Arrival and Departure Behavior of Common Murres at Colonies: Evidence for an Information Halo?

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Abstract.—I analyzed the arrivals, departures and commuting behavior of Common Murres (*Uria aalge*) breeding at colonies in Witless Bay, Newfoundland to test aspects of the information center hypothesis. No evidence was found for information exchange at nest sites. Departing murres seldom left in groups and successful foragers were not followed on foraging trips. Similarly, murres on the ledges were not well positioned to assess the directions of incoming birds and they appeared to pay little attention to these birds. Intracolony movements and circling near the ledges resulted in a high noise:information ratio around the ledges. Birds on the ocean 100-600 m from the nest sites, however, appeared to have a clear view of the orientation of incoming flocks, and of successful adults carrying fish. I propose that this zone acts as an information halo, where naïve birds can obtain information on the location of their mobile, patchy prey. In 60% of departures, breeding adults splashed down within this 100-600 m zone, and were more likely to land there if they had not recently delivered a meal, or had spent more than an hour at the colony. Meals were subsequently delivered to chicks after 69% of such splashdown departures, but most birds did not catch these prey within the 100-600 m zone. Meals were delivered after 82% of direct departures in which murres flew from the ledges to >800 m out to sea. Outgoing murres usually flew solitarily or in small flocks within 2 m of the sea, which would further enhance their abilities to track the paths of the high-flying incoming flocks.
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The information center hypothesis (ICH) suggests one possible benefit to colonial breeding and communal roosting (Ward and Zahavi 1973, Wittenberger and Hunt 1985). Central to the ICH is the notion that naïve or unsuccessful individuals might locate food patches and improve their foraging success by following or observing successful conspecifics at the colony or roost (Bayer 1982, Wittenberger and Hunt 1985, Brown 1986, Greene 1987). Like many other seabirds, murres (*Uria* spp.) forage in situations where information exchange on prey locality would be beneficial: they feed on small, epipelagic fish and crustaceans which are highly mobile and patchy (Tuck 1961, Bradstreet and Brown 1985, Vermeer *et al.* 1987), and they often commute many km between colonies and food patches, frequently in conditions of poor visibility (Gaston and Nettleship 1981, Bradstreet and Brown 1985, Wanless *et al.* 1990). Murres would often be unable to track the movements of their prey, particularly when obliged to spend many hours at the colony incubating or brooding (Gaston and Nettleship 1981, Verspoor *et al.* 1987).

Both Common Murres (*Uria aalge*) and Thick-billed Murres (*U. lomvia*) nest in large, dense colonies, but tests of the ICH at these colonies have been few, largely anecdotal and inconclusive (Birkhead 1985). Gaston and Nettleship (1981) concluded from observations of Thick-billed Murres that information exchange did not take place at the cliff ledges, but naïve outgoing murres might gain information from the headings of incoming or outgoing flocks. They suggested that the murres obtained this information either on the water at the base of the colony or *en route* to foraging areas, by tracking the stream of murre flocks returning to the colony.

I report observations made at colonies of Common Murres in Newfoundland, focusing on the arrival and departure behavior of breeding adults and the applicability of the ICH. In particular, I examined Gaston and Nettleship's (1981) suggestion that the colony itself might not act as an information center, but birds sitting on the ocean within a few hundred meters of the colony might be better positioned to gain information on the location of prey patches.

Observations were made during the chick-rearing period (20 June - 20 July) in four seasons (1982-1985) at Gull and Green islands in Witless Bay, Newfoundland (47°16'N, 52°47'W). These islands, 2.0 km apart, supported 690 and 74,000 pairs of Common Murres, respectively, in addition to 600 Thick-billed Murres at Green Island (Nettleship 1980). Detailed behavioral observations were made at a cliffside site on Gull Island, and observations were made from Gull Island of the flight behavior of murres commuting to and from Green Island.

Arrivals, departures, exchanges in brooding duties (timed to the nearest minute) and deliveries of fish to chicks were recorded in all 4 years at a sub-colony of about 25 pairs nesting within 8-17 m of a blind on the east side of Gull Island. These observations overlapped with another study in which prey types, parental time budgets and foraging durations were analyzed (Burger and Piatt 1990). Meals delivered to chicks were clearly visible in the beaks of the adult birds, and comprised 89% capelin (*Mallotus villosus*), 9% sand lance (*Ammodytes* spp.) and 2% other fish (Burger and Piatt 1990).

