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Effects of Interspecific Dominance Among Egrets Commensally Following Roseate Spoonbills

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Egret species participate as followers in several "beater-follower" associations (Rice 1954, Christman 1957, Parks and Bressler 1963, Emlen and Ambrose 1970, Leck 1971, Courser and Dinsmore 1975). This type of relationship in which one species, the "follower," increases its foraging efficiency through exploitation of prey items disturbed by the foraging activities of another species, the "beater," may be important in the evolution of many mixed-species associations (Rand 1954, Moynihan 1962, Friedmann 1967). To understand the composition of this kind of association we need to know both the benefits animals obtain by participating in them and the factors that limit the magnitude of these benefits. In associations with a single follower species Heatwole (1965) and Dinsmore (1973) showed that egrets increase their foraging efficiency by following, and Grubb (1976) showed that intraspecific aggression limits the number of followers that can take advantage of any beater. Where there are multiple follower species interactions between them will affect the advantages each can obtain by following and will thereby influence the tendency for members of each species to occur in the association. This paper compares the increase in feeding efficiency achieved by interspecifically dominant Great Egrets (*Casmerodius albus*) with that achieved by interspecifically subordinate Snowy Egrets (*Egretta thula*) when they both participate as followers in a feeding aggregation.

From 26 to 29 January 1975 I observed feeding aggregations of Great Egrets, Snowy Egrets, Roseate Spoonbills (*Ajaia ajaja*), White Ibises (*Eudocimus albus*), Glossy Ibises (*Plegadis falcinellus*), immature Little Blue Herons (*Florida caerulea*), and American Jacanas (*Jacana spinosa*) in a marsh in Costa Rica. The aggregations form when a group of Roseate Spoonbills begins foraging in emergent water hyacinth. In contrast to the slow lateral sifting movements they use while foraging over submerged vegetation, in emergent hyacinth the spoonbills move rapidly and jerk their bills forward through the vegetation, acting as beaters. Roseate Spoonbills, White Ibises, Great Egrets, and Snowy Egrets are regularly present in the aggregations, the other species irregularly. There is considerable variation in the composition of the aggregations, but typically the spoonbills and White Ibises are present in roughly equal numbers and form one or more clumps that the egrets surround and frequently attempt to penetrate. Snowy Egrets are usually at least as numerous as the spoonbills and roughly five times as numerous as Great Egrets.

Great Egrets and Snowy Egrets also feed solitarily in the same area. Therefore, I could observe each species foraging in and away from the aggregations under similar conditions and compare the increase in foraging efficiency they obtained by joining the aggregations.

TABLE 1. Feeding attempt rates, capture success proportions, and expected feeding rates of Great Egrets and Snowy Egrets foraging with and away from Roseate Spoonbills

	Attempt rate (attempts/min.) $\bar{x}$ (n)	Capture success proportion (captures/attempt) $\bar{x}$ (n)	Expected feeding rate (items/min.)
Great Egrets:			
with spoonbills	1.21^{a} (24)	0.54 (15)	0.65
alone	0.55^{a} (25)	0.61 (20)	0.37
Snowy Egrets:			
with spoonbills	2.28^{b} (36)	0.36^{c} (29)	0.84
alone	0.82^{b} (24)	0.82^{c} (10)	0.67

[a,b,c] Common superscripts indicate significant differences, Mann-Whitney *U*-test, $P < 0.05$

Foraging efficiency is directly related to feeding rate and inversely related to energy expenditure during foraging. I recorded successful, unsuccessful, and indeterminate feeding attempts of actively foraging Snowy Egrets in 2-min focal-animal samples (Altmann 1973) and of Great Egrets in 3-min focal-animal samples, and calculated feeding attempt rates, capture success proportions (successful attempts/total attempts), and expected feeding rates (attempt rate × capture success proportion) (Table 1).

