Brood amalgamation of Trumpeter Swans *Cygnus cygnus buccinator*

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We documented post-hatch brood amalgamation in Trumpeter Swans in the northern Rocky Mountains of the United States. During 1987-90, 11.5% of swan broods were involved in amalgamation, and the rate of amalgamation did not vary by year. There were significantly more broods, and a higher density of broods on wetlands where amalgamation occurred than on wetlands where amalgamation did not occur. Possible mechanisms for amalgamation are discussed.

Keywords: Brood, Cygnet, Post-hatch Brood Amalgamation, Rocky Mountains, Trumpeter Swan, Waterfowl

Brood amalgamation in Anseriformes has received increased attention in recent years (Eadie *et al.* 1988, Afton & Paulus 1992). Although post-hatch brood amalgamation (PHBA, also referred to as crecheing, gang-brooding, adoption, or kidnapping) is widespread in wildfowl, there are few reports of PHBA in *Cygnus*. In a recent review of brood amalgamation in North American Anatidae, Eadie *et al.* (1988) did not report PHBA in Trumpeter Swans *Cygnus cygnus buccinator*, possibly because records are few and from only one locale. Banko (1960) and Page (1976) did, however, report rare occurrences of PHBA in Trumpeter Swans at Red Rock Lakes National Wildlife Refuge (RRL), Montana, USA. During 1987 through 1990, we documented additional PHBA in Trumpeter Swans in the Centennial Valley (CV).

Objectives

The objectives of this paper are to: (1) review and update records of PHBA in Trumpeter Swans; (2) document the extent of PHBA in Trumpeter Swans in the CV; and (3) evaluate environmental and demographic covariates associated with PHBA in our study area. We were unable to evaluate rigorously various ultimate causes of PHBA (Eadie *et al.* 1988) because we did not work with marked individuals, were not able to observe behaviours associated with amalgamation, and were not able to assess lifetime reproductive success of individuals involved/not involved in PHBA. We do, however, provide comments regarding the likelihood that various ultimate factors apply to PHBA in Trumpeter Swans at RRL.

Study area

Data were collected in the CV of southwestern Montana (44°37' N 112°45' W) at RRL and adjacent wetlands (see Banko 1960 for additional details). Elevation on the valley floor is 2,012 m. Summers are short and cool, and winters are long and cold. Mean annual temperature is 1.6°C, with a frost free period of 51 days (Page 1976). The 1,000 km^2 valley holds numerous scattered wetlands, a 17 km^2 reservoir, and approximately 26 km of lacustrine habitat. RRL is a 163 km^2 wetland-upland complex located at the east end of the CV and is dominated by four large lakes and numerous smaller wetlands and impoundments totaling approximately 5,666 ha. Water depths range from 0.3 to 2.8 m, but most areas are $\leq$0.6 m (Banko 1960). Waters are slightly alkaline (pH = 8, Banko 1960), cool (15° to 18.6°C, Gale *et al.* 1987) and support a diverse community of aquatic macrophytes (Banko 1960, Paullin 1973).

Methods

During aerial surveys conducted in 1987-90 to monitor Trumpeter Swans in the CV wetlands, locations and sizes of all broods were recorded during three flights per summer. The entire area was surveyed from a fixed-wing Cessna aircraft flying at 120 kph and 30 m above ground level. Trumpeter Swan pairs were circled until complete brood counts could be made (<3 passes). For each flight, data on date, weather conditions, aircraft, observer and location and number of adult swans and cygnets were recorded on a portable tape recorder. Brood locations were also plotted in pencil on aerial photographs and transferred to a 16 mm:1 km scale map for permanent reference after each flight was completed. Survey dates were as similar as possible among years, but intervals varied due to weather and logistical constraints. Flights were conducted in each of the following intervals each year: 6 to 18 July, 8 to 16 August, and 10 to 19 September. No broods or adults were marked during the study because the refuge restricted activities in nesting habitats during the breeding season to protect the swans.

Numbers and sizes of broods on each discrete wetland were compared during consecutive flights to determine changes in brood sizes and numbers of broods between counts. Hatching dates ranged from approximately 31 May to 1 July. Therefore, brood counts conducted prior to 1 July were excluded from analysis because additions of newly hatched broods made it impossible to determine clearly whether or not PHBA had occurred since the last flight. Numerical differences between consecutive surveys conducted after 1 July that could have simply resulted from cygnet mortality or brood movement were excluded from further analysis. Thus, documented cases of PHBA were limited to unequivocal increases in brood size or recombinations of the broods and cygnets on an individual wetland. We assumed all PHBA involved one donor brood and one recipient brood but acknowledge that more complex donor-recipient combinations were possible. Thus, our results should be considered as minimum estimates of the frequency of PHBA for Trumpeter Swans in the CV.

