Geographic variation in Trumpeter Swan *Cygnus buccinator* clutch size and egg weights

DAVE OLSON[1]*, BILL LONG[2] & CARL D. MITCHELL[3]

[1]U.S. Fish and Wildlife Service, Region 6, Migratory Bird Program, PO Box 25486-Denver Federal Center, Denver, Colorado, USA.
[2]Wyoming Wetlands Society, PO Box 3216, Jackson, Wyoming, USA.
[3]55 Eagle Creek Road, Wayan, Idaho, USA.
*Correspondence author. E-mail: dave_olson@fws.gov

Abstract

Because larger clutch sizes and heavier eggs may indicate fitness as well as resource availability, we investigated whether there were significant differences in clutch size and egg weights between the Interior Population (IP) and Rocky Mountain Population (RMP) of Trumpeter Swans *Cygnus buccinator* in North America. A total of 1,113 eggs were measured or weighed at 283 nests. Average clutch size ranged from 3.5–5.8 eggs across study sites, and average egg mass ranged from 333.25–373.80 g. Average clutch size was significantly larger for IP swans (5.8 eggs per clutch) than for those from the RMP (mean clutch size = 4.3 eggs). Egg weights were also significantly heavier in the IP (mean = 366.43 g) than in the RMP (mean = 336.98 g). Mean clutch sizes and egg weights were within the range of other studies involving Trumpeter Swans. The results may provide some indication why the IP is increasing at a faster rate than the RMP of Trumpeter Swans.

Key words: clutch size, *Cygnus buccinator*, egg size, geographic variation, Trumpeter Swan.

Many studies have investigated spatial or temporal variation of both clutch size and egg weights in avian species, including waterfowl (*e.g.* Klomp 1970; Dunn & MacInnes 1987; Blackburn 1991a; Christians 2002; Svagelj *et al.* 2012). Geographic variation in clutch size is common in birds, with the most frequent trend across species being an increase in clutch size with latitude (Klomp 1970). Similarly, egg size also varies within clutches of many species of bird (Ricklefs 1980; Christians 2002).

Previous studies have compared egg and clutch size patterns specifically for waterfowl (Dunn & MacInnes 1987; Rohwer & Eisenhauer 1989; Flint & Grand 1999; Figuerola & Green 2005). Rohwer (1988) and Rohwer & Eisenhauer (1989) considered clutch size and egg weights in Trumpeter Swans *Cygnus buccinator*; comparing data recorded in Alaska for birds

from the Pacific Coast Population (PCP) and Montana for Rocky Mountain Population (RMP) swans. Since that time, most but not all Trumpeter Swan populations have increased significantly across their range, the exception being the portion of the RMP which breeds in the United States (the RMP-U.S.). Trumpeter Swans have been reintroduced successfully into Wisconsin, Michigan, Minnesota and Iowa. These latter swan flocks are now designated as the Interior Population (IP) (Fig. 1) and have been steadily increasing in number (Groves 2012).

The IP increased by 13% during 1968–2012 and by 16% during 2005–2012 (Groves 2012). In contrast, the RMP increased by only 6.3% from 1968–2010 and by 13% from 2005–2010. Larger clutch sizes and heavier eggs may be an indication of higher resource availability (Krapu & Reinecke 1992; Erikstad *et al.* 1993; Blums *et al.* 2002) and fitness (Charnov & Krebs 1974). Given the current population trends, we therefore aimed to determine whether egg weight and clutch size differed significantly between these two populations, by investigating egg weight and clutch size

Figure 1. Locations where Trumpeter Swan clutch size and egg weight data were obtained (green arrows = clutch size data only; red arrows = both egg weight and clutch size data). Map is from the 2010 North American Trumpeter Swan Survey (Groves 2012). Shaded areas represent current Trumpeter Swan distribution in North America, with dotted lines indicating separation of the three populations.

for several individual breeding flocks of Trumpeter Swans across the IP and RMP. Clutch size and egg weight data recorded for IP and RMP swans were also compared with these measures for captive Trumpeter Swans in Wyoming, and with wild Trumpeter Swans in Wyoming and Idaho. Captive Trumpeter Swans, which are being used for regional restoration programmes, are provided with food year-round and therefore are considered likely to be in better nutritional state than birds in the wild. As such, and as better nutrition would contribute to larger eggs and/or clutch sizes (Blums *et al.* 2002), we hypothesised that clutch and egg sizes would be greatest for the captive birds.

