Our observation was made 50 m beyond the driveable portion of the Mazaroni Val Trail, at 480 m elevation, where tree falls had created a semi-open clearing within the forest. Several trees 30–35 m in height stood isolated above a 5 m high jumble of secondary growth. As we passed this spot at 15:00 our attention was attracted by a series of high-pitched, insect-like notes from above. We saw a male White-throated Manakin fly up from the crown of one of the isolated trees. It flew in a shallow arc above the canopy, its white throat puffed-out, wings beating furiously, as it delivered its call in mid-air, then dove into the crown of a tree 12–15 m distant at the edge of the clearing, terminating the display with a wing snap. A tape-recording of the flight song, of insufficient quality to allow production of a sonogram, is on file at the Cornell University Laboratory of Ornithology sound library. A phonetic description is as follows: a 9-sec series of eight high-pitched notes starting at slightly above 7 kHz rising to about 8 kHz with increasing intensity, terminating with a snap, e.g., *seeee·seeee·seeee·seeee·seeee·seeee·seeee·seeee-snap*. The song flight was delivered back and forth between the same two trees four times in 5 min. The male then disappeared for 15 min, then displayed once again, then departed. About 5 min later, a male reappeared chasing a female through the forest about 10 m overhead with short, agitated bursts of flight. During the chase, one of the birds uttered a sharp *seee·ee*. I revisited this spot in November 1980 and February 1981 and observed no further displays.

Snow (pp. 553–561 *in* Proc. XIII Inter. Ornithol. Congr., Ithaca, New York, 1963) mentions display flights in his synopsis of manakin displays. However, his summary does not indicate that any of the species known to possess display flights performed them high above their normal habitat. The unique flight-song display above the forest canopy here described for the White-throated Manakin is also exhibited by another closely allied, allopatric member of *Corapipo*. John Rowlett (pers. comm.), of Austin, Texas, was birding in elfin forest habitat above Cerro Azul, Panama, during February 1978 when he witnessed several male white-ruffed Manakins (*C. leucorrhoa*) in flight song display. Up to three males were involved at a given moment. Each bird flew straight up to about 15 m above the canopy, hovered briefly, then plummeted back into the forest. A series of high-pitched *seee* notes was delivered in flight, but Rowlett was uncertain if these were uttered as the birds were climbing or dropping. Also, the terminal wing snap was not detected.

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Notes on the agonistic behavior of Common Murres.—Common Murres (*Uria aalge*) nest colonially and in fact breed at greater densities than almost any other bird species (see Tuck, The Murres, Can. Wildl. Serv. Monogr. Ser. 1, 1961). However, once away from breeding sites they occur singly or in loose aggregations (Williams, M.Sc. thesis, Univ. Sheffield, Sheffield, England, 1972). The social situation during the non-breeding season is quite different from that during breeding, where extreme crowding is possible through the inhibition of intense aggression and escape tendencies. The problems presented by this highly stressful situation (breeding conditions) have been well defined by Birkhead (J. Anim. Ecol. 46:751–764, 1977).

Williams (1972) appraised the forms and origins of Common Murre behaviors, while Birk-

head (Anim. Behav. 26:321–331, 1978) analyzed quantitatively the 14 displays described for this species. The present study was carried out to increase our knowledge of murre agonistic behaviors. The basic terminology used and the behaviors observed follow the scheme of Birkhead (1978). Agonistic behaviors are considered to be those that increase or decrease interaction distance from overt attack to escape (Scott, Am. Zool. 6:683–701, 1966; Manning, An Introduction to Animal Behaviour, 2nd ed., Addison-Wesley Publ. Co. Don Mills, Ontario, 1972).

Observations were made at various distances from several breeding ledges in a new and rapidly expanding colony on Gull Island, Witless Bay, Newfoundland, in 1977 and 1978 (Mahoney, M.Sc. thesis, Memorial Univ., St. John's, Newfoundland, 1979). Sites were chosen to minimize disturbance. The oblique nature of the slopes above the ledges and the presence of rock outcroppings allowed us to approach within 10–15 m of the birds without causing alarm, although we usually remained 50 m away. Observations were made using 7 × 35 binoculars and a 15–60× spotting scope.