Watches covered all daylight hours and lasted 4-17 h. The breasts of all breeding adults (incubating or brooding) at the observation site were individually marked in each year with drops of picric acid squirted from the clifftop. The activities and orientation of each marked breeding adult present at the colony were recorded at 5-min intervals using the instantaneous-scan technique (Altmann 1974). In addition, scans at 30-s intervals were made to record the behavior, body position and departure time of adults which had been relieved of incubation or brooding duties. The orientation of the breast and beak of each on-duty (incubating or brooding) and off-duty (actively breeding but not incubating or brooding) murre was allocated to one of four categories: facing the cliff, facing seawards or perpendicular to the cliff face (left or right).

The behavior and flight bearing of marked murres leaving the focal colony were observed, using binoculars to track the birds and a stop-watch to time their flight. Distances flown were estimated from flight times, assuming a speed of 78 km h^{-1} (Bradstreet and Brown 1985). Distances within 200 m were also confirmed with reference to fishing buoys, whose positions had been measured with a rangefinder. For departing birds which flew further than 800 m, I allocated the direction in which the bird was last seen flying to 1 of 6 45° sectors covering the 270° visible horizon. Additional observations of the flight orientations were made from the base of the cliff below the focal colony and from a boat positioned 150 and 600 m offshore.

Murres commuting to and from the large Green Island colony were observed from the southeastern point of Gull Island. The altitude of flying birds was estimated, and recorded as low (within 2 m of the sea), medium (2-15 m) or high (>15 m). Arrivals of flocks (birds flying on the same course within 10 m of each other) were observed to determine the distance at which birds began to leave flocks and where the flocks were no longer recognizable amid the murres circling the colony. Flocks of 4 or more birds approaching at right angles to the observation point were selected at random when 500-600 m off Green Island. They were tracked with a 20× telescope, fitted with an eyepiece pointer and a goniometer for measuring horizontal angles. Angles, measured with 0.5° precision, were converted to linear distances with a precision of 17 m. Some additional imprecision in estimating distances resulted from flight paths which were not exactly perpendicular to the observer's line of sight.

RESULTS

Behavior at the Ledges

Murres at the ledges did not orientate themselves for optimal observation of incoming or departing conspecifics. The breasts of brooding and incubating murres always faced the cliff, and their beaks faced seaward only 11% of the time (319 scans of 15 nest sites on 23-26 June 1985). Off-duty adults, relieved of brooding, remained on the ledges for a mean of 11.4 min (SD = 20 min, range <1-179 min, N = 169, data from 1984 and 1985 pooled), with their breasts facing seaward 2% of the time and their beaks 25% (469 scans averaging 31 birds, 11-16 July 1985). Although they faced seaward more often than incubating or brooding birds, this did not occur more often than expected by chance (25%).

Many of the murres frequenting the ledges were not constrained by breeding activities and frequently flew from one part of the colony to another, creating a swarm of circling birds near the ledges. In a sample of 803 arrivals, 21% were by marked breeding adults, 12% by failed breeders or adults whose chicks had fledged, and 67% by unmarked birds (not breeding at the observation site and including some prospecting birds). A murre following a randomly selected departing conspecific would have little chance of ending up at a foraging site. In a sample of 100 randomly selected departures, 60% of the birds returned to the cliff after a short flight, 21% flew seaward out of sight and 14% disappeared around the island and might have landed at other cliff sites.

