duetting in semi-captive Bar-headed Geese (*Anser indicus*) at Seewiesen in Germany. He characterized the duetting call as the distance call. The young of a pair of Bar-headed Geese were abducted, and the duetting was led by the female (the incubator and primary brood care giver) on return while looking for her goslings at the site from which they had been removed. Lamprecht et al. (1985) suggested that the response of the male relieved the female from visually monitoring her mate's whereabouts.

Hall (2004) discussed 10 hypotheses that addressed the function of duetting in birds. In only one of the 10 hypotheses she suggested that duetting may function as a means to protect birds and their young from predation or to confuse predators during a predation attempt. Duetting does not appear to protect Trumpeter Swans from Snapping Turtle attacks nor to confuse Snapping Turtles. However, duetting and clamouring appear to be a form of mobbing (McFarland 1987), which might be added to the 10 hypotheses of Hall (2004).

*Pleistocene distribution*

The range of the Snapping Turtle extends from southern Canada west to the foothills of the Rocky Mountains and east to the Atlantic coast and as far south as Florida and northeastern Mexico (Conant 1975) (Figure 7).

Prior to European settlement, the range of Trumpeter Swan was very extensive (Mitchell and Eicholz 2010). It extended from southern and central Alaska south and east through central Canada and the northern half of the United States (Mattson et al. 1985). It bred from the Atlantic coast (Lumsden 2013) to the Pacific.

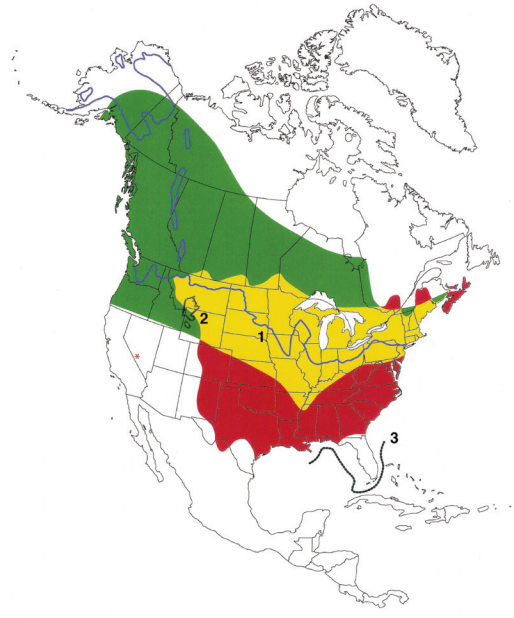


FIGURE 7. Map of North America showing the distribution of Trumpeter Swans (*Cygnus buccinator*) (green) (Mattson et al. 1985), Snapping Turtles (*Chelydra serpentina*) (red), (Conant 1975) and where the two species' ranges overlap (yellow) during the Pleistocene. The red asterisk denotes the location of a Snapping Turtle fossil uncovered in Glendale, Nevada. The southern limits of the Wisconsin glaciation are shown by the solid blue line (1), and the limits of the Yellowstone glacier are shown by the solid black line (2). The 300-foot marine contour (3) indicates the strandline (shoreline) during the Pleistocene.

Historically, the range boundaries of these two species did not remain static. There were 18 to 20 glacial cycles during the 2.6 million years of the Pleistocene (Graham 2011). Each of the four major glacial advances of Pleistocene ice had a fundamental impact on the distribution of both species. They would have been confined to areas well south of the Great Lakes in the east and south of the 49th parallel in the west. The southern limit of the Wisconsin glaciation is shown in Figure 7. Thus, at the peak of glaciation, all of the breeding range of the Trumpeter Swan east of the Rocky Mountains would have been confined within the range of the Snapping Turtle.

The glacial ice sheets changed sea levels, temperatures, and precipitation patterns, which in turn influenced the distribution of the Snapping Turtle and the Trumpeter Swan. In the Gulf of Mexico, the Pleistocene shoreline, now submerged, indicates a substantial marine retreat. The strandline has been located about 300 feet below current sea levels (Muhs et al.

