AGGRESSIVE COMMUNICATION BY *LARUS GLAUCESCENS*  
PART V: ORIENTATION AND SEQUENCES OF BEHAVIOR  
by  
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(With 15 Figures)  
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INTRODUCTION  
The agonistic behaviour of Larids has been well documented as a major factor in the establishment and maintenance of a territory. Particular attention has been given to the function of individual displays and their communicative values (TINBERGEN, 1959; STOUT, WILCOX & CREITZ, 1969; STOUT & BRASS, 1969). It has been further suggested (STOUT & BRASS, 1969; GALUSHA & STOUT, 1977) that aggressive tendencies during displays are communicated by head position, that is, the lower the head, the more aggressive the bird.

Important differences in the communicative functions of a given display, resulting from body orientation have been suggested for several species of Larids (TINBERGEN, 1959; MANLEY, 1960; BROWN, BLURTON-JONES & HUSSELL, 1967). In all their descriptions, differences in body orientation are cited as helping other birds distinguish between "sexual" and "agonistic" displays. MANLEY (1960) provides examples of changes in behavior, which he calls "abrupt inhibitions" resulting from a distinct change in posture and/or orientation. The present study considers the effect of body orientation during the aggressive displays on aggressive communication as exhibited by the Glaucous-winged Gull (*Larus glaucescens*) during natural aggressive interactions and in response to moving model gulls.

Much of the previous work on Larid behavior (STOUT et al., 1969; STOUT & BRASS, 1969; STOUT, 1975; GALUSHA & STOUT, 1977; MOYNIHAN, 1955; TINBERGEN, 1953; 1968; 1959; 1960) focused on the descriptions and

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meanings of individual behaviors. Stout (1975) suggested, however, that sequences of individual behaviors might provide information not conveyed by the individual behaviors alone. He suggested that the meaning of a string of behaviors could be altered by changes in the relative positions of the included behaviors.

Sequential analyses of interactions between individuals have been made for a number of species including rhesus monkeys (Altman, 1965), hermit crabs (Hazlett & Bossert, 1965), great tits (Blurton-Jones, 1968), mantis shrimps (Dingle, 1969), ring doves (Wortis, 1969) and crayfish (Heckenlively, 1970). One purpose of this paper is to provide a description of sequential communicative behavior used by *L. glaucescens* during natural aggressive interactions.

Experiments with automated models were also done to test the hypothesis that the meaning of a behavior can be modified by behaviors that precede it in the interaction sequence.

Previous papers (Stout et al., 1969; Stout & Brass, 1969; Stout 1975; Galusha & Stout, 1977) presented evidence for interpreting various aggressive behaviors including Choke, Aggressive Mew and Upright Still as representing various levels of "threat". This view supports a similar hypothesis forwarded by Tinbergen (1959). We have further evaluated these behaviors in light of orientation and sequence data.

**MATERIALS AND METHODS**

Observations and experiments on aggressive communication by *Larus glaucescens* were conducted on Colville Island located 11.7 km west of Rosario Beach, Skagit County, Washington, U.S.A., between 15 June and 15 August, 1971 to 1974. Colville Island contains one of the largest breeding colonies of *L. glaucescens* in the San Juan Islands. Observations and experiments were usually conducted from blinds erected at strategic locations on the island.

Approximately 4000 m of 16 mm motion picture film of gull behavior were taken using a Bolex Rex-5 camera with a Vario-Switar automatic zoom lens at 24 frames/second during the summers of 1967 and 1968. The film was viewed with a Kodak Analyst reversible movie projector with variable speed control.

The film interactions were coded independently three different times for the different segments of this work. All strings were initially coded for use in work on sequences of behavior. One hundred seventy-eight strings with a change in orientation between the defending and intruding birds were coded for the work with change in orientation. All strings were again coded and included both behaviors and orientations. In addition such things as intruder initially near or far from the defender and defender or intruder moving fast or slow were coded. The initial distance was determined according to the following arbitrary classification: Near = five bird lengths or less; Far = more than five bird lengths. Speed of entry was the most subjective measure used. A slow entry was one in which the bird walked slowly or "deliberately" into the territory. A fast entry was one in which the bird flew or ran into the territory considerably faster than at a normal walking pace, usually after being chased out of a neighboring territory.

Angles of orientation between two interacting birds were coded. The orientations