The proportion of broods involved in PHBA was compared: (1) among years, (2) between August and September, (3) between wetlands with small (<750 ha) versus large (≥750 ha) areas of open water, and (4) between wetlands with poorly developed shorelines (actual shoreline length was 1-10 times greater than the shoreline of an elliptical basin) versus well-developed shorelines (shoreline length ≥10 times that of an elliptical basin) using Chi-square tests (Conover 1980). Randomisation tests with 1,000 bootstrap samples were used to compare mean number of broods and brood density on open water areas where PHBA did and did not occur (Manly 1991). In the randomisation tests, we only used data for wetlands that had at least two broods, *ie*, only places where amalgamation was possible. We used a significance level of 0.1 to better balance Type I and Type II statistical errors given our sample sizes (Steel & Torrie 1980).

Results

Frequency and timing of PHBA

We documented eight instances of PHBA in 1987-90 (**Table 1**). The annual percentage of broods involved in PHBA averaged 11.5% (SE=2.2) and did not vary significantly by year (χ^2=2.59, df=3, P=0.46). Similarly, frequency of PHBA did not differ by month (χ^2=0.00, df=2, P=1.00): four amalgamations occurred between July and August surveys and an additional four occurred between August and September surveys.

Number of cygnets exchanged

After PHBA occurred, recipient broods had an average of 8.6 cygnets (range = 3-11). Mean size of broods that were not known to have been involved in PHBA was 3.5 (range = 1-8). Recipient broods gained a minimum of one to

Table 1. Post-hatch brood amalgamation (PHBA) of Trumpeter Swans in the Centennial Valley (CV), Montana, USA, 1987-90.

	Year			
Variable	1987	1988	1989	1990
Broods in the CV (*n*)	38	32	8	36
Broods involved in PHBA				
Broods (*n*)	4	6	0	6
Broods (%)	10.5	18.8	0	16.7

four cygnets during PHBA. (Numbers received represent minimums because, with unmarked birds, we could not be certain that recipient broods had all original cygnets survive and received only the cygnets indicated by changes in brood size.)

Environmental and demographic covariates

PHBA occurred on four different wetlands in the CV. We observed higher brood density (P=0.06) and more broods (P=0.01) on wetlands where PHBA occurred than on wetlands where PHBA did not occur. Wetlands with PHBA averaged 1.1 broods/100 ha (SE=0.3) and 6.5 broods/wetland (SE=0.9), whereas other wetlands averaged 0.4 broods/100 ha (SE=0.1) and 3.0 broods/wetland. Five of eight (62.5%) instances of PHBA involved broods that had recently moved to the wetland where PHBA was documented. Frequency of PHBA did not vary by the size of a wetland's open water area (χ^2=1.17, df=1, P=0.28) or a wetland's shoreline development (χ^2=0.59, df=1, P=0.53).

Discussion

Frequency of PHBA in Cygnus

Banko (1960) and Page (1976) provided earlier reports of PHBA in Trumpeter Swans at RRL but concluded that it occurred rarely. Banko (1960) stated that, 'close family ties... coupled with a pair's territorial proclivities virtually eliminates the possibility of two or more broods combining, especially in the younger age classes when both factors are more strongly expressed.' Our data indicates that PHBA may be more common than previously believed and that any costs or benefits of PHBA likely apply to a significant proportion of broods present in the CV. During 1987-90, at least 16 broods (11.5% of broods present) were involved in PHBA. Furthermore, additional PHBA may have occurred but gone undetected during this study because, without unmarked broods, we were unable to document all PHBA. In particular, we were unable to detect any PHBA that may have occurred during June, *ie*, in young broods.

PHBA has not been reported in Trumpeter Swans from other areas (Mitchell 1994) but has been reported in Black Swans *Cygnus atratus* (Williams 1981), Whooper Swans *Cygnus cygnus* (Rees *et al.* 1990), and Mute Swans *Cygnus olor* (Minton 1968, Bacon 1980, Meng & Parkin 1991). The rate of PHBA documented in this study falls between rates found in other species. Williams (1981) estimated 68% of the Black Swan cygnets at Lake Ellesmere (a colonial nesting area of up to 1,600 nests) were found in creches in 1976. Black Swan creches also occurred at colonies on Lake Wairarapa, Vernon Lagoon, Okarito/West Coast, and Waituna Lagoon. Bacon (1980) suggested that 1-3% of Mute Swan cygnets near Oxford were 'adopted' by adjacent pairs.