Departure Behavior

The distribution of inter-departure intervals of marked breeding adults differed significantly from that expected from random departures with a Poisson distribution (Fig. 1; Kolmogorov-Smirnov test, Z = 6.254, N =
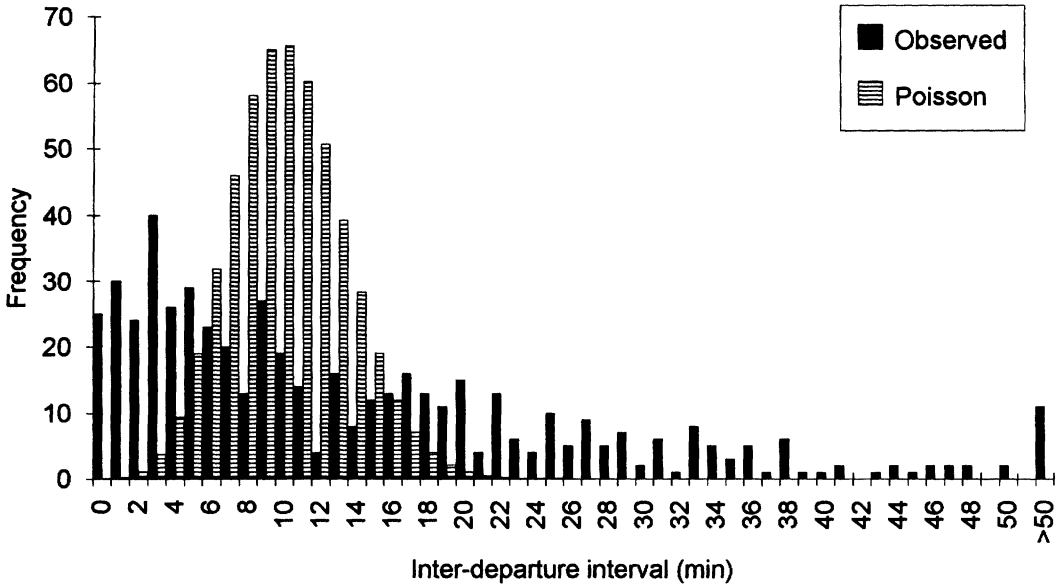
Figure 1. Frequency distribution of 525 intervals between departures of breeding adults at a sub-colony of 25 pairs of Common Murres at Gull Island, Newfoundland.

52 categories, P < 0.001). Departures were clumped, with inter-departure intervals of 5 min or less occurring more often than expected. This might be construed as departures of groups, with birds following one another out to sea, but a closer inspection of the data revealed that this was unlikely. More than 95% of the 525 inter-departure intervals exceeded 1 min, and in that time a murre would have flown more than 1 km. Hence, it is unlikely that many birds followed their neighbors to foraging grounds.

During 4 breeding seasons, 265 departure flights of marked breeders were observed, excluding instances when birds circled and returned immediately to the colony. On 105 occasions (40%), the murre flew continuously until lost from sight, usually more than 1 km from the colony (hereafter referred to as a direct departure). Only 7 of these (3% of all departures) involved birds joining conspecifics and departing as a flock. The proportion forming flocks was not significantly different when the departing bird had delivered a meal in the preceding hour (2 of 51 departures), compared to those that had not (5 of 214 departures; $\chi^2_1 = 0.40$, P > 0.05). In all other departures (60%), the murres splashed down near the colony (hereafter called a splashdown departure), and in 88% (140/160) of these cases the focal bird landed within 3 m of conspecifics already on the water. Ninety-three percent of splashdown departures ended 100–600 m from the colony.

A murre's departure behavior was influenced by its preceding activities. Direct departures occurred more frequently among murres which had delivered a meal to a chick in the preceding hour (88%, N = 51) than among murres which had not recently delivered a meal (28%, N = 214; $\chi^2_1 = 62.8$, P < 0.001). The proportion of direct departures declined with increasing time spent by the bird at the colony before leaving, whether the bird had delivered a meal or not (Fig. 2). Among adults with chicks, the type of departure had no significant effect on whether the adult returned to the colony with a meal for the chick or not: meals were delivered after 82% of 72 direct departures and 69% of 110 splashdown departures ($\chi^2_1 = 3.76$, P > 0.05).

