Interspecific and Intraspecific Aggression Among Foraging Greater and Lesser Yellowlegs

William Moskoff

Introduction

Studies of shorebird foraging behavior have largely ignored the implications of mixed-species social associations (but see Burger et al. 1979 and Barnard and Thompson 1985), even though shorebird social organization during migration differs from that of the breeding period (Recher and Recher 1969). Here I examine the influence of intra- and interspecific foraging associations between Lesser Yellowlegs and Greater Yellowlegs on their aggressive interactions during their southward migration. Lesser Yellowlegs (*Tringa flavipes*) and Greater Yellowlegs (*T. melanoleuca*) are two shorebirds well known to associate with each other on both their wintering grounds (Dott 1985, Bolster and Robinson 1990, Hayes and Fox 1991) and during migration (Burger et al. 1977, Paulson 1993). From one perspective, the association between the yellowlegs species may seem surprising in view of the substantial overlap in their behavior and habitat use. They use similar foraging techniques, pecking for their prey, making repeated stabs at the water surface, rather than probing in mud or sand for their prey (Zusi 1968, Paulson 1993). They also consume many of the same foods: snails (*Physa* sp.), dragonflies (*Epicordulia princeps* and *Erythemis simplicicollis*), soldier flies (*Odontomyia* sp.), and predaceous diving beetles (*Agabus disintegratus* and *Hygrotus* sp.) (Brooks 1967). In addition, based on studies of migratory shorebird interactions in California, Recher and Recher (1969) predicted that morphologically similar shorebird species such as the yellowlegs should be interspecifically aggressive.

The similarity in prey, foraging microhabitats, and foraging techniques between the two yellowlegs species creates the basis for potential competitive interactions. However, the two species may be different enough in size that competition for food does not occur (Abrams 1975, 1983); Greaters (about 170 g) are about twice the mass of Lessers (about 80 g) (Cramp and Simmons 1983). There is also a difference in absolute bill size, suggesting that the two species may partition prey based upon size. The fact that they regularly differ in the use of vertical habitat suggests that the two species encounter a different category of prey at least part of the time. This is not unusual for species that share the same horizontal habitat (Schoener 1974): for example, in south central Alaska, Greater Yellowlegs eat many small fish, whereas Lesser Yellowlegs concentrate on small invertebrates (L. Tibbitts, pers. comm.).

Study Area and Method

The study was conducted at the Chincoteague National Wildlife Refuge (NWR) on Assateague Island, Virginia (37° 52' N, 75° 22' W), approximately 70 km northeast of Norfolk, Virginia, in July and August 1995, 1996, and 1997. Birds were observed either through 10 x 40 Zeiss binoculars or a tripod-mounted scope with a 25X lens.

During this three-year period, the foraging activities of 121 Lesser Yellowlegs and 83 Greater Yellowlegs were studied. Observations on focal individuals were made daily during the morning (0630-1130) and late afternoon (1600-1800). Work was not conducted in the early afternoon because birds were seldom seen in open areas, likely because of the high heat and humidity. On the migratory grounds Lessers and Greaters foraged in loosely integrated associations, rather than in dense and highly organized flocks. Flock sizes were generally small, ranging typically from 3-12 individuals. The criterion for selection of a focal animal was that it had to be within 9 m of a conspecific or congener when observations of a foraging bout began. I examined the frequency of aggression when the individual was foraging with conspecifics only, with congeners only, and with both congeners and conspecifics. Aggressive behavior largely took the form of short chases on the water, but in some cases there were aerial chases. Focal animals were observed until an aggressive interaction ended the foraging bout, or for a maximum of 15 minutes. These observations were used to establish the presence or absence of aggression by social association and the number of foraging bouts ended by aggression.

Results

The pattern of intraspecific aggression under the different social associations for Lesser Yellowlegs closely resembled that of Greater Yellowlegs (Table 1). There was no consequential difference in the distribution of aggression by social association

Table 1. Percent of foraging bouts involving intraspecific aggression by social association for yellowlegs (number of foraging bouts involving aggression / total foraging bouts observed)

	Lesser Yellowlegs	Greater Yellowlegs
w/Conspecifics only	40.0 (16/40)	57.9 (22/38)
w/Consp. and Congeners	10.0 (3/30)	13.0 (3/23)
w/Congeners only*	7.8 (4/51)	4.5 (1/22)

*Intraspecific aggression occurred in this foraging association when a conspecific flew in and initiated some form of aggression with the conspecific that had heretofore been the only member of the species present in the group.

between the two species. Intraspecific aggression was high when an individual foraged only with conspecifics. It fell dramatically when foraging with the other yellowlegs species, to about one-fourth the level occurring when foraging only with conspecifics. When there were aggressive interactions, it ended the foraging of the focal animal in 68.8 percent of the conspecifics-only foraging bouts among Lesser

Yellowlegs (11/16) and 81.8 percent of the conspecifics-only foraging bouts among Greater Yellowlegs (18/22).

