

ning of 27 March 1991, I found two struggling at the entrance to the garden. They confronted one another like fighting roosters and attacked with their bills. At intervals one fell, but promptly regained its feet to resume the conflict, which continued until an entering car drove the birds away. While the two fought, a third wood-rail could be seen nearby, making smacking sounds.

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Interspecific Aggression by Tundra Swans Toward Snow Geese on the Sagavanirktok River Delta, Alaska

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Interspecific aggression in the Anseriformes has been reported in several studies (McKinney 1965, Kear 1972, Savard 1982, 1984, Livezey and Humphrey 1985a, b, Nuechterlein and Storer 1985a, b, Ely et al. 1987). Swans, in particular, are noted for intense aggression in captivity, but aggression by swans toward other waterfowl in the wild had been considered rare (Scott 1977, Kear 1972, Brazil 1983). Recent work from the Yukon-Kuskokwim Delta (Ely et al. 1987) and our observations from the North Slope of Alaska indicate that such aggression may be common.

During research on Lesser Snow Geese (*Chen caerulescens caerulescens*; 1985-1990), we observed frequent aggressive interactions between Tundra Swans (*Cygnus columbianus*) and the geese. The study area was located on the central Sagavanirktok River delta in an oil-development area near Prudhoe Bay, Alaska. Most of the Snow Geese that nest in Alaska occupy a small colony (150-300 pairs, nearly all white phase) on Howe Island in the outer delta. Following the hatch in late June or early July, Snow Geese are distributed in compact groups in widely-spaced brood-rearing areas along the coast, up to 25 km from Howe Island. Nonbreeders and most failed breeders undertake a molt migration (to an unidentified location), so these groups consist almost entirely of brood-rearing geese. Brood-rearing areas are discrete patches of arctic salt marsh vegetation dominated by *Carex subspathacea*, *C. ursina*, and *Puccinellia phryganodes*; the areas are shared with brood-rearing Brant (*Branta bernicla*) and other geese.

Swans, in contrast, are highly territorial throughout the breeding season and nest at relatively low densities (0.01-0.03 nests/km²) across the North Slope of Alaska. Nest densities are somewhat higher in river deltas (R. King unpubl. data) and are as high as 0.9 nests/km² in the Sagavanirktok River delta (R. J. Ritchie unpubl. data). Both Snow Geese and Tundra Swans in the study area initiate nesting in late May or, in late seasons, as soon as snow disappears from nest sites. Snow Geese usually hatch between late June and early July, whereas Tundra Swan nests hatch from early to mid-July.

Systematic observations of Snow Geese were conducted during incubation (late May-early July) and brood rearing (late June-late July) of 1985-1990. During incubation, 368 h of observations were made from a blind on the mainland about 700 m south of Howe Island. In 1988-1990, these observations included the single pair of Tundra Swans that nested on the island each year. During brood-rearing, 471 h of observations were made from blinds located near heavily used brood-rearing areas and from a vehicle on the oil field road system. Tundra Swans were observed when they approached brood-rearing Snow Geese and when Snow Geese approached an active swan nest.

During the six years of the study, we observed 38 direct attacks on Snow Geese by Tundra Swans. Attacks occurred between 30 June and at least 23 July (when observations ceased), which is early in the brood-rearing period for swans. Almost all attacks involved geese that were either unable or unwilling

to fly, and flight-capable swans. In 30 of the attacks, swans made physical contact with at least one goose. In three attacks the swan was paired and had young; otherwise, the reproductive status of the swans was unknown. Swans nesting on Howe Island never attacked incubating Snow Geese or Brant, although some goose nests were within 20 m of the swan nest. In contrast, nesting swans were frequently observed in aggressive territorial interactions with other swans.

An attack was initiated when one swan flew or ran (always with wings flapping), from as much as 1 km away, directly toward a group of brood-rearing Snow Geese. The geese usually responded to attacks as they did to any severe disturbance, by attempting to flee as a group. Thus, escape was delayed as the geese attempted to circle the swan and reassemble the group. Frequently, one or more adult males defended or counter-attacked, allowing females and goslings to escape.

The swan typically captured one goose, usually an adult male or a gosling, and subjected it to a prolonged beating. If other geese were nearby when the victim escaped or was released, the swan then captured another individual, often beating several geese during a single attack. Most attacks ended with a series of raised-wing or quivering-wing displays by the swan (DeVos 1964, Cooper 1979; first described for Tundra Swans by Hawkins 1986), followed by its withdrawal.