Timing

Banko (1960) felt that PHBA in Trumpeter Swans was least likely to occur in young broods. Although we were unable to assess frequency of PHBA in young broods, our data clearly indicate that PHBA occurred regularly from mid-July through mid-September. This is in striking contrast to Bacon's (1980) suggestion that Mute Swan cygnets 10 to 20 days old were accepted by adjacent pairs, whereas older cygnets were not.

Number of cygnets exchanged

We were unable to quantify the upper limits of how many cygnets were added to broods but did document recipient broods acquiring one to four cygnets. Our numbers are well below the maximums reported in Black Swans and Mute Swans. Williams (1981) found Black Swan creches with as many as 40 cygnets. Meng & Parkin (1991) described an amalgamated Mute Swan brood of 15 cygnets. Minton's (1968) report of PHBA in Mute Swans involving broods of three and five cygnets (two instances) is similar to what we observed in Trumpeter Swans.

Number of broods involved

Although we assumed that only one donor and one recipient brood were involved in each instance of PHBA, more broods may have been involved. Previous instances of PHBA at RRL (*n*=4) involved two and three broods (Banko 1960) and two and up to five broods (Page 1976). At least 15, and as many as 30, different Black Swan broods contributed cygnets to the brood of 40 documented by Williams (1981). PHBA in Mute Swans typically involves one donor and one recipient brood (Minton 1968, Bacon 1980, Meng & Parkin 1991).

Permanency of PHBA

Brood amalgamation in waterfowl is not always permanent (Afton & Paulus 1992). Page (1976) noted that two Trumpeter Swan broods that amalgamated in August were observed back in the original two family groups in September. In this study, amalgamated broods remained as such until annual surveys ended in September.

Environmental and demographic covariates

PHBA appears to be more likely to happen at higher brood densities. In 1989, the only year in which no PHBA was documented, a cold, wet spring and abnormally high water levels in the CV wetlands caused swans to initiate comparatively few nests. Consequently, in 1989 relatively few broods were present, brood densities were low, and opportunities for PHBA were reduced. Comparisons of brood density and numbers on wetlands where PHBA occurred and did not occur provide further evidence of the importance of brood numbers/density to PHBA, brood density and number were approximately twice as high on wetlands where PHBA occurred. In Black Swans, high frequency of PHBA and extremely large amalgamated broods occurred in an area with 1,600 nests. In Whooper Swans, PHBA occurred after a dispute between brood-rearing pairs on adjacent territories caused one pair of adults, but not their cygnets, to leave the site (Rees *et al.* 1990). Obviously, PHBA opportunities increase with density and interactions between brood-rearing pairs; however, ultimate causes for donating or accepting cygnets are not known (Eadie *et al.* 1988).

We also found cygnet movement to be associated with most instances of PHBA in the CV. Similarly, Williams (1981) stated that PHBA in Black Swans at Lake Ellesmere occurred when large numbers of broods concentrated in a confined feeding area. Patchy food resources and non-aggressive parents allowed frequent brood mixing there. PHBA also occurred in Mute Swans after brood movements, *ie* when young cygnets were washed over weirs in the river during floods (Minton 1968, Bacon 1980). Thus, PHBA appears to be regularly associated with brood movements of various origins. Movements likely create a variety of situations (high brood or cygnet densities, intrusion into another territory) that facilitate or instigate PHBA (see Eadie *et al.* 1988).

Ultimate causes of PHBA

Eadie *et al.* (1988) presented a variety of alternative hypotheses for explaining the presence of PHBA. The accidental mixing hypothesis, which predicts that mixing occurs inadvertently before strong bonds develop between parent(s) and young, was not supported by our data. PHBA regularly occurred in Trumpeter Swan broods 30 to 115 days old. This does not mean that amalgamation is not accidental but does indicate that PHBA occurs after strong parent-cygnet bonds have had time to develop. The validity of other hypotheses could not be tested in our study, our data do not reject any of the hypotheses and each provides a plausible explanation for why PHBA occurred. Studies of marked birds that monitor PHBA, survival, and reproductive success in Trumpeter Swans are needed to distinguish the ultimate causes of PHBA in this species.

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