Common Murres breed so densely that aggressive confrontations occur frequently. Three levels of intensity were recognizable: level 1—"jabbing," directed at the opponent's bill without contact; level 2—similar to level 1, but contact was made and the target included the neck and head; level 3—"jabbing" with half-open beaks, leading to locked bills, twisting heads, and beating with the wings. Only 30 level 3 encounters were recorded in two seasons of fieldwork, which is far fewer than Birkhead's (1978) 200 in four seasons. It indicates that intense aggression is less frequent on Gull Island than on Skomer, with the difference probably being due to colony size and lay-out.

Jabbing was the most frequent expression of overt aggression, with one bird thrusting its bill towards another, sometimes making contact and sometimes in a ritualized form. In the initial stages of confrontation jabbing was directed only at the head and bill of the opponent, but during later stages intensity of jabs increased.

Level 2 was usually preceded by "threat display," and normally occurred with the birds about 0.3 m apart and facing the cliff. The birds maintained a distance in which actual physical contact could occur. Once a level 2 encounter intensified to level 3 the "critical distance" was broken down and fighting occurred. The critical distance was well defined; threat posturing between two birds greater than 0.5 m apart occurred in only 3 of 200 (1.5%) threat displays observed. In 76 (38%) of these, threat was accompanied by a low "gargling" call. These threat displays developed to level 3 intensity in only four (2%) cases, or 13% of the total level 3 encounters observed (N = 30). Level 3 encounters seldom exceeded 2 min, but one fight lasted 17 min, with both combatants becoming bloodied. In long encounters the birds became fatigued and often rested with beaks and necks entwined. As soon as one bird gripped its opponent by the lack of the neck struggling ceased. The low frequency of violent confrontations indicates strong inhibitions against them. Such inhibitions, coupled with the gradations in the intensity of encounters, essentially perform the function of aggression, namely protection of site, mate, and self.

During level 3 encounters antagonists seemingly lost all inhibitions towards the crossing of territories, and scrambled about the ledge. Incubating birds never responded to these intrusions even though they were often struck by the wings of the fighting birds, and birds not incubating were seen to retaliate only twice (6.6% of the occasions). This absence of retaliation by non-combatants presumably prevented damage to chicks and eggs. On the other hand, trepassing birds shuffling among incubating birds were normally attacked (level 1) by territory owners. The trespasser rarely retaliated and usually fled (see Williams 1972). Challenges invariably ended with head-shaking (Williams 1972; this study); the head was lowered as shaking occurred until eventually it touched the breast or shoulder at which point preening commenced. Thus, head-shaking connects the alert challenge posture of potential

aggression with an appeasement gesture. In contrast to Birkhead (1978), it was noted here and in Williams' (1972) study that head-shaking occurred before any winner or loser in an encounter could be determined. Ainley (Behaviour 50:16–51, 1974) noted a similar movement in Adélie Penguins (*Pygoscelis adeliae*) and suggested that it may be concerned with the removal of water, salt gland fluids, and other extraneous materials from the nostrils. This behavior also occurred frequently in non-agonistic situations and was usually associated with gape-distension similar to the "jaw-stretch" in ducks (McKinney, Behaviour 25:120–220, 1965) and "yawn" in penguins (Ainley 1974). In the latter context it was a comfort movement. Body maintenance behaviors are likely candidates for ritualization as they contain no threat components. Gape-distension, accompanied by loud calls, was also observed in the female during copulation.

Both Birkhead (1978) and Williams (1972) commented on seasonal aspects of murre aggressive behavior. On 63 occasions, unprovoked, random attacks (level 1), followed immediately by appeasement gestures, were observed during incubation and fledging. Fewer than 10 such behaviors were noted in the pre-laying period, and none when the birds first returned to the ledges. The latter is in direct contrast to the situation reported by Birkhead (1978).

Aggressive encounters were usually associated with territory defense or exhibited by the mate in cases of attempted rape. In 42 such attempts, the female resisted while her mate attacked the rapist, the latter never retaliating. On only two occasions was intra-pair aggression observed, both of which involved copulation, with the female jabbing vigorously at the male. Birkhead (1978) also noted a low level of intra-pair aggression on Skomer.

On Gull Island aggressive jabs frequently and abruptly gave way to appeasement. Obviously, if mechanisms to mitigate aggression had not evolved, dense coloniality could never have become successful. Birkhead (1978) separated murre appeasement into passive displays which prevent aggression, and active displays which terminate it, and noted that certain displays in different contexts function in either capacity. This latter point is well illustrated in the case of "side-preening," the most frequent appeasement behavior seen on Gull Island. It was performed upon return of a bird to its site, at the end of fights in the middle of level 2 encounters, and as an ending to threat-only confrontations. Birkhead's (1978) contention, conflicting with that of Williams (1972), that no directional component is involved in this behavior, was supported by our observations.

