

Winning with warts? A threat posture suggests a function for caruncles in Ross's Geese

M. ROBERT McLANDRESS

Introduction

Agonistic behaviour in geese has been described by numerous investigators (e.g. Johnsgard 1965). Dominant geese in flocks acquire more or better quality resources (Raveling 1970). But aggression is energetically costly and fighting can cause injury. It is not surprising then that geese have evolved agonistic displays which reduce fighting. A display which has not been reported in other species appears to have become stereotyped in Ross's Geese *Anser rossii*. An area of warty protuberances (caruncles) on the base of the upper mandible of the bill (Figure 1), which is a species diagnostic characteristic, is the focal point of the display.

Methods

Ross's Geese were studied in the field from September 1975 to May 1977 in western North America. Approximately 1000 geese were neck-banded and hence individually identifiable. Unmarked birds were subjects of most observations, however, because less than 1% of the population was tagged (McLandress 1979). Detailed behavioural data were gathered only at distances of less than 20 m. The number of hours of useful observations was limited (ca. 100 hr.) because of difficulty in keeping track of individuals within enormous flocks of Ross's and Lesser Snow Geese *A. caerulescens caerulescens*.

Development of caruncles on the



Figure 1. Extensively developed caruncles on the bill of an adult Ross's Goose.

bills of adult Ross's Geese were recorded at two migration staging areas; west-central Saskatchewan (Canada) in September-October of 1975 and 1976 and, northeastern California (U.S.A.) in March-April of 1976 and 1977. Ross's Geese have a very restricted migration corridor (Bellrose 1980), therefore geese examined were fairly representative of the population as a whole. Birds in Saskatchewan were trapped at lake roosting areas with rocket nets and those in California were obtained following avian cholera epizootics. Caruncle development was assigned to one of four subjective classes. These were: 1) no swelling or warts at the base of the bill, 2) distinct swelling at bill base but no warts, 3) distinct warts on sides of the bill, 4) extensive lateral warts and distinct warts on the dorsal surface of the bill. In the autumn of 1976 and spring of 1977 'yearling' adult geese (14 to 20 months old) were identified by penis characteristics or the presence of 5-10 mm Bursas of Fabricius (Hanson 1967).

Results and discussion

Display description

Fighting (reciprocal striking) between

Ross's Geese was not observed at winter roost sites. Even at feeding sites, physical contact was limited to 'surprise' attacks. Typically, one goose rushed toward and struck the back or tail of another which fled. Head to head confrontations were seen only at roost sites and were restricted to subtle displacements of one bird by another. In such instances, the aggressor maintained a slightly crooked neck that was typical of resting geese and simply 'bowed' its head toward an opponent (Figure 2). The threatened goose then retreated a few steps or returned the threat which caused the initiator to retreat. Occasionally, the dominant bird continued to bow its head and moved toward the displaced bird resulting in further retreat by the latter. This form of agonistic display, termed 'bow-threat', was seen at all times of the year. Threat postures described for other species (Fischer 1965; Raveling 1970; Owen 1980) were common only at migration staging areas in spring and early autumn and on nesting territories in spring (see also Ryder 1967).

Typically, the bow-threat involved an aggressor and one or two subordinates. But, on one occasion (3 April 1977) at a marsh roost site near Tule Lake, California, 30 Ross's Geese were involved in bow-threat displays. The group con-



Figure 2. Two Ross's Geese (left) use bow-threat to displace conspecifics (right) at a roost site in California.

tained both males and females. Geese faced one another and assumed the bow-threat posture which was usually followed by 'neck-dipping' (Fischer 1965), a precopulatory display. Occasionally, the larger geese (probably males) attacked one another. Other behaviour which might indicate motivation for this group interaction was not observed, but a similar account was concluded to be the 'beginning of pair formation' (Palmer 1976).

Origin of the bow-threat

I conclude that the bow-threat is a stereotyped display in Ross's Geese. Postures that involve bent necks and heads tilted forward during agonistic encounters are exhibited in other *Anser* spp. when terminating a chase (e.g. see Figure 20 in Fischer 1965). The most subtle threats of Canada Geese *Branta canadensis*, Snow Geese, and White-fronted Geese *Anser albifrons*, involve small changes in neck extension on either the vertical or horizontal plane (personal observation) and little, if any, head 'bowing'. Similarities in head and neck positions indicate that the bow-threat may have been derived from positions intermediate to the bent neck and erect neck postures. Recall that the neck remains crooked during the bow-threat. In other species of geese, this neck position is at least neutral and the extreme bent-neck posture ('Duckmauserhaltung' — Fischer 1965) may inhibit attack by other geese.