Discussion

Foraging associations are believed to benefit individuals in two ways: predator avoidance (Waite and Grubb 1987, Lovvorn 1989, Cresswell 1994) and the facilitation of food acquisition (Barnard and Thompson, 1985). Foraging associations in shorebirds have been shown to achieve both of these benefits as well, although not for all species under all conditions (Abramson 1979, Fleischer 1983, Goss-Custard 1984). Goss-Custard (1970) argued that shorebirds flock to protect against predation and increased bird density may lead to a reduction in per capita vulnerability to predators, as Myers (1980) showed for Buff-breasted Sandpipers (*Tryngites subruficollis*). Moreover, for species responsive to alarm calls given by conspecifics, as is the case with both Lessers and Greaters, associating with conspecifics may be justified by the sentinel function. Flocking, however, may also raise interference costs (Puttick 1984). The evidence from the foraging behavior of both yellowlegs species suggests high intraspecific interference costs.

Secondarily, group foraging provides public information about the quality of a foraging patch that may not be found during solitary foraging (Valone and Giraldeau 1993). Sometimes the costs of intraspecific aggression may be less than the costs of searching for one's own patch and having to obtain information on one's own about where food is available. The fact that intraspecific aggression was low when conspecifics associate with at least one congener is an important outcome, because it suggests that yellowlegs can reduce the energy they expend on aggression by foraging with congeners. One possible explanation for reduced aggression when individuals simultaneously associate with conspecifics and congeners is that, because any given patch will permit only a certain number of birds, the encounter rate of an individual with conspecifics is reduced and so too is the opportunity for intraspecific aggression. A second possible explanation is that the foraging behavior of one species facilitates access to food by the other. That is, one species in essence acts as a beater for the other, a phenomenon documented in other waterbirds (Emlen and Ambrose 1970). Nevertheless, the primary way in which yellowlegs probably reduce aggression is by spacing themselves on the migratory grounds, foraging as single individuals, a phenomenon noted among other waders (Vines 1980). When birds avoid each other, as yellowlegs seem to, it decreases the possibility that a foraging individual will be attacked (Puttick 1984).

A possible reason for the absence of interspecific aggression between Greater and Lesser yellowlegs is that, in spite of consuming some of the same foods, their feeding niches are sufficiently different to effectively reduce competition (Connell 1980, Rosenzweig 1991), an outcome facilitated by bill size differences in the two species (Eldridge and Johnson 1988).

Mixed-species foraging may be more efficient because there is less intraspecific aggression for both species, and that, in turn, lowers the expenditure of energy. Why, then, do not all Lessers and Greaters affiliate with their respective congener? The desirability of associating with congeners may be density dependent. For instance, as the number of Lesser Yellowlegs associating with Greater Yellowlegs in any given patch increases, there may be diminishing marginal returns to additional Lesser Yellowlegs and vice versa. As the latter's numbers increase and density increases, intraspecific aggression will concomitantly rise due to increased competition for the remaining resources in the patch. The high density of Lesser Yellowlegs and the accompanying aggressive behavior would, under these circumstances, swamp out the moderating influence represented by a Greater Yellowlegs. Thus, some Lesser Yellowlegs could be better off foraging alone because of reduced intraspecific aggression and a higher return to their foraging effort. But, all other things being equal, if there were Greater Yellowlegs on one of these patches, Lesser Yellowlegs should use that patch because the number of aggressive encounters will be lower. They can relax with congeners, but not when alone or with conspecifics. Associating with Greater Yellowlegs, in essence, increases the benefit per unit of foraging time. The analysis is the same when assessing Greater Yellowlegs behavior.

The approach taken in this work has been to measure two effects: that of congeners on a Greater or Lesser Yellowlegs, and that of conspecifics on a Greater or Lesser Yellowlegs. But there are other pathways that may explain yellowlegs behaviors, and therefore additional studies of the Lesser Yellowlegs-Greater Yellowlegs relationship that may be valuable. For example, independent of social association, prey size and distribution may influence the behavior of yellowlegs. Resource depression through either prey depletion or prey exploitation may also be important. This is potentially a two-way relationship. Yellowlegs can depress the level of food abundance through interference behavior and overt aggression. Prey abundance, in turn, can affect the level of vigilance and the peck rate, for example. In view of the evidence on aggressive behavior, it may also be useful to measure the encounter rate of conspecifics per unit time. Since there may also be some behavioral effect of one species upon the other, an effort to control experimentally for this may be in order.