Birds making direct departures often changed direction, usually within 600 m of the colony, and so the final orientation of direct departures was assessed for birds tracked for more than 800 m. Murres from the observation sub-colony made direct de-
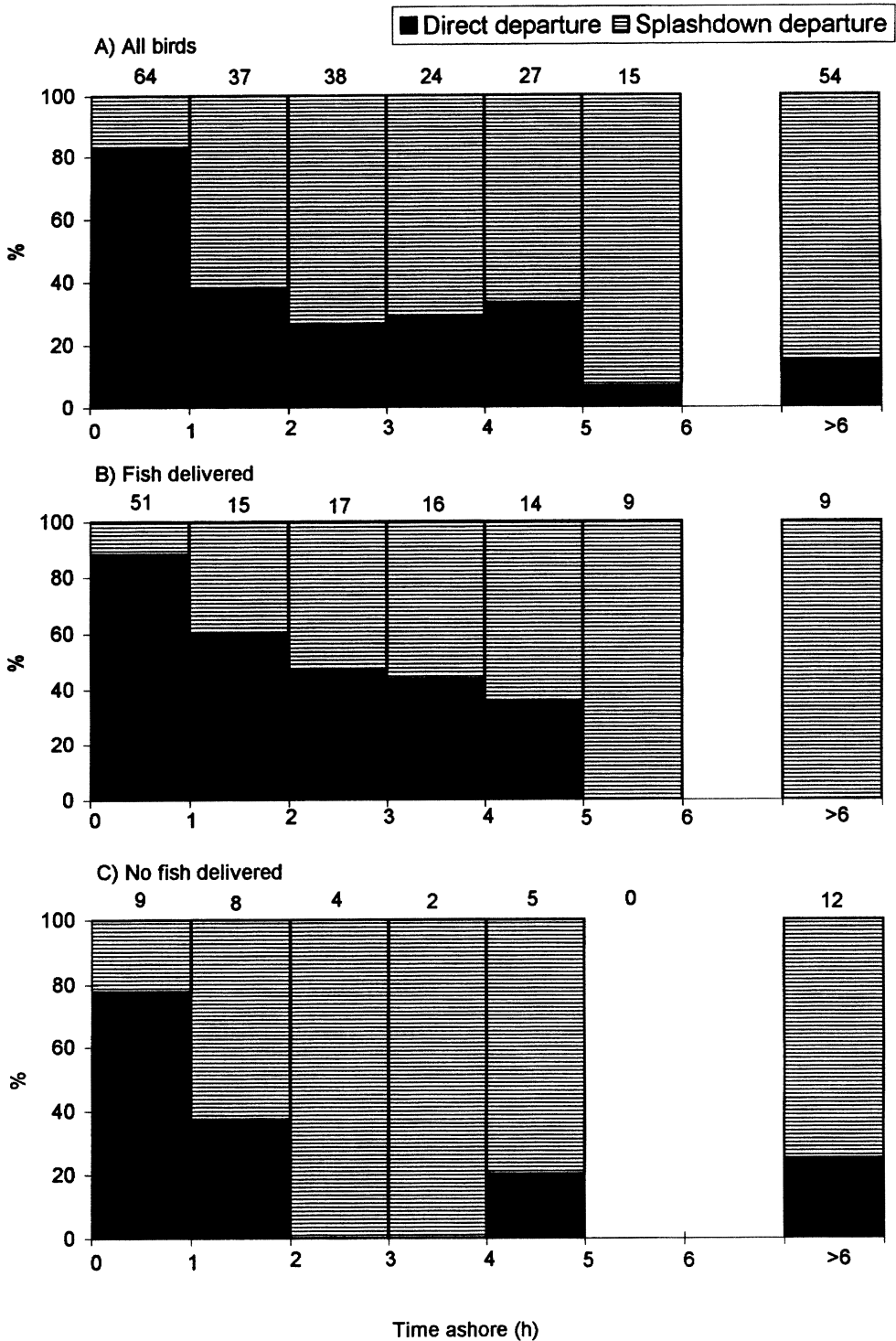
Figure 2. Changes in the departure behavior of marked breeding Common Murres after increasing periods of time ashore. Departing birds either flew directly out of sight, usually more than 1 km distant (direct departures) or splashed down on the sea near the colony (splashdown departures). Graph A includes all birds whether with or without chicks, B and C show departures by adults with chicks which had delivered a meal to a chick (B) or not delivered a meal (C) before the observed departure. Sample sizes are the numbers of departures observed.

partures in all directions, including around the island to forage near the shores of Witless Bay (birds seen flying around the island subsequently returned with prey). Marked individuals making successive departures on the same day showed a tendency to return to the same 45° sector (64% of 11 pairs of successive flights). When more than 1 day separated departures, a slightly lower proportion returned to the same sector (47% of 19 pairs of departures) but the change was not significant ($\chi^2_1 = 0.741$, P > 0.05).