The group interaction observed at Tule Lake indicated another possible derivation for the bow-threat. The bowed head and bent neck appears in precopulatory displays in other species of geese (Klopman 1962; Fischer 1965). This posture probably serves as appeasement to prevent attack by partners during sexual interactions and may have secondarily become an agonistic display in Ross's Geese.

Relative to other species, Ross's Geese are extremely gregarious. In winter flocks, dominance in other species is positively correlated with family size (Boyd 1953; Hanson 1953; Raveling 1970). Status among geese from families of equal size is less definitive and birds

probably rely heavily on individual status recognition to avoid conflicts. Compared with species of larger geese studied in winter (Boyd 1953; Raveling 1970; Prevett & MacInnes 1980), Ross's Goose families break up readily (unpubl. data). Thus, at least in winter, individual signals may be more important than family size in reducing conflict among Ross's Geese.

The Ross's Goose is colonial when nesting and achieves one of the highest nesting densities recorded for any species of goose (McLandress 1983). Mechanisms may have evolved in this species that inhibit the energetically costly aggression that is common to other species of geese during territorial establishment (Ewaschuk & Boag 1972; Mineau & Cooke 1979; Owen & Wells 1979). It is likely that many intraspecific conflicts are resolved through threat displays which incorporate a maximum amount of information about an individual's status.

Caruncles

Ross's and Lesser Snow Geese are sympatric but hybrids are rare (McLandress & McLandress 1979). Bill features are the most striking morphological differences between these species. If caruncles are important as species isolating mechanisms, extensive development would be expected when pairing occurs in the second winter. Some swelling at the base of the bill was noticeable in a higher proportion of yearlings examined in spring (47% of 15 males, 50% of 14 females) than in autumn (30% of 27 males, 13% of 24 females), but yearling geese (14-20 months old) rarely had distinct warts (7% males, $n = 42$; 0 females, $n = 38$).

Ross's Geese that were adults (more than 1 year old in 1975) were identifiable through two years because 'yearlings' could be excluded from birds examined in autumn 1976 and spring 1977. As time progressed more of these adults exhibited increased development of caruncles (Table 1). By spring 1977, however, more than 40% of the 1975 adults (i.e. 32 months of age or older) still did not have distinct warts.

Age is correlated with reproductive success in geese (Finney & Cooke 1978; Raveling 1981). Apart from grey feather-

Table 1. Progression in caruncle development in the 1975 adult cohort of Ross's Geese.

When obtained	Minimum age (months) ¹	N	% of geese by wart rank ²				Average rank
			1	2	3	4	
Males ($r_s = 0.251$) ³							
Autumn 1975	14+	116	37	27	20	16	2.16
Spring 1976	20+	82	44	23	23	10	1.99
Autumn 1976	26+	45	20	22	47	11	2.49
Spring 1977	32+	49	8	35	35	18	2.71
Females ($r_s = 0.440$) ³							
Autumn 1975	14+	110	57	26	14	3	1.63
Spring 1976	20+	49	47	31	22	0	1.76
Autumn 1976	26+	55	27	27	42	4	2.22
Spring 1977	32+	31	10	32	48	10	2.58

¹ Yearling adults (i.e. immature in 1975) were excluded in autumn 1976, spring 1977.

² See text for description of wart classes.

³ Spearman's Rank Correlation Coefficient, both $P < 0.01$.

ing of immature birds, age class differences in Ross's Geese were evident only in the variation in extent of caruncles and possibly through behaviour. The bow-threat provides an adversary with full view of these 'warts'. Therefore, I propose that the caruncles on the bills of Ross's Geese function as a 'badge' (Dawkins & Krebs 1978) for signalling status. Differences in the extent of caruncles within adult age classes (Table 1) should then be related to individual status. A distinct advantage of a badge signalling system is that 'contests' can be averted because individuals can predict their status in any group of conspecifics (Rohwer & Ewald 1981).

Caruncles could enhance the bow-threat by inhibiting aggression of other geese, which could be innate or learned from unsuccessful conflicts with older 'warty' geese. Inhibition of aggression would explain the highly gregarious

nature and low levels of fighting in Ross's Geese.