Methods

Study sites

Data on clutch size and egg weights were collected from the literature and from field studies (Fig. 1, Table 1). IP egg data were recorded at the Seney National Wildlife Refuge, Michigan (2006–2009) and at various nest sites in south-central Minnesota (2007–2008). RMP-U.S. data came from Red Rock Lakes National Wildlife Refuge, Montana (RRLNWR, in 1955, 1987, 1989–1990 and 2010), the Yellowstone National Park of Wyoming, Montana and Idaho (YNP, in 1985), wild Trumpeter Swans clutches in non-YNP parts of Wyoming and Idaho (in 2000–2001 and 2004–2006), and from a captive flock at the Wyoming Wetlands Society (WWS) captive swan rearing facility near Jackson, Wyoming (in 2001–2007). Wild Trumpeter Swans in western Wyoming and eastern Idaho nest and winter in similar habitats, and have the same genetic origins. Therefore we combined clutch and egg size data from these states for our analysis. RMP-Canada egg data were obtained from publications of clutch sizes recorded at Grand Prairie, Alberta (Holton 1985; MacKay 1987).

Data collection and analysis

Clutch size and egg weight data were obtained both from our own field studies and from earlier publication (Tables 1 and 2). Clutch size data were available for all study sites. Egg weights were determined either by weighing them directly or by measuring the eggs, depending on when and by whom the data were collected. The ratio of eggs measured, to calculate their weight, in relation to those that were weighed was 4 : 1. Eggs were weighed to the nearest gram using a Pesola spring balance. On measuring the eggs, length and width were recorded to the nearest 0.5 mm using a vernier calliper; egg mass was then calculated following the equation:

$$\text{Egg mass} = \text{constant}*(\text{length}*(\text{breadth})^2)$$

The constant of 0.555 (g/cm^3) was calculated from data recorded for a variety of waterfowl species (Hoyt 1979); there are currently no better data available on the relationship between size and mass for Trumpeter Swan eggs.

Multiple linear regression analysis was used to determine which variables (flock affiliation, study site and year) were associated with clutch size and egg weight. Flock affiliation was classified as either Interior Population (IP) or Rocky Mountain

Table 1. Mean clutch sizes and egg weights recorded in different study areas, for the Interior Population (IP) and Rocky Mountain Population (RMP) Trumpeter Swans of North America.

Population affiliation	Location	Years data collected	Number of nests	Mean clutch size	Number of eggs measured and/or weighed	Mean egg weight (g)
Interior	Seney NWR, Michigan	2006–2009[1]	76	5.5	411	362.1
	Minnesota	2007–2008[2]	46	5.8	261	373.8
Total (IP)			**122**		**672**	
RMP	Red Rock Lakes NWR, Montana	1955[3], 1987[1], 1989–1990[1], 2010[4]	37	5.0	180	340.1
	Yellowstone National Park, Wyoming	1985[5]	56	4.1		
	Wyoming (wild)	2000–2002,[1] 2004–2006[1]	29	3.5	97	333.3
	Wyoming Wetland Society (captive)	2001–2007[1]	40	4.2	164	346.4
	Grande Prairie, Alberta	1985[6], 1987[7]	87	5.8		
Total (RMP)			**249**		**441**	
Total (All)			**371**		**1,113**	

Data obtained from: [1]Authors; [2]Spaeth (2014); [3]Red Rock Lake NWR (1955) and Banko (1960); [4]U.S. Fish and Wildlife Service unpubl. data; [5]Gale *et al.* (1987); [6]Holton (1985); [7]Mackay (1987).

Table 2. Clutch size data and results of Mann Whitney U tests, used to determine whether there are significant differences in clutch sizes for Trumpeter Swans across geographic locations (n.s. = not significant).