Commuting Behavior

Flight patterns of murres, observed 2.0 km from their Green Island colony, differed according to the destination and windspeed. With low to moderate winds (<30 km h^{-1}) incoming murres flew higher than outgoing (Fig. 3; $\chi^2_2 = 7,350$, P < 0.001). Strong offshore winds exceeding 30 km h^{-1} caused a change in flight patterns; the incoming birds flying into the wind tended to be much lower, near the sea surface, than in calmer conditions, while some outgoing birds flew higher, possibly to take advantage of tail winds or avoid the incoming birds (Fig. 3). Outgoing birds flew alone or in small flocks, but incoming birds were usually in large flocks (Fig. 4; Kolmogorov-Smirnov test, P < 0.001).

Murres began to leave flocks of 4 or more incoming birds when they were within 500-600 m of Green Island, and nearly all incoming flocks were unrecognizable by the time the birds reached the colony (Fig. 5). Incoming flocks were clearly comprised of birds from many parts of the colony, indicating that near-neighbors did not usually travel in the same flocks. A dense swarm of incoming, departing and circling murres surrounded Green Island, usually extending 100-150 m out to sea, obscuring the orientation of incoming flocks (Fig. 5). A murre at the colony would not readily be able to assess the orientation of incoming murres carrying prey.

Observations made beneath the much smaller colony at Gull Island indicated that here too, many birds circled above the base of the cliff within 100 m of the shore, but none 600 m offshore. The flight paths of

streams of incoming murres, and birds carrying fish in their beaks, were clearly visible to observers in the boat 100-600 m offshore.

DISCUSSION

Patchy Prey and the Need for Information Exchange

There are several compelling reasons why murres breeding in Witless Bay would benefit from the exchange of information on the locality of prey patches. Both capelin (Templeman 1948, Brown and Nettleship 1984, Schneider and Methven 1988, Piatt 1990, Methven and Piatt 1991) and sand lance (Reay 1970, Winters 1983) were patchily distributed, mobile fish whose densities, depths and horizontal distributions were affected by diurnal cycles, tides, sea temperature and winds. Capelin were often common within Witless Bay and off the adjacent coast, but their schools were seldom predictably located within this large area (Piatt 1990, Schneider et al. 1990, Methven and Piatt 1991). Furthermore, murres aggregated at large schools of capelin, ignoring the many smaller schools (Piatt 1990). The prey resources available to the murres during this study were adequate for successful breeding (Burger and Piatt 1990).

The murres often travelled long distances to feeding grounds. Foraging trips preceding prey deliveries at Gull Island were typically 90 minutes or more (Burger and Piatt 1990), and had a potential range up to 200 km (Cairns 1990). Aggregations of murres occurred many km from the colony and in 1985 a major aggregation was 70 km from Witless Bay (Schneider et al. 1990). Relocating profitable prey schools in such vast areas of ocean after a visit to the colony would be difficult if the bird relied only on memory and cues available at the foraging site, especially if the school was moving.