2004) (Figure 7). As the glaciers advanced, marine, freshwater, and terrestrial habitats would have expanded or changed. The new habitat and cooler conditions would have permitted Trumpeter Swans to expand their breeding range southward.

The range of the Snapping Turtle also expanded, probably southward and westward into the Mohave Desert during these glacial cycles. Fossil Snapping Turtle bones were excavated near Glendale, Nevada (36°39′N, 114°34′W) (indicated by asterix in Figure 7), well outside the current range of the Snapping Turtle. The fossils date from about 35 000 Years Before Present, just before the peak of the Wisconsin glaciation (Van Devender and Tessman 1975). Increased precipitation and changes in wetland conditions likely provided habitat for the Snapping Turtle and perhaps Trumpeter Swans in what is now the Mohave Desert.

There are no Snapping Turtles within the present breeding range of the Rocky Mountain population of the Trumpeter Swan (R. Shea, personal communication). Trumpeter Swans from this Rocky Mountain population were used in the restoration program in Ontario (Lumsden 2002), and they exhibit the stamping behaviour. This suggests that this population must have been exposed to Snapping Turtle predation at some time in the past.

At the peak of the Wisconsin glaciation, much of the breeding range of the Rocky Mountain population of the Trumpeter Swan was covered by the Yellowstone glacier (Pierce 2003) (Figure 7). Both the Wisconsin glaciation and the Yellowstone glacier would have been bordered by a zone of tundra that was underlain by permafrost 80–200 km wide (Graham 2011) which graded into an open spruce forest. The duration of the ice-free period in this permafrost zone would have been too short for Trumpeter Swans to complete their nesting cycle, according to Hansen et al. (1971), Trumpeter Swans breeding in Alaska need 140–154 ice-free days to complete their nesting cycle). During the Pleistocene, Trumpeter Swans would have been widely displaced to the south beyond the tundra zone, and individuals from lower elevations would have recolonized the area as the ice retreated. These colonists would have been birds that had evolved under the selective pressure of Snapping Turtle predation.

To my knowledge, the Pacific coast population of the Trumpeter Swan, which breeds west of the Rocky Mountains and in Alaska, has never encountered Snapping Turtles during the nesting season. Evolutionarily, this population was under no selective pressure to develop behaviours that deter Snapping Turtle predation. Many of the Trumpeter Swans that were used to restore populations in the U.S. Midwest came from Alaskan stock. The speed with which this genetically distinct (Oyler-McCance et al. 2007) stock, whether or not it possessed an anti-turtle defence, established itself in the mid-western United States suggests that Snapping Turtle predation was not an important factor.

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## Literature Cited

**Abel, B.** 1992. Snapping Turtle attacks on Trumpeter Swan cygnets in Wisconsin. Passenger Pigeon 54: 209–213.

**Alexander, M. M.** 1943. Food habits of the Snapping Turtle in Connecticut. Journal of Wildlife Management 7: 278–282.

**Conant, R.** 1975. A Field Guide to Reptiles and Amphibians. Eastern and Central North America. Houghton Mifflin Co., Boston, Massachusetts.

**Coulter, M. W.** 1957. Predation by Snapping Turtles upon aquatic birds in Maine marshes. Journal of Wildlife Management 21: 17–21.

**de Vos, A.** 1964. Observations on the behaviour of captive Trumpeter Swans during the breeding season. Ardea 52: 166–189.

**Ernst, C. H., J. E. Lovich,** and **R. W. Barbour.** 1994. Turtles of the United States and Canada. Smithsonian Institution. Washington D.C.

**Ferguson-Lees, I. J., Robert Gillmor, P. A. D. Hollom, Robert Hudson, E. M. Nicholson, M. A. Ogilvie, P. J. S. Olney, K. H. Voous,** and **J. Wattel.** 1977. Ostrich to Ducks. Vol. 1 of The Handbook of the Birds of Europe, the Middle East and North Africa: the Birds of the Western Palearctic. *Edited by* S. Cramp and K. E. L. Simmons. Oxford University Press, Oxford, U.K.

