

Assortative Mating by Brant

KENNETH F. ABRAHAM,¹ C. DAVISON ANKNEY,¹ AND H. BOYD²

¹Department of Zoology, University of Western Ontario, London, Ontario N6A 5B7, Canada, and

²Canadian Wildlife Service, Ottawa, Ontario K1A 0E7, Canada

Brant (*Branta bernicla*) exhibit much variation in the darkness of abdominal plumage, height of the white "necklace," and the extent to which the necklace encircles the neck (Manning et al. 1956, Boyd and Maltby 1979). In North America, individuals of the western subspecies ["Black Brant" (*B. b. nigricans*)] have darker abdomens but taller and more complete necklaces than do populations of the eastern subspecies ["Atlantic Brant" (*B. b. hrota*)]. There is variation within breeding populations as well (e.g. Boyd and Maltby 1979). Although the genetics of the variation is unknown, the continuous rather than discrete nature of the variation suggests a polygenic basis. The white necklace has a signal function (Johnsgard 1965: 56) and possibly also contributes to individual recognition. These plumage characters may therefore play a role in mate selection.

We gathered data on plumage variation on Southampton Island, Northwest Territories for HB's continuing study of plumage variation among Brant populations. Here, we report on possible assortative mating based on necklace type.

We studied Brant at East Bay, Southampton Island, (63°58'N, 81°50'W) in the summers of 1979 and 1980. Each year we intensively searched an 8-km² area for Brant nests and marked them with numbered stakes. We revisited the nests during incubation to obtain data about necklace types of mated birds. We used the scoring system of Boyd and Maltby (1979): "2" = necklace completely encircles the neck, "1½" = necklace incomplete either front or back, "1" = necklace incomplete front and back, "½" = necklace very incomplete, and "0" = necklace absent. Sometimes only the female of a pair stayed at the nest long enough to be scored. The data collected each year were kept separate for statistical testing, because some pairs were probably scored in both years. Five people scored necklaces in 1979 and four in 1980; only one person scored necklaces in both years. Each observer monitored a separate portion of the study area. Although a few pairs were scored by more than one person, there were too few of these to permit the best assessment of observer variability. The similarity in observed pair types between 1979 and 1980 ($\chi^2 = 0.83$, $P > 0.25$), however, suggests little observer variability.

All nesting Brant seen by us had either "1" or "½" necklaces. The proportion of "1" necklaces was much higher ($P < 0.005$) among males than females (Table 1A). Because both "1" and "½" necklaces are incomplete front and back, our results mainly show a sex difference in the amount of white, rather than in completeness. This agrees with the Boyd and Maltby

(1979) finding that mean necklace height of males was greater than that of females (i.e. within a completeness category males were whiter than females) in the four populations they examined. Female scores could potentially have been biased, because male necklaces averaged whiter than females (i.e. when a pair was scored, the female could have received a lower score if she were scored *relative* to the male). Clearly, that did not happen, as female scores were independent ($P > 0.25$) of male presence or absence (Table 1B).

Positive assortative mating by necklace type occurred among East Bay Brant (Table 2); more pairs had birds with the same necklace scores than would be expected if pairing were random. Cooke et al. (1976) showed that positive assortative mating in the dimorphic Lesser Snow Goose (*Chen caerulescens caerulescens*) results from early learning. Birds raised in a monomorphic family showed a mating preference for birds of the familial morph, while birds from mixed families mated with birds of either morph in proportion to the relative frequency of the morphs among potential mates. Assortative mating of Brant by necklace type could result from such early learn-

TABLE 1. Necklace scores of nesting Brant at East Bay, Southampton Island, Northwest Territories.

	Necklace score		
	½	1	
A. Necklace scores of males and females from mated pairs			
1979			
Females	77	111	$\chi^2 = 33.23$ $P < 0.005$
Males	27	161	
1980			
Females	61	107	$\chi^2 = 22.92$ $P < 0.005$
Males	23	145	
B. Necklace scores of females scored when male present (+) and when male absent (-)			
1979			
+	77	111	$\chi^2 = 0.22$ NS
-	42	68	
1980			
+	61	107	$\chi^2 = 1.29$ NS
-	27	65	

TABLE 2. Pair types of nesting Brant at East Bay, Southampton Island, Northwest Territories.