Common Murres typically spent long periods at the colony. Incubation, daytime brooding and overnight brooding shifts measured by Verspoor et al. (1987) averaged 17 h (range 1-38 h), 4h (1-14 h), and 12 h (7-20 h), respectively. During the time ashore the vertical and
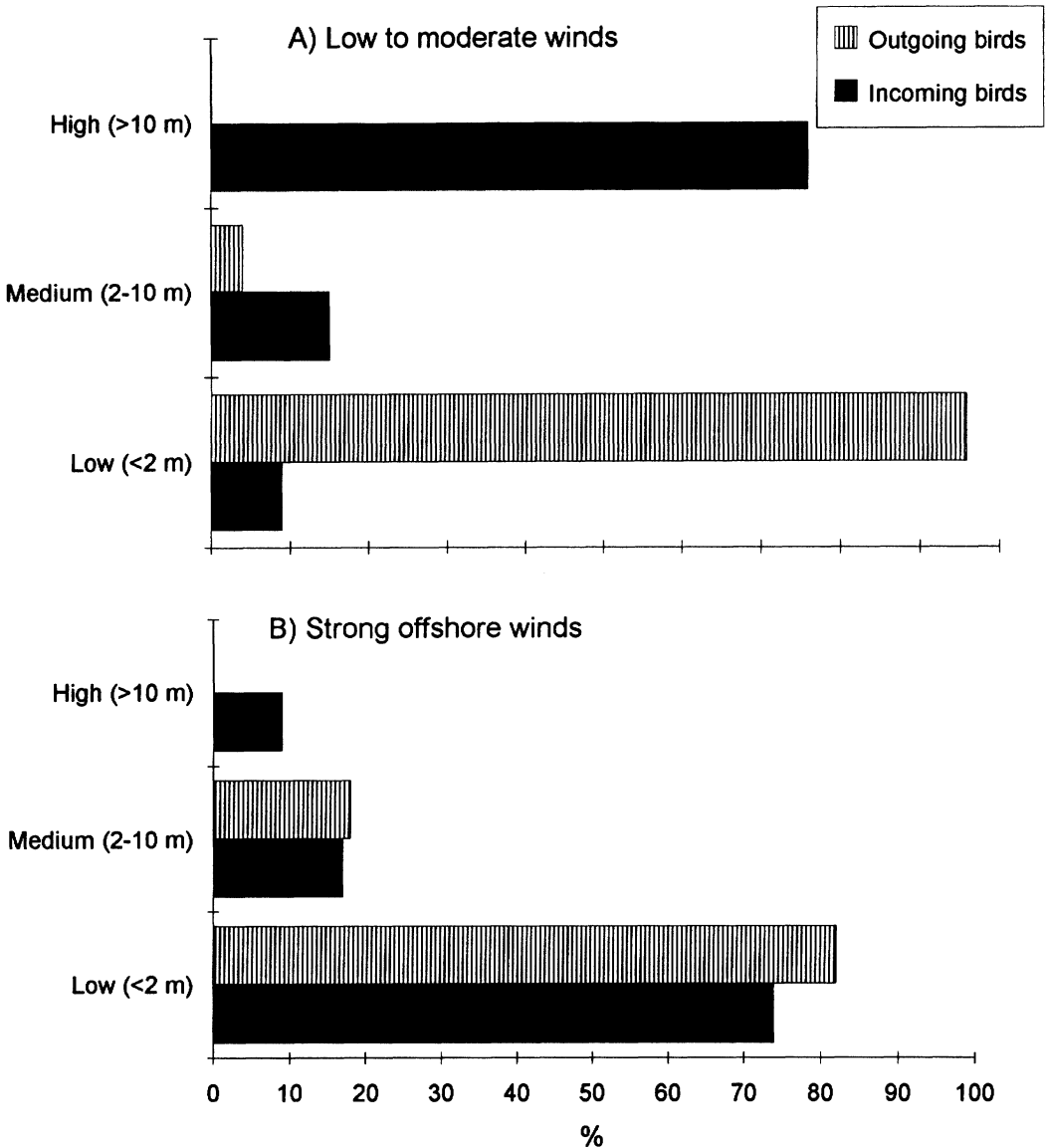
Figure 3. Estimated altitudes of incoming and outgoing Common Murres observed 2 km from the Green Island colony. Graph A shows behavior when winds were low to moderate (<30 km h⁻¹) and B when offshore winds, facing the incoming birds, exceeded 30 km h⁻¹. Sample sizes were 7,041 and 3,271 incoming and outgoing birds, respectively in graph A, and 2,844 and 898, respectively, in graph B.

horizontal distribution of prey would be likely to change, and birds would be unlikely to re-encounter previously exploited schools.