Location	Mean clutch size ± s.d. (*n*)	Range (no. eggs)	*P*-value
Interior Population	5.6 ± 1.7 (122)	1–9	≤ 0.001
Rocky Mountain Population	4.9 ± 1.7 (249)	1–9	
RMP-U.S.	4.2 ± 1.4 (162)	1–8	≤ 0.001
RMP-Canada	5.8 ± 1.4 (87)	2–9	
Wyoming-wild	3.5 ± 1.0 (29)	1–6	0.006
Wyoming Wetland Society (captive)	4.2 ± 1.1 (40)	2–7	
Michigan	5.5 ± 1.6 (76)	2–9	0.443 (n.s.)
Minnesota	5.8 ± 1.9 (46)	1–9	

Population (RMP). Study sites were included in one of seven groups: Red Rock Lakes NWR, Yellowstone National Park, Seney NWR, Minnesota, Wyoming wild Trumpeter Swans, Wyoming Wetlands Society captive swans and Grand Prairie-Alberta. Data used in the analysis were recorded over several decades, from 1955 through to 2010, so year was also included as a variable to test for trends in clutch size and egg weight over time. Non-parametric Mann-Whitney U tests were also used to determine which sites differed significantly from each other in their clutch size and egg weight data. Egg weights were available for the following study sites only: Red Rock Lakes NWR, Seney NWR, Minnesota, Wyoming wild Trumpeter Swans and Wyoming Wetlands Society captive swans. Clutch sizes were available for all study sites.

Results

In addition to information found in the literature, a total of 1,113 eggs (n = 846 measured; n = 267 weighed) were sampled directly from 283 nests (Table 1). Multiple linear regression analysis indicated that Flock Affiliation, Site Affiliation and Year all had a significant effect on clutch size ($F_{1,364}$ = 26.36, $F_{1,364}$ = 16.77 and $F_{1,364}$ = 27.55 respectively; $P < 0.001$ in each case). However, for egg weights, only Flock Affiliation was an important explanatory variable ($F_{1,216}$ = 34.38, $P < 0.001$); neither Site Affiliation ($F_{1,216}$ = 0.40, P = 0.12, n.s.) nor Year ($F_{1,216}$ = 2.60, P = 0.11, n.s.) were found to be significant.

Clutch size

Clutch size over all study sites ranged from 1–9 eggs with a mean of 5 eggs per nest.

The IP mean clutch size of 5.6 eggs (s.d. = 1.7, n = 122) was significantly larger (U_{369} = 9243, $P \leq 0.001$) than the RMP mean clutch size of 4.3 eggs (s.d. = 1.4, n = 249; Table 2). Similarly, clutch sizes differed significantly (U_{247} = 2118, $P \leq 0.001$) between RMP-U.S. (mean ± s.d. clutch size = 4.2 ±1.4, n = 162) and RMP-Canada (mean ± s.d. clutch size = 5.8 ± 1.4, n = 87; Table 2). There was also a significant difference (U_{67} = 337.5, P = 0.006) between clutch sizes from the captive and wild flocks in Wyoming/Idaho, but not between clutch sizes at Seney NWR and those at nest sites in Minnesota (U_{120} = 1486, P = 0.44, n.s.).

Egg weights

Egg weights across all study sites ranged from 147.9–455.2 g, with a mean of 351.9 g (n = 1,118). Egg weights recorded for IP swans (mean ± s.d. = 366.4 ± 32.5 g, n = 672) differed significantly (U_{1116} = 83851, $P \leq 0.001$) from those recorded for the Rocky Mountain population (mean ± s.d. = 337.0 ± 32.3 g, n = 446; Table 3). There was no statistical difference (U_{249} = 5624, P = 0.071, n.s.) between the Wyoming captive flock's mean egg weight of 346.4 g (s.d. = 32.8, n = 164) and the Wyoming/Idaho wild flocks egg weight of 333.3 g (s.d. = 37.0, n = 97). However there was a statistical difference (U_{670} = 38893, P = 0.011) between the Seney NWR, Michigan mean egg weight (362.1 g, s.d. = 29.5, n = 411) and the Minnesota mean egg weight of 373.80 g (s.d. = 36.3, n = 261; Table 3).

Discussion

Clutch size and egg weights varied significantly between the Rocky Mountain and Interior populations of Trumpeter Swans. Life history strategies (Lack 1968), individual fitness factors (Rockwell *et al.* 1987), and environmental variation (Smith

Table 3. Egg weight data (measured in grams) and results of Mann Whitney U tests used to determine whether there are statistically significant differences in egg weights for Trumpeter Swans across geographic locations (n.s. = not significant).

