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Impact of Interspecific Aggression and Herbivory by Mute Swans on Native Waterfowl and Aquatic Vegetation in New England

MICHAEL R. CONOVER[1] AND GARY S. KANIA[2]

[1]*Berryman Institute and Department of Fisheries and Wildlife, Utah State University, Logan, Utah 84322, USA; and*

[2]*Department of Wildlife Management, National Rifle Association, 11250 Waples Mills Rd., Fairfax, Virginia 22030, USA*

One of the greatest threats to American avifauna is the establishment of free-ranging exotic avian populations (Temple 1992). Despite evidence of substantial harm caused by exotic birds, most exotic species are so poorly studied that many of their alleged environmental impacts remain largely undocumented (Temple 1992). One such exotic species is the Mute Swan (*Cygnus olor*), a Eurasian species that has been introduced several times into North America, beginning in the late 1800s (Allin et al. 1987). By the 1970s, free-ranging populations existed in Michigan, Minnesota, Wisconsin, Wyoming, British Columbia, Ontario, and in Atlantic coastal states from Maryland to Massachusetts (Allin 1981). In the Atlantic Flyway, free-ranging populations increased from 200 birds in 1955 to 5,300 in 1987 (Allin et al. 1987).

Some biologists are concerned that the increasing population of free-ranging Mute Swans may have an adverse impact on native waterfowl, owing to the swan's aggressive nature (Reese 1975, Williams 1989). Swans sometimes attack other waterfowl, causing injury or death (Stone and Marsters 1970, Willey and Halla 1972, Allin et al. 1987). Furthermore, aggressive swans may displace other waterfowl (Willey and Halla 1972). An additional concern is that the foraging behavior of swans may adversely affect aquatic plant biomass, reducing the food available for other waterfowl. Currently, data are insufficient to judge whether these concerns are real or whether swan populations should be controlled. At present, Mute Swans are protected in some states and unprotected in others; in still others, government employees attempt to control swan populations by shaking eggs and removing adults (Allin et al. 1987). In this study, we examined interspecific aggression by free-ranging adult Mute Swans with breeding territories in freshwater ponds and the impact of their herbivory on aquatic vegetation.

Methods.—Territorial pairs of free-ranging Mute Swans were observed at 15 freshwater ponds (2 to 30 ha) in New Haven County, Connecticut from 1982 to 1987. These ponds represented all freshwater sites in the study area known to have nesting pairs of free-ranging Mute Swans in 1982. Observations were limited to freshwater sites because these were the main areas where Mute Swans came into contact with native waterfowl.

Data on the impact of interspecific aggression were collected on both members of a swan pair simultaneously; data for males and females were analyzed separately. Sex of pair members was determined by the larger body size and larger fleshy knob on the forehead of males (Bellrose 1980). Pairs were observed year-round for 30-min periods, randomly selected among daylight hours. Observations were made from shore, usually from a car to minimize disturbance of the birds. During an observation period, we noted all aggressive behaviors by swans, the other species involved, and the outcomes. Agonistic behaviors by swans included threats (raising wings above back), chases, and physical attacks. All sites were searched weekly from a boat or shore for nesting waterfowl.

Sample sizes for all statistical tests were the number of subjects under observation. Paired t-tests were used to ascertain if there were sexual differences in aggressive behavior. To test whether seasonal variation occurred in swan aggressiveness, data on each swan's behavior during March to May, June to August, and September to February were analyzed using a two-way ANOVA (seasons vs. subjects). Linear regressions were used to compare interspecific aggression rates of individual swans to their intraspecific aggression rates.

To determine whether waterfowl were avoiding areas near swans, we prepared a map of each site noting water depths. At the beginning of each observation period, we noted a swan's location and randomly selected from the map another point of similar depth. At 5-min intervals, we then visually estimated the distance from the nearest individual of every waterfowl species present to both the swan and the randomly selected point. For each individual swan, these data from all observation periods were then combined to yield a single mean distance value between it and each waterfowl species. A similar mean value was obtained for the paired random points. Hence, sample sizes consisted of the number of individual swans under study. A paired t-test was then used to test whether mean distances between a waterfowl species and a swan differed from the distance between that species and a random point.

The experiment on the impact of swan herbivory was conducted at 12 of the freshwater ponds used in the other part of this study. Exclosures were erected in late May or early June at two ponds in 1983, six ponds in 1984, two in 1985, one in 1986, and one in 1987. At each pond, we located two sites (3 × 3 m each) between 20 and 50 m apart that were similar in water depth (between 0.5 and 1.0 m) and appeared to have similar vegetation. One of these sites was randomly selected to serve as an open site where swans could graze (hereafter referred to as grazed site) and marked with a wooden post. The other site served as the ungrazed site and a 3 × 3 m swan exclosure was centered on it. The exclosure was built by attaching a 0.3 to 0.5 m wide chicken-wire fence to eight posts. The fence was built so that its bottom edge was level with the water surface so that it would exclude swans but not other aquatic herbivores such as fish, turtles, diving ducks, and muskrats. Another pair of grazed and exclosure sites was set up on the opposite side of the pond. Data from these two pairs were always combined for analysis to provide a single grazed and ungrazed value for each pond.