Memory of the location of previously exploited patches could be used for repeated forays, and this appeared to be a short-term strategy used by murres at Gull Island. Birds leaving the colony within an hour of delivering a meal usually flew directly out to sea and in 82% of direct departures, the bird re-turned with another chick meal. Marked individuals followed the same bearing in 64% of successive direct departures on the same day and 47% of departures separated by more than one day, suggesting that they were visiting widely dispersed patches. Radio-tagged Common Murres studied by Wanless et al. (1990) showed similar widely dispersed foraging efforts. Repeated visits to prey patches would be beneficial only as long as
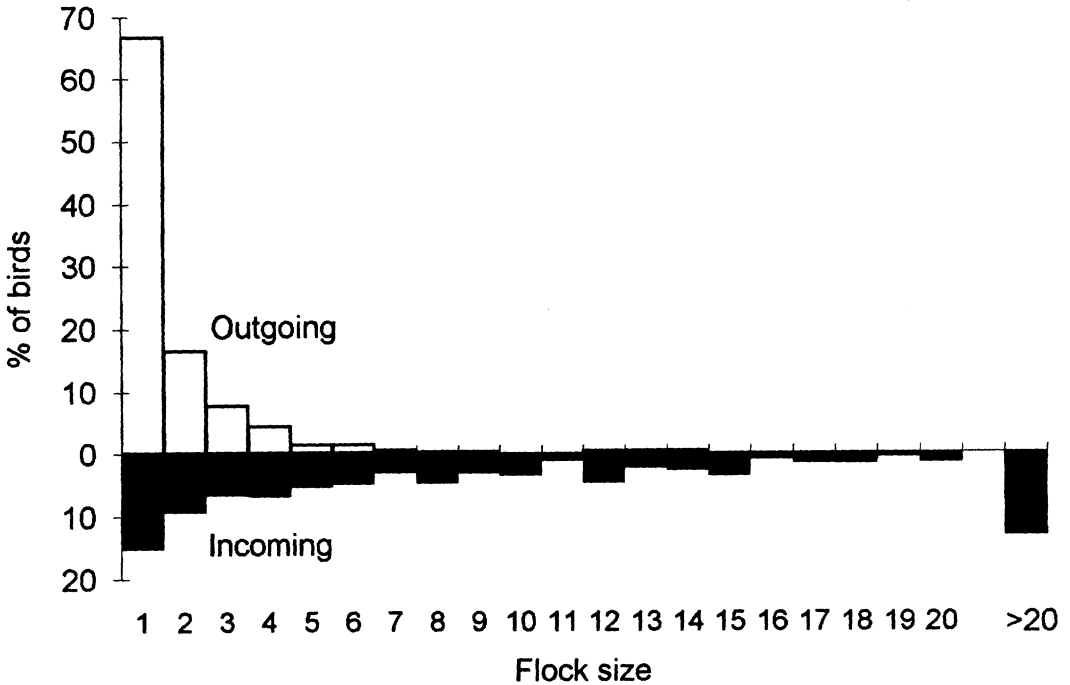
Figure 4. Flock sizes recorded for 9,885 outgoing and 4,169 incoming Common Murres observed 2 km from Green Island. The data are plotted as percentage distributions of birds rather than flocks to avoid underestimating the numbers of birds in large flocks.

the patch remained profitable and relatively stationary (Waltz 1982), and reliance on memory to locate patches would not be a successful strategy for murres over periods of more than a few hours.

As an alternative to getting information at colonies, outbound murres could locate food by joining conspicuous feeding flocks, i.e., by local enhancement (Ward and Zahavi 1973). Murres do this in Witless Bay (Piatt 1990) and elsewhere (Hoffman et al. 1981, Porter and Sealy 1982). Many foraging aggregations were, however, tens of km from the colonies (Schneider et al. 1990), suggesting that birds relying on local enhancement alone would spend considerable flight time searching for feeding flocks. Information obtained at or near the colony would decrease energetically expensive search time.

Lack of Evidence for Information Exchange at Nest Sites

The most commonly proposed mechanism whereby information is exchanged at colonies or roosts is when naïve or unsuc-

cessful birds follow successful birds returning to the foraging patch (Ward and Zahavi 1973, Wittenberger and Hunt 1985, Brown 1986). This did not occur at the Witless Bay murre colonies. Breeding adults were joined by conspecifics in only 3% of direct outbound flights, and there was no evidence that murres which had recently delivered a fish were joined more frequently than those that had not. In most cases, the departing flocks formed over the ocean more than 100 m from the colony and did not involve near-neighbors. Murres leaving the very large Green Island colony tended to fly singly or in small groups even after 2 km of flight. The hypothetical benefits of following randomly selected conspecifics (Waltz 1982) also could not apply at nest sites, since very few departing murres, randomly selected, flew directly to foraging areas. Most returned immediately to the ledges.

Birkhead (1976) and Ashcroft (1976), working at Skomer Island, Wales, found that Common Murres and Atlantic Puffins (Fratercula arctica), respectively, did not leave the

FIRST BIRD LEAVES THE FLOCK

FINAL BREAKUP OF FLOCK

OUTER EDGE OF CIRCLING BIRDS

GREEN I.