Acknowledgements

I thank D. G. Raveling and D. F. Lott for constructive criticism of the paper. C. R. Ely and J. S. Sedinger provided valuable discussion. The Canadian Wildlife Service supported this study through a contract to R.I.M. Ecology Ltd., Winnipeg, Canada. Concern for caruncles was stimulated by W. J. L. Sladen.

Summary

A subtle agonistic display of Ross's Geese *Anser rossii*, the 'bow-threat', is described. The display appears to have arisen from attack-inhibiting postures or sexual appeasement behaviour. Caruncles may serve to enhance the display. The extent of caruncle 'warting' increases with age. Ross's Geese may signal status with the bow-threat, thereby averting high levels of aggression.

References

- Bellrose, F. C. 1980. *Ducks, geese and swans of North America*. Harrisburg, P.A.: Stackpole Books.
- Boyd, H. 1953. On encounters between wild White-fronted Geese in winter flocks. *Behaviour* 5: 85-129.
- Dawkins, R. & Krebs, J. R. 1978. Animal signals: information or manipulation? Pp. 282-309 in Krebs, J. R. & Davies, N. B. (eds.). *Behavioural Ecology*. Sunderland: Sinauer Associates.
- Ewaschuk, E. & Boag, D. A. 1972. Factors affecting hatching success of densely nesting Canada Geese. *J. Wildl. Manage.* 36: 1097-1106.

- Finney, G. & Cooke, F. 1978. Reproductive habits in the Snow Goose: the influence of age. *Condor* 80: 147-58.
- Fischer, H. 1965. Das Triumphgeschrei der Graugans (*Anser anser*). *Z.F. Tierpsychol.* 22: 247-304.
- Hanson, H. C. 1953. Inter-family dominance in Canada Geese. *Auk* 70: 11-16.
- Hanson, H. C. 1967. Characters of age, sex, and sexual maturity in Canada Geese. *Illinois Nat. Hist. Surv. Biol. Notes* No. 49, 15 p.
- Johnsgard, P. A. 1965. *Handbook of waterfowl behavior*. Ithaca, N.Y.: Cornell Univ. Press.
- Klopman, R. B. 1962. Sexual behavior in the Canada Goose. *Living Bird* 1: 123-9.
- McLandress, M. R. 1979. Status of Ross' Geese in California. Pp. 255-265 in Jarvis, R. L. & Bartonek, J. C. (eds.). *Management and biology of Pacific flyway geese*. Corvallis, O.R.: O.S.U. Book Stores, Inc.
- McLandress, M. R. 1983. Temporal changes in habitat selection and nest spacing in a colony of Ross' and Lesser Snow Geese. *Auk* 100: 335 - 43.
- McLandress, M. R. & McLandress, I. 1979. Blue-phase Ross' Geese and other blue-phase geese in western North America. *Auk* 96: 544-50.
- Mineau, P. & Cooke, F. 1979. Territoriality in Snow Geese or the protection of parenthood — Ryder and Inglis' hypothesis re-assessed. *Wildfowl* 30: 16-19.
- Owen, M. 1980. *Wild geese of the world*. London: Batsford.
- Owen, M. & Wells, R. 1979. Territorial behaviour in breeding geese — a re-examination of Ryder's hypothesis. *Wildfowl* 30: 20-26.
- Palmer, R. S. 1976. *Handbook of North American birds*, Vol. 2, part 1. New Haven, Connecticut: Yale Univ. Press.
- Prevett, J. P. & MacInnes, C. D. 1980. Family and other social groups in Snow Geese. *Wildl. Monogr.* 71.
- Raveling, D. G. 1970. Dominance relationships and agonistic behavior of Canada Geese in winter. *Behaviour* 37: 291-319.
- Raveling, D. G. 1981. Survival, experience, and age in relation to breeding success of Canada Geese. *J. Wildl. Manage.* 45: 817-29.
- Rohwer, S. & Ewald, P. W. 1981. The cost of dominance and advantage of subordination in a badge signaling system. *Evolution* 35: 441-54.
- Ryder, J. P. 1967. The breeding biology of the Ross' Goose in the Perry River region, Northwest Territories. *Can. Wildl. Serv. Rept. Ser.* No. 3.
- M. Robert McLandress, Division of Wildlife and Fisheries Biology, University of California at Davis, Davis, California 95616, U.S.A.