For vegetation sampling, each grazed and ungrazed site was considered as being composed of five sections. Each time a site was sampled, all of the above-ground vegetation was harvested within a 0.33 × 0.33 m sampling frame placed within each section. Subsequent sampling was taken elsewhere in each section so that no area was harvested more than once. Sampling was conducted in late May or early June when the exclosures were established (year 1, spring), three months later (year 1, fall), and 15 months later (year 2, fall). Vegetation was segregated by species, dried for more than 24 h at 110°C, and weighed. Paired t-tests were used to compare the biomass of grazed and ungrazed sites. One grazed and one ungrazed sample were obtained from each pond with each sample consisting of 10 sample frames collected from the same pond (five sample frames per exclosure × two exclosures per pond). Hence, for these statistical tests, the sample size equalled the number of ponds under study.

TABLE 1. Number of aggressive interactions per hour ($\bar{x} \pm$ SE) initiated by free-ranging male ($n = 15$) and female ($n = 15$) Mute Swans against swans and other waterfowl at 15 freshwater sites in Connecticut.

Species being attacked	Male	Female	P^a
Mute Swan	0.62 ± 0.21	0.31 ± 0.11	0.03
Mallard	0.10 ± 0.03	0.07 ± 0.01	0.07
American Black Duck	0.03 ± 0.01	0.01 ± 0.001	0.10
Canada Goose	0.38 ± 0.29	0.01 ± 0.01	0.11
Human	0.25 ± 0.07	0.16 ± 0.06	0.08
Total interspecific aggression	0.80 ± 0.30	0.31 ± 0.09	0.04

[a] Paired one-tailed t-test comparing males and female swans.

Results.—During 405.0 h of observation on 15 males and 398.5 h on 15 females, we observed 870 aggressive interactions by free-ranging Mute Swans; 410 were directed against other swans and 460 against other species. Swans were aggressive towards humans 174 times (usually involving a threat display directed at people trying to feed them). They were also aggressive towards Great Blue Herons (*Ardea herodias*) three times, gulls (*Larus* spp.) three times, scaups (*Aythya* spp.) twice, Gadwalls (*Anas strepera*) once, domestic ducks seven times, and domestic geese 21 times. On all other occasions, interspecific aggressive behavior was directed at Mallards (*Anas platyrhynchos*), American Black Ducks (*A. rubripes*), and Canada Geese (*Branta canadensis*; Table 1).

There were no significant differences among years in the aggressive behavior of swans. Hence, data were summarized for each individual subject across years and statistical tests conducted on the combined data. Males were more aggressive than females towards both conspecifics and other species (Table 1). Rates of interspecific and intraspecific aggression were not

TABLE 2. Mean number of aggressive encounters per hour initiated by free-ranging male and female Mute Swans during different seasons at five freshwater sites in Connecticut.

Species being attacked	Season: March–May	Season: June–August	Season: September–February
Male swans			
Mute Swan	0.72	0.42	1.70[a]
Mallard	0.24	0.04	0.11
American Black Duck	0.05	0.19	0.03
Canada Goose	0.25	0.06	0.14
Human	0.24	0.51	0.05
Total interspecific interaction	0.79	0.91	0.40
Female swans			
Mute Swan	0.47	0.01	0.69
Mallard	0.07	0.05	0.09
American Black Duck	0.05	0.00	0.14
Human	0.23	0.09	0.14
Total interspecific interaction	0.35	0.21	0.26

[a] None of differences among seasons were significant ($P < 0.05$) based on two-way ANOVA (2,8 df).

correlated in either males ($r^2 = 0.01$, $P = 0.80$) or females ($r^2 = 0.01$, $P = 0.76$).

Swans occupied their territories throughout the year except when ponds froze. Five males and five females were observed often enough in each season (more than 10 observation periods/season) to be included in the seasonal analysis. Aggression rates for both male and female swans did not vary by season (Table 2). Males varied in their aggressiveness toward American Black Ducks, Canada Geese, and all interspecific interactions combined; females did not (Table 2).

Aggressive interactions usually ended when ducks moved a few meters away from a threatening swan. However, Canada Geese often had to swim more than 50 m, had to fly away, or were chased into water less than 5 cm deep or onto dry land before a swan stopped chasing them (Table 3). Swans got close enough on 50 occasions to bite individuals of other species. Mallards, American Black Ducks, Canada Geese, and domestic geese were bitten, but injuries did not appear serious. Once a swan used its wing to strike a goose.