Female necklace score	Male necklace score			
	1979		1980	
	1/2	1	1/2	1
1/2	17 (11.1) ^a	60 (65.9)	13 (8.4)	48 (52.6)
1	10 (15.9)	101 (95.1)	10 (14.6)	97 (92.4)
	$\chi^2 = 6.31, P < 0.025$		$\chi^2 = 4.71, P < 0.05$	

^a Observed (expected generated by contingency table analysis).

ing or from a nonrandom distribution of birds with different necklace types at the time of pair formation (the "prevalence" hypothesis of Cooke et al. 1976). New York and New Jersey wintering Brant did not differ in necklace type composition (116/177 "1" in New York vs. 191/260 "1" in New Jersey; $\chi^2 = 3.1$, $P > 0.05$; data from 1979–1982 with sexes combined). Cooke et al. (1976) knew of no case, except Lesser Snow Geese, in which early learning of familial phenotype led to intraspecific positive assortative mating in the wild. To us, the "early learning" hypothesis is the simplest explanation for the assortative mating by Brant.

As Brant subspecies are largely segregated in winter (Palmer 1976), the major period of pair formation, hybridization is minimized. Boyd and Maltby (1979) however, reported that paler Parry Islands Brant winter or migrate, in part, with the darker "Black Brant." Manning et al. (1956) reported that the subspecies nesting ranges overlapped and suggested that mate loss and subsequent pairing in such areas could produce "mixed pairs." Assortative mating based on early learning could hinder such interbreeding.

Lensink (1968) found that, within a population of "Black Brant," neckbanded birds had a lower productivity than did legbanded birds. He suggested that neckbands hindered pair formation and caused a breakdown of established pair bonds by interfering with normal behavior. The necklace of Brant functions in threat displays (Johnsgard 1965: 56), which establish the rank of competing birds, and our results indicate that the necklace may also be important in mate choice. Neckbands could interfere with both processes, either by covering up the necklace (threat displays are given with the neck extended and head forward) or by increasing the amount of white (contrast) on a bird's neck. If Brant choose mates on the basis of familial necklace phenotype, a neckband might effectively create a phenotype unacceptable to a bird's present or potential mate. Also, if the necklace functions in individual recognition, a neckband could cause pair-bond breakdown. Finally, pairs of neckbanded Brant may have lower productivity than do unbanded pairs because they have lower success in agonistic encounters.

The hypothesis that early learning of familial neck-

lace type leads to positive assortative mating in Brant could be tested using captive Brant in experiments similar to those of Cooke et al. (1972) and Cooke and McNally (1975), who manipulated phenotype composition of families. For Brant, the whiteness of the necklace could be enhanced or reduced, and the influence of neckbands could be tested directly. The possibility of winter segregation of birds with different necklace types is easily tested by scoring Brant from several locations. Two other lines of research could be pursued. First, biologists studying other Brant populations could gather data on necklace types to determine whether or not assortative mating occurs. Second, the genetics of necklace variation could be studied with captive breeding birds; this is not feasible in field studies, because the necklace of young Brant does not begin to develop until the first autumn, unlike the dimorphism in Lesser Snow Geese, which is apparent at hatch.

We thank D. Boyd, W. Chappell, S. Johnson, P. Kehoe, D. Koval, and K. Maronets for assistance in the field. We thank F. Cooke, P. Handford, J. P. Ryder, and D. M. Scott for commenting on the manuscript. Our Brant studies on Southampton Island were funded by a contract with Department of Supply and Services, Canada; the Canadian Wildlife Service; the United States Fish and Wildlife Service; the Atlantic Flyway Council; and a Natural Sciences and Engineering Research Council operating grant to CDA.

LITERATURE CITED

- BOYD, H., & L. S. MALTBY. 1979. The Brant of the western Queen Elizabeth Islands, N.W.T. Pp. 5–21 in *Management and biology of Pacific flyway geese* (R. L. Jarvis and J. C. Bartonek, Eds.). Corvallis, Oregon, Oregon State Univ. Bookstores, Inc.
- COOKE, F., & C. M. McNALLY. 1975. Mate selection and colour preferences in lesser snow geese. *Behaviour* 53: 151–170.
- , P. J. MIRSKY, & M. B. SEIGER. 1972. Colour preferences in the lesser snow goose and their possible role in mate selection. *Can. J. Zool.* 50: 529–536.
- , G. H. FINNEY, & R. F. ROCKWELL. 1976.