Location	Mean egg weight ± s.d (n)	Range (g)	P value
Interior Population	366.4 ± 32.5 (672)	147.9–455.2	≤ 0.001
Rocky Mountain Population	337.0 ± 32.3 (446)	256.0–431.0	
Wyoming (wild)	333.3 ± 37.0 (97)	262.0–431.0	0.071 (n.s.)
Wyoming Wetland Society (captive)	346.4 ± 32.8 (164)	256.0–430.0	
Michigan	362.1 ± 29.5 (411)	147.9–448.3	0.011
Minnesota	373.8 ± 36.3 (261)	226.3–455.2	

& Fretwell 1974; Rohwer 1992) are a few of the multiple drivers that might explain differences in clutch size and egg weights. Essentially, these drivers can be broken down into two categories: genetic and environmental factors (Perrins & Jones 1974; Figuerola & Green 2005).

Low levels of genetic variation have been linked to reduced fitness in some species (O'Brien & Evermann 1988; Quattro & Vrijenhoek 1989; Wayne *et al.* 1991). Within the RMP swans, there is slight but not significant genetic variation (Oyler-McCance *et al.* 2007). The IP was reintroduced from many birds from multiple distinct and unrelated source flocks, which bolstered genetic variation (Ransler *et al.* 2011). It is possible that the lack of genetic variation may lead to smaller clutch sizes and lighter eggs for Trumpeter Swans over time.

Previous studies looking at clutch size and egg weights in Trumpeter Swans (Banko 1960; Hansen *et al.* 1971; Rohwer & Eisenhauer 1989) have shown that swans from Montana had smaller clutch sizes and smaller egg weights than those from Alaska. The IP reintroduction programme for Trumpeter Swans used swans coming from Alaskan stock. Since heredity may allow characters such as clutch size and egg weight to persist, this might have contributed to the Interior Population swans having larger clutches and heavier eggs (Alisauskas & Ankeny 1992).

The wetlands used by swans in the IP are at lower elevations with a longer growing season than the higher elevation wetlands used by RMP swans. At lower elevations, earlier ice-free conditions in spring, warmer water temperatures, earlier aquatic plant phenology and a longer aquatic vegetation growing season tend to occur, which may contribute to greater plant food resources being available to the swans for a longer period, and thus influence the fitness of the IP birds. Breeding habitat had a significant effect on the body mass of Whooper Swan *Cygnus cygnus* cygnets in Finland where cygnets reared on peatlands and oligotrophic lakes were over 1,000 g lighter than those reared on eutrophic lakes (Knudsen *et al.* 2002). The "Resource Limitation" hypothesis is supported by the trade-off between egg size and clutch size at an interspecific level (Lack 1968; Klomp 1970; Blackburn 1991a,b). Although this argument is considered weak in waterfowl (Rohwer 1992, 1988), there is further support for the hypothesis in that females in better body condition lay larger clutches (Alisauskas & Ankeny 1992; Erikstad *et al.* 1993). It has been suggested that RMP-Canadian Trumpeter Swans gain a nutritional advantage by migrating to their breeding grounds through areas with post-harvest crop residues and with numerous small productive ponds at lower elevations. The breeding area of the RMP-U.S. swans however overlaps with the winter habitat they share with RMP-Canadian Swans and food resources needed to improve pre-breeding body condition were consumed during the winter. As a result, the RMP-U.S. flocks must wait for their high elevation breeding grounds, which freeze during winter, to thaw and for submerged aquatic vegetation to become available before they can feed. Canadian-breeding Trumpeter Swans therefore are likely to arrive on their

breeding grounds in better condition than the RMP-U.S. birds and can lay larger clutches than Trumpeter Swans nesting in the United States. The IP has submerged aquatic vegetation available earlier than the RMP-U.S. swans because wetlands used by the IP occur at lower elevations and have a longer growing season. The IP Trumpeter Swans therefore seem likely to come into the breeding season in better nutritional condition than those from the RMP-U.S., albeit this hypothesis has yet to be tested. The higher clutch size found in captive Wyoming Trumpeter Swans similarly may be attributable to their having continuous access to supplemental food, potentially allowing them to persist on a higher nutritional plane than Trumpeter Swans in the wild. We hypothesise that the difference in egg weights between Minnesota and Michigan Trumpeter Swans are also due to variation in nutrition and habitat, but lack the data on the movements and site use by the IP swans required to analyse this in greater detail.

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Photograph: Carl D. Mitchell getting ready to candle Trumpeter Swan eggs, by Laura Briley.