Canada Geese were observed nesting or with young at 7 of the 15 study sites, Mallards at 12 sites, and American Black Ducks at 1 site. We did not observe any instances where swans foiled a nesting attempt by another waterfowl species. Despite the swans' aggressive nature, there was no evidence that any waterfowl species avoided areas near swans. Distances between the closest waterfowl to a random point and to a swan did not vary for most waterfowl species (Table 4).

When the exclosures were erected in May to assess the impact of swan herbivory, above-ground plant biomass for all plant species and for the three most ubiquitous species did not differ between grazed and ungrazed sites (Table 5). In the fall, there was slightly more plant biomass in the exclosures than in the grazed sites, but the differences were not statistically significant. During the winter, exclosures at five ponds were destroyed by shifting ice or vandalism. At the remaining seven ponds, plant biomass in the fall of the second year was slightly higher in the exclosures than at the grazed sites, but the differences were not statistically significant.

Discussion.—In southern England, some Mute Swans occupy and defend their territories year-round, depending upon winter weather and availability of food resources on the territory (Scott 1984). Free-ranging Mute Swans in Connecticut also occupied their territories almost year-round (except during midwinter when freshwater sites became frozen). Whenever present on their territories, Mute Swans engaged in both interspecific and intraspecific aggression. Consequently, they threatened or attacked both breeding waterfowl and those migrating through or wintering in Connecticut.

Mute Swans spent as much time in interspecific aggression as in intraspecific aggression. Intensive interspecific aggression is rare among most birds, but is common in one group: steamer-ducks (*Tachyeres*

TABLE 3. Different responses by waterfowl to aggressive encounters with free-ranging male or female Mute Swans at 15 freshwater sites in Connecticut.

Species being attacked	*n*	Percent of all waterfowl responses: Moved <10 m	Moved 10–50 m	Moved >50 m	Swam ashore	Flew to far side	Flew away
Male swans							
Ducks	75	55	29	3	7	3	4
Canada Goose	115	30	24	21	11	10	4
Female swans							
Ducks	34	74	24	0	3	0	0
Canada Goose	29	69	0	14	7	0	10

TABLE 4. Distance ($\bar{x}$ ± SE) between a free-ranging Mute Swan (or a random point) and closest waterfowl to them at 15 freshwater sites in Connecticut.

Species being attacked	n (sites)	Distance (m) to Swan	Distance (m) to Random point
		Male swans	
Mallard[a]	13[b]	49.3 ± 9.1	60.0 ± 7.5
American Black Duck	7	34.7 ± 9.4	57.0 ± 19.5
Wood Duck	5	46.2 ± 15.6	58.2 ± 18.3
Other ducks	4	57.8 ± 13.9	53.5 ± 22.4
Canada Goose	4	82.8 ± 27.4	81.2 ± 34.1
		Female swans	
Mallard	14	51.6 ± 10.4	61.9 ± 10.8
American Black Duck	9	33.6 ± 11.5	43.6 ± 10.5
Wood Duck	6	27.8 ± 5.6	39.9 ± 16.3
Other ducks	6	69.5 ± 22.6	42.3 ± 6.7
Canada Goose	4	82.5 ± 19.9	109.8 ± 30.3

[a] The only significant difference ($P < 0.05$) based on paired t-tests (two-tailed) was distance between American Black Ducks and male swans.

[b] Sample sizes are less than 15 because some waterfowl species were not observed at all sites.

TABLE 5. Above-ground plant biomass (g/m^2) of all plants and for three ubiquitous species at sites where Mute Swans could graze and at ungrazed sites that were surrounded by exclosures when first erected (Year 1, Spring; $n = 12$ ponds), three months later (Year 1, Fall; $n = 12$ ponds), and 15 months later (Year 2, Fall; $n = 7$ ponds).

Sampling period	Biomass (g/m^2) Grazed	Biomass (g/m^2) Ungrazed	t[a]
	All plant species		
Year 1, Spring	36.0	37.9	0.80
Year 1, Fall	59.1	40.2	1.38
Year 2, Fall	75.4	60.9	0.62
	***Potomogeton* spp.**		
Year 1, Spring	1.8	7.3	1.00
Year 1, Fall	1.5	0.1	1.19
Year 2, Fall	0.1	0.0	1.00
	Nymphaea odorata		
Year 1, Spring	2.3	1.2	1.47
Year 1, Fall	12.3	16.2	1.45
Year 2, Fall	12.6	18.3	1.23
	Elodea canadensis		
Year 1, Spring	1.0	1.0	0.00
Year 1, Fall	4.6	3.4	1.01
Year 2, Fall	1.6	1.6	0.00

[a] All comparisons nonsignificant ($P > 0.05$).

spp.; Livezey and Humphrey 1985, Murray 1985, Nuechterlein and Storer 1985). This raises the question of whether steamer-ducks and swans share characteristics that can explain their intraspecific aggression. Steamer-ducks have massive heads, thick skin, and a large size advantage over their interspecific opponents; these traits reduce the risk of defeat or injury from interspecific aggression (Nuechterlein and Storer 1985). Likewise, swans have a large size advantage over their interspecific avian opponents and face little risk of injury during their attacks on other birds. None of the birds we observed being threatened or attacked by swans fought back.