The "preening" during side-preening was token in nature, and emphasized the ritualization of the posture. During 340 observed returns-to-site, all of which could have resulted in aggression, 311 (91%) birds side-preened immediately or just after "bill-arring" with their mate. In 167 (54%) of returns that included appeasement, neighbors adopted a challenge or threat posture, and in 42 (25%) they jabbed the newly arrived individual. In all but seven of the latter, aggression terminated with the appeasement posture. Thus, in only 2% of the cases did post-appeasement aggression occur. Birds returning to an unoccupied site (mate absent) always side-preened, indicating that non-mate conspecifics may solicit this response. In the 9% of returns-to-site where side-preening was not recorded, all birds performed bill-arring.

"Stretch-away" and "turn-away" appeasement occurred after an aggressive encounter involving the bird showing appeasement, or in response to a nearby high level encounter, and in response to the movement of nearby birds. Stretch-away was performed only by incubating birds and was mainly a passive gesture (88% [76 of 86 observations]). During active appeasement the neck extension was sometimes maintained even while the bird was jabbed by its opponent.

Turn-away occurred infrequently as passive appeasement, and in 121 of 127 observations (95%) it occurred immediately after level 2 or level 3 confrontation. It followed threat encounters in only 3% of cases. In five level 2 encounters, where turn-away was used to terminate aggression, the initial jabs were responses to the stretch-away elicited by the move-

ment of a nearby bird. Paradoxically, one appeasement gesture elicited aggression and thereby necessitated a different appeasement display. These observations underline the high tension inherent in murre breeding colonies and demonstrate how sudden movements often elicit aggression.

A passive appeasement behavior, the "post-landing display," was observed in 324 of 360 instances (90%) where birds alighted within 1 m of conspecifics or where they followed landing with movement through the colony. Murres landing and remaining on the periphery of a group seldom performed post-landing display, which is in contrast to Williams' (1972) observations. Birkhead (1978) also noted that birds were more likely to perform it in the proximity of other birds. This display is probably a combination of recovery after landing and preparation for attack, defense or fleeing (see van Tets, Ornithol. Monogr. No. 2, 1965). After landing, a murre must usually cross several territories in order to reach its egg or mate. On Gull Island, if the bird could walk past a group at a distance of 2 m or more no posture was assumed. However, if it had to walk by at less than this distance it usually (78% [161 to 207 observations]) adopted "ritualized-walking I," which included head-down and wings-up-and-back components. In 35% of observations the latter component was abandoned. This indicates that head-down is the most essential component of the display, and certainly, if, as Birkhead (1978) suggests, the wing component draws attention to the moving bird, then it may be that the post-land display, which preceded ritualized-walking I, accomplished this already.

When a murre had to move through a nesting group it adopted "ritualized-walking II," which was practically identical to post-landing display, except that in 23 of 63 instances (37%) the wings-up-and-back component was lacking. This usually occurred where the latter aspect might have elicited aggression from birds struck by the wings. The appeasement function of this display was demonstrated in two ways. First, of 15 situations where birds did not adopt this posture, 14 (93%) resulted in threats or level 2 encounters. Second, in eight (57%) of these situations, birds once threatened or attacked, stretched the neck high and positioned the bill almost vertically. If the attacker was to one side or behind them, the birds hurried out of range; if their path was blocked by the aggressor, then they stopped and usually accepted several jabs without retaliation. Aggression was always alleviated by exaggeration of the basic posture and level 3 encounters never developed.

We observed no behaviors not also recorded by Birkhead (1978). A possible exception was the exaggerated form of the ritualized-walking II display, which bore a strong resemblance to Birkhead's (D. Phil. thesis, Oxford Univ., Oxford, England, 1976) "head-vertical" posture. He interpreted this display as one of advertising performed almost exclusively by non-territorial (non-mated) males. The posture illustrated by Birkhead (1976) is apparently identical to the one observed on Gull Island and it may be that the posture functions in both contexts—male advertising and active appeasement—both being situations requiring conspicuous non-aggressive intent.

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