Snow Geese nearly always moved away from attacking swans, with 90.5% of the individuals in a group exhibiting running or a more intense response. The mean distance moved was 170 m (Table 1), with greater distances moved during longer attacks. Geese failed to move away only in response to a few low-intensity and/or short attacks. Attacks inflicted crippling injuries on at least three adult geese and at least one gosling died. Disappearances of both adults and goslings after swan attacks suggested delayed mortality in four other cases.

In the three cases in which family groups of swans were observed during attacks, one adult (presumably the female) adopted a concealment posture and fled with the cygnets away from the geese. The other swan flew at low altitude directly toward the geese and attacked. The female and cygnets moved up to 1 km, apparently continuing to flee until rejoined by the male. Both adults then exhibited a series of triumph displays (Heinroth 1911, Cooper 1979), consisting of trumpeting calls, wing-flapping and head-bobbing.

As measured by the proportion of geese reacting, the duration of reactions, and the distances moved, attacks by Tundra Swans were the most severe type of disturbance of Snow Geese that we observed. Other disturbances included vehicles (particularly those that slowed or stopped, or from which humans emerged), humans on foot, aircraft, foxes, and raptors. Geese fled overland from both attacking swans and humans on foot, until the threat was no longer visible. In

TABLE 1. Descriptive statistics on 38 attacks on brood-rearing Snow Geese by Tundra Swans on the Sagavanirktok River delta, Alaska, 1985-1990.

	$\bar{x} \pm SE$
Group size (no. adults)	26.3 \pm 2.9
Number of juveniles ^a	22.9 \pm 5.0
Nearest distance of swan (m)	0.9 \pm 0.4
Duration of disturbance (min)	9.6 \pm 1.9
Distance moved (m)	170.4 \pm 45.6

^a $n = 20$ (juvenile count missing in 18 cases).

response to other disturbances, they usually moved only as far as the nearest water body.

Snow Geese appeared generally wary of Tundra Swans throughout the brood-rearing period. Brood-rearing geese appeared to avoid active swan nests and often exhibited moderately severe reactions to swans that were merely flying overhead. (43.7% responded to such "fly-bys" with running or a more intense response, and the mean distance moved was 30.5 m.)

Savard and Smith (1987) outlined four possible explanations for the occurrence of interspecific aggression: (1) deterrence of predators (Verner 1975, Walters 1979, Stephens 1984); (2) sexual selection, in which males exhibit aggression to communicate their fitness to potential mates (Nuechterlein and Storer 1985a); (3) exclusion of competitors for food or other resources (Kilham 1958, Kruuk 1967, Cody 1968, MacRoberts 1970, Dow 1977); and (4) misdirected intraspecific aggression.

Aggression by Tundra Swans toward Snow Geese did not appear to be related to predator deterrence. Because of their large size, swans (and their eggs and young) are not often troubled by predators (Kear 1972, Scott 1977). In the Sagavanirktok River delta, swans responded to large predators (bears and humans) by adopting concealment postures and fleeing, whereas small predators generally were ignored. Arctic foxes (*Alopex lagopus*) were attacked only when they approached within 10 m of nesting or brood-rearing swans. In contrast, swans attacked Snow Geese at distances of hundreds of meters.

In some respects, interspecific aggression in swans is consistent with the sexual-selection hypothesis. Tundra Swans exhibit sexual dimorphism in both size (Limpert et al. 1987) and aggressiveness (Scott 1977, Earnst 1992), factors that affect female choice in other large waterfowl (Raveling 1970, Black and Owen 1987). Some "attacks" were primarily ritualized displays; 8 of 38 ended without direct contact with geese, and 5 of 38 ended without substantial displacement of geese. Attacks were followed by ritualized nuptial displays (e.g. the triumph display). However, attacks on Snow Geese and on Greater White-fronted Geese (*Anser albifrons*; Ely et al. 1987) occurred only during the brood-rearing period. In all cases in which social status was known, attacking swans were paired and had young. Therefore, although we cannot eliminate a function

in pair-bond maintenance, it appears unlikely that sexual selection is the primary reason for aggression against Snow Geese by Tundra Swans.