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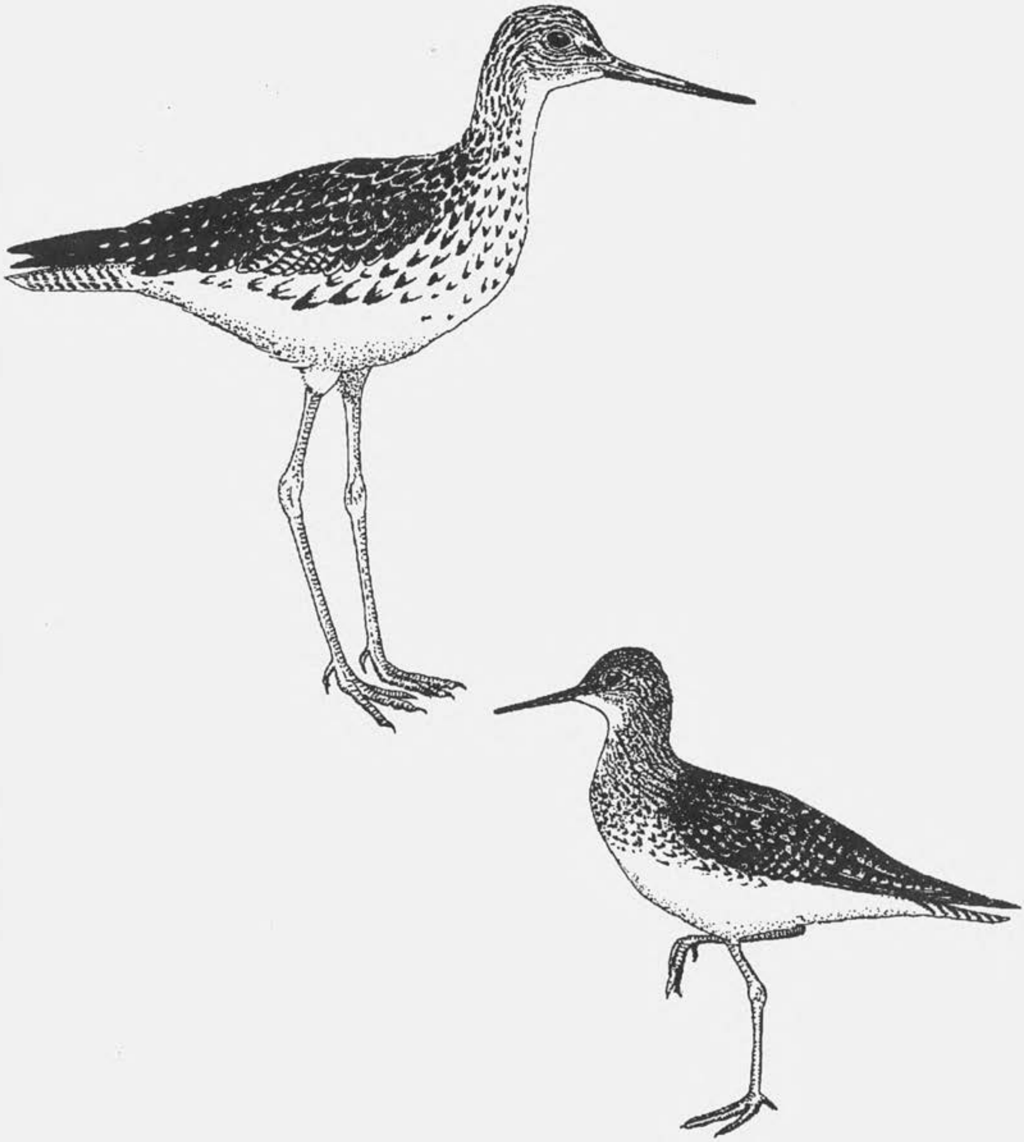
William Moskoff is Hollender Professor Emeritus of Economics and Biology at Lake Forest College, Lake Forest, Illinois. He thanks Mary Ashley, Joel Brown, Anne Houde, Scott Robinson, Marta Hersek, and most especially Christopher Whelan for comments on an earlier version of this paper. Refuge Manager John Schroer and biologist Irvin Ailes of the Chincoteague NWR were immensely helpful in facilitating field work.



GREATER AND LESSER YELLOWLEGS, GEORGE C. WEST