Both species significantly increase their attempt rates while in the aggregations, presumably indicating that prey items become available more frequently due to the activity of the spoonbills. The capture success proportion of Great Egrets is only slightly decreased by the crowded conditions of the aggregations, while that of Snowy Egrets is significantly decreased. Consequently, Great Egrets obtain considerably more feedings per unit time when participating in the aggregations while the expected feeding rate for Snowy Egrets is only slightly increased (Table 1).

To estimate relative energy expenditure during foraging I recorded the activity of foraging individuals every 2 s (Table 2). Foraging was scored as active when the bird was walking (or flying, which occurred less than 1% of the time) while searching for or pursuing prey, and inactive when it was standing still visually searching for prey nearby or striking at prey from a standing position. Each species spent a smaller percentage of its foraging time in the active state when with the spoonbills than when away from them (Table 2). Presumably walking in pursuit of prey consumes more energy than standing still waiting for prey to become available. The data in Table 2 indicate, therefore, that each species reduces its energy expenditure during foraging by joining the aggregations. The amount of energy expended in the increased agonistic encounters is probably not large enough to affect this conclusion.

A precise comparison of the increases in foraging efficiency achieved by the two species would require more information about the energy costs of foraging and the distribution of prey items in and away from the aggregations. However, the decrease in proportion of foraging time spent in motion is of the same order for the two species (71% decrease for Snowy Egrets, 64% decrease for Great Egrets, from Table 2) while the increase in feeding rate is considerably greater for Great Egrets than for Snowy Egrets (76% and 25% increases, respectively, from Table 1). In combination these data indicate that Great Egrets increase their foraging efficiency by a greater amount than Snowy Egrets when they join the feeding aggregations. I attribute this difference primarily to the differences in their interspecific relationships.

Inter- and intraspecific agonistic interactions were more frequent within aggregations than away from them. Great Egrets were the most dominant and Snowy Egrets the most subordinate species regularly

TABLE 2. Activity budgets of Great Egrets and Snowy Egrets foraging with and away from Roseate Spoonbills

	Percent time engaged in				n (2-s intervals)
	Foraging		Agonistic Encounters	Preening	
	Active	Inactive			
Great Egrets:					
with spoonbills	6.0	93.4	0.7	0.0	557
alone	18.7	81.3	0.0	0.0	1,647
Snowy Egrets:					
with spoonbills	7.3	91.6	1.0	0.1	3,172
alone	27.9	70.6	0.5	1.1	3,735

participating in the flocks. In over 22 h of focal animal observations and several hours of unscheduled observations Great Egrets invariably won interspecific encounters among regularly participating species and Snowy Egrets invariably lost them. While Great Egrets were only rarely disturbed by other Great Egrets when foraging in aggregations, Snowy Egrets were frequently disturbed by brief fights with each other and with Great Egrets and by being supplanted by foraging spoonbills and ibises. This frequent disturbance is probably responsible for the lower capture success proportion of Snowy Egrets, which is the main factor responsible for their lesser increase in foraging efficiency.

Thus, it appears that individual Great Egrets derive a greater benefit from associating with Roseate Spoonbills than do individual Snowy Egrets and that this difference is mainly due to their higher interspecific dominance status. This effect is similar to that described by Willis (1966, 1973) for ant-following birds. In both cases the presence of individuals of dominant species limits the advantage individuals of subordinate species can obtain by joining the association. This suggests that the controlling effect that Willis found interspecific dominance to have on the composition of ant-following bird flocks may be more general among beater-follower associations.

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Osprey Trapped by Water Chestnut

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Little is known on the mortality of the Osprey (*Pandion haliaetus*) after leaving the nest (Tyrrell 1936, Auk 53: 261–268, Bent 1937, Life Histories of North American Birds of Prey, Dover Publications Inc., New York, pp. 352–379, Henny and Wight 1969, Auk 81: 173–185). Lafontaine and Fowler (1976, Auk 93: 390) reported a Golden Eagle (*Aquila chrysaetos*) killing and eating a mature Osprey, and Paul Spitzer (pers. comm.) mentions that juvenal Ospreys sometimes break a wing when diving into shallow water.

On 9 September 1976 at 1300, it was reported to me that a large hawk-like bird was struggling in the