Advantages steamer-ducks or Mute Swans gain from interspecific aggression are unclear. Nuechterlein and Storer (1985) proposed that male steamer-ducks exhibit interspecific aggression to display their fighting ability to females and to reduce food competition. Livezey and Humphrey (1985) argued that the advantages which steamer-ducks gain from interspecific aggression may include protection of young, defense of food from marginal competitors, sexual advertisement, and practice for intrageneric combat.

Biologists are concerned that the expanding populations of Mute Swans in the United States may have an adverse impact on native waterfowl either because of their aggressive nature or their herbivory on aquatic plants (Reese 1975, Allin et al. 1987, Kania and Smith 1986, Williams 1989). We found that Mute Swans engaged in high rates of aggression against native ducks and geese, but that these episodes consisted mainly of threats and chases, and rarely resulted in physical contact. Hence, one cost for native waterfowl that shared a pond with a Mute Swan was the energetic cost of evasion. There was, however, considerable variation among individual swans in the tolerance of other waterfowl. The more aggressive ones chased other waterfowl, especially geese, that were in their vicinity. The more tolerant swans did not.

The swans' interspecific aggression also could adversely impact other waterfowl by interfering with breeding attempts, but such was not observed. Unlike Kania and Smith (1986), we were unable to document any incidents of a swan causing a nesting attempt to fail.

Nuechterlein and Storer (1985) reported that steamer-ducks were able to exclude molting Red Shovelers (*Anas platalea*) from their territories. We found no indication that the distances between waterfowl and a swan differed from the distance between waterfowl and a random point. If waterfowl were avoiding areas near Mute Swans, a nonrandom distribution would have been expected, but such was not found. One difference between our observations and those of Nuechterlein and Storer (1985) is that we did not limit our observations to molting waterfowl. The birds in our study could easily escape from a swan if threatened. However this would not be true when geese were molting and unable to fly. Hence, aggressive Mute Swans may exclude molting geese from their territories.

Swans also could have a deleterious impact on native waterfowl if their herbivory impacted aquatic plant biomass, thereby reducing either the vegetative or macroinvertebrate (Krull 1970) food resources used by native waterfowl. In this study, we were unable to document any effect of swan herbivory on aquatic vegetation. However, swan populations in the area are increasing (Allin et al. 1987) and breeding territories are becoming smaller. For instance, in 1983 there were two breeding pairs on Lake Whitney, but by 1990 there were six. Hence, while current swan densities are not having an impact on aquatic plant biomass in New England ponds, this may change if swan densities increase substantially.

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Siblicide and Cannibalism at Northern Goshawk Nests

CLINT W. BOAL AND JOHN E. BACORN
School of Renewable Natural Resources, University of Arizona, Tucson, Arizona 85721, USA

In many asynchronously hatching birds, brood size decreases during the nestling period in a characteristic pattern, starting with the last-hatched chick. This has been widely interpreted as a system by which family size is adjusted to match available levels of essential parentally provided resources (Lack 1954). One cause of this mortality in some raptors and other predatory birds is fatal sibling aggression (e.g. O'Connor 1978, Stinson 1979, Mock et al. 1990), after which the victim's tissues are sometimes ingested by family members (Ingram 1959, Mock 1984, Bortolotti et al. 1991). There is some controversy over how often consumption of the victim occurs and, as a separate issue, how important an evolutionary component the cannibalism per se may be (reviews in Elgar and Crespi 1992, Stanback and Koenig 1992).

Siblicide and cannibalism is uncommon among avian species (Mock 1984, Mock et al. 1990, Stanback and Koenig 1992). Most reports are based on indirect evidence, such as remains of nestlings found in nests (Heintzelman 1966, Pilz 1976, Moss 1979, Bechard 1983), and may fail to unequivocally identify the cause of death. Observational accounts of siblicidal and cannibalistic events are few (Newton 1978, Pilz and Seibert 1978, Jones and Manez 1990, Bortolotti et al. 1991, Negro et al. 1992). The key events tend to be brief (Mock 1984) and may go unwitnessed unless a nest is under constant observation.

We report the observation of a nestling Northern Goshawk (*Accipiter gentilis*) killing and cannibalizing a sibling after the adult female disappeared from the nest area. In addition, we describe a separate incident