Assortative mating in Lesser Snow Geese (*Anser caerulescens*). Behav. Gen. 6: 127-140.

JOHNSGARD, P. A. 1965. Handbook of waterfowl behavior. Ithaca, New York, Cornell Univ. Press.

LENSINK, C. J. 1968. Neckbands as an inhibitor of reproduction in Black Brant. J. Wildl. Mgmt. 32: 418-420.

MANNING, T. H., E. O. HÖHN, & A. H. MAC-

PERSON. 1956. The birds of Banks Island. Natl. Mus. Can. Bull. 143: 1-144.

PALMER, R. S. 1976. Handbook of North American birds, vol. 2. New Haven, Connecticut, Yale Univ. Press.

Received 5 October 1981, accepted 30 June 1982.

Natal and Juvenal Plumages of the Blue-and-White Swallow (*Notiochelidon cyanoleuca*)

KEITH A. ARNOLD,¹ EVA JOLENE BOYD,¹ AND CHARLES T. COLLINS²

¹Texas Cooperative Wildlife Collections, Department of Wildlife and Fisheries Sciences, Texas A&M University, College Station, Texas 77843 USA, and

²Department of Biology, California State University, Long Beach, California 90840 USA

Although much information is available on the pterylosis of some Old World and North American hirundinids (Nitzsch 1867; Shufeldt 1890; Lowe 1938; Wetherbee 1957, 1958), there is a dearth of such data on most neotropical passerines (Collins 1963a, 1973). The pterylosis of the neotropical genus *Notiochelidon* (*sensu lato*) is completely unknown (Clench in litt. to

Arnold). Here we describe the natal and juvenal plumages of the Blue-and-White Swallow (*N. cyanoleuca*) based on five nestlings of the following stages of Wetherbee (1957): Stage B—TCWC 10947, 10948; Stage D—TCWC 10945, 10946, and 10976. All five birds were salvaged after falling from nests in a house located in the Parque Nacional de Guatopo, Est. Miranda,

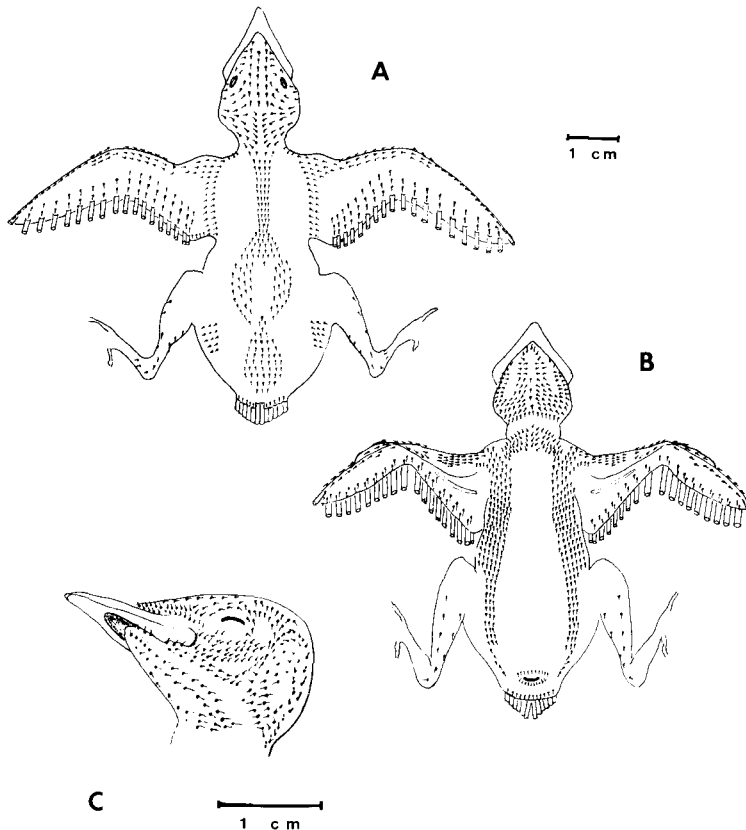


Fig. 1. Pterylosis pattern of the Blue-and-White Swallow, drawn directly from specimens. A. Dorsal view. B. Ventral view. C. Ventro-lateral view of head. Views A and B drawn to the same scale.