**Graham, A.** 2011. A natural history of the New World: the ecology and evolution of plants in the Americas. University of Chicago Press, Chicago, Illinois.

**Hall, M. L.** 2004. A review of hypotheses for the function of avian duetting. Behavioural Ecology and Sociobiology 55: 415–430.

**Hansen, H. A., P. E. K. Shepherd, J. G. King,** and **W. A. Troyer.** 1971. The Trumpeter Swan in Alaska. Wildlife Monographs 26: 1–83.

**Igl, L.,** and **D. Peterson.** 2010. Common Snapping Turtle preys on an adult Western Grebe. Waterbirds 33: 105–109.

**Johnsgard, P. A.** 1968. Waterfowl: their biology and natural history. University of Nebraska Press, Lincoln, Nebraska.

**Lagler, K. F.** 1943. Food habits and economic relations of the turtles of Michigan with special reference to fish management. American Midland Naturalist 29: 257–312.

**Lamprecht, J., A. Kaiser, A. Peters,** and **C. Kirchgessner.** 1985. Distance call duets in Bar-headed Geese (*Anser indicus*): co-operation through visual relief of the partner? Zeitschrift für Tierpsychologie 70: 211–218.

**Lorenz, K.** 1970. Studies on human and animal behaviour. Volume 1. Butler and Tanner, London, U.K.

**Lumsden, H. G.** 1986. Response of Mute Swans (*Cygnus olor*) to Snapping Turtle (*Chelydra serpentina*) attack on a cygnet. Canadian Field-Naturalist 100: 267–268.

**Lumsden, H. G.** 2002. Hatchability of eggs from captive Trumpeter Swans. North American Swans 3(1): 2–4.

**Lumsden, H. G.** 2013. Isotherms and winter distribution of Trumpeter Swans. Ontario Birds 31(1): 46–50.

**Mattson, S., S. Craven,** and **D. Compton.** 1985. The Trumpeter Swan. University of Wisconsin Cooperative Extension Publication G3647.

**McFarland, D.** *Editor*. 1987. The Oxford Companion to Animal Behaviour. Oxford University Press, Oxford, U.K.

**Mitchell, C. D.,** and **M. W. Eicholz.** 2010. Trumpeter Swan (*Cygnus buccinator*). Revised. No. 105 *in* The Birds of North America. *Edited by* A. Poole. Cornell Lab of Ornithology, Ithaca, New York. Retrieved from the Birds of North America Online.

**Moriarty, J. J.** 1990. Snapping Turtle bites off more than it can chew. Newsletter of Minnesota Herpetological Society 10:4.

**Muhs, D. R., J. F. Wehmiller, K. R. Simmons,** and **L. L. York.** 2003. Quaternary sea-level history of the United States. Pages 147–183 *in* The Quaternary Period in the United States. *Edited by* A. R. Gillespie, S. C. Porter, and B. F. Atwater. Vol. 1 of Developments in Quaternary Science. *Edited by* J. van der Meer. Elsevier.

**Oyler-McCance, S. J., F. A. Ransler, L. K Berkman,** and **T. W. Quinn.** 2007. A rangewide population genetic study of Trumpeter Swans. Conservation Genetics 8: 1339–1353.

**Pierce, K. L.** 2003. Pleistocene glaciations of the Rocky Mountains. Pages 63–76 *in* The Quaternary Period in the United States. *Edited by* A. R. Gillespie, S. C. Porter, and B. F. Atwater. Volume 1 of Developments in Quaternary Science. *Edited by* J. van der Meer. Elsevier.

**Pryor, G. S.** 1996. Observations of shorebird predation by Snapping Turtles in eastern Lake Ontario. Wilson Bulletin 108: 190–192.

**Van Devender, T. R.,** and **N. T. Tessman.** 1975. Late Pleistocene Snapping Turtle (*Chelydra serpentina*) from southern Nevada. Copeia 1975: 249–253.

**Willey, C. H.,** and **B. F. Halla.** 1972. Mute Swans of Rhode Island. Rhode Island Department of Natural Resources, Division of Fish and Wildlife. Wildlife Pamphlet No. 8.

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