If interspecific aggression serves primarily to exclude potential competitors for food, the degree to which intruding species are attacked should be related to the amount of dietary overlap with the dominant species (Savard and Smith 1987). Brood-rearing swans in the Sagavanirktok River delta rarely used the habitats in which they attacked Snow Geese, suggesting little dietary overlap. However, we cannot eliminate resource competition as an explanation for aggression against other species, such as Greater White-fronted Geese (see Ely et al. 1987).

Our observations are most consistent with the hypothesis that aggression by Tundra Swans toward Snow Geese represents misdirected intraspecific aggression. The behavior of swans during attacks on Snow Geese closely resembled intraspecific territorial defense, including sequestering of the cygnets and ritualized displays toward both the victims and the mate (Scott 1977, Hawkins 1986). Attacks on the geese appeared to be more severe than attacks on other swans (possibly because the geese lack effective defense or ritualized response), but otherwise there was little to distinguish them from attacks on other swans.

Kear (1972) reported that, in captivity, the level of interspecific aggression by swans is related to similarity of victims to swans in both color and size. White swans persecute Snow Geese in preference to other geese, geese in preference to small ducks and coots, white ducks in preference to darker ducks, and large pelicans, herons, and cranes in preference to smaller water birds. Black-plumaged swans preferentially attack dark-colored or otherwise similarly marked geese.

In the wild, Tundra Swans have been reported to attack Greater White-fronted Geese (Ely et al. 1987), Canada Geese (*Anser canadensis*), Emperor Geese (*Chen canagicus*; C. R. Ely and C. A. Babcock unpubl. data), and Snow Geese (this report). However, swans in our study area did not attack other waterfowl species when Snow Geese were present, perhaps because the Snow Geese are most similar in appearance to swans. It also is possible that attacks were triggered by the presence of goslings; in all instances it was brood-rearing geese that were attacked. Swans are known to attack and kill strange cygnets, and goslings may resemble cygnets more than adult geese resemble adult swans.

Attacks against Snow Geese have no obvious benefits for Tundra Swans, but misdirected intraspecific aggression may persist even when it is not adaptive (i.e. reproductive success is affected neither by aggression nor by competition for food or other resources; Murray 1971). Maladaptive or nonadaptive interspecific territoriality may persist indefinitely when selection against it is weak (Nuechterlein and Storer 1985a) or when such selection is swamped because it occurs largely at the edge of the dominant species' geographic range or at the edges of contig-

uous but unshared habitats (Murray 1971). All of these criteria probably apply in the case of Tundra Swans and Snow Geese. As with steamer-ducks (*Tachyeres* spp., Nuechterlein and Storer 1985a), Acorn Woodpeckers (*Melanerpes formicivorus*, MacRoberts 1970), and Noisy Miners (*Manorina melanocephala*, Dow 1977), the energetic costs of interspecific aggression by swans appear to be minor and the risks small, so selection against the behavior is probably minimal. Although their annual ranges overlap extensively, the distribution of Snow Goose colonies is such that few Tundra Swans ever encounter Snow Geese during brood rearing, so gene flow may prevent selection against interspecific aggression. It also appears that habitat preferences differ in areas of sympatry and that aggression is expressed mainly along the borders of habitats preferred by swans.

Aggression by Tundra Swans against Snow Geese seems to represent a case of misdirected intraspecific aggression, resulting from the morphological similarity of the two species combined with the generally highly aggressive behavior of swans. While the behavior appears to have no particular benefits for swans, it is likely to persist because there appears to be little or no selection against it.

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Age of First Breeding in Common Murres

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An accurate assessment of the age of first breeding is an essential prerequisite for the formulation of population models. Relevant quantitative data, however, are difficult to collect in species having long periods of delayed maturity. We report on the ages of first-recorded breeding of Common Murres (*Uria aalge*) obtained from long-term studies at two Scottish colonies: the Isle of May, Firth of Forth (56°11'N, 2°33'W) in the North Sea; and Canna, Inner Hebrides (57°03'N,

6°35'W) on the Atlantic coast. On the former island, data reported here were collected from 1981 through 1992, a period during which numbers declined slightly. On Canna, the population more than doubled between 1974 and 1983, but then declined slightly before stabilizing from 1987 through 1992.

Methods.—On the Isle of May, murre breeding ledges are accessible, and chicks have been banded in small numbers for over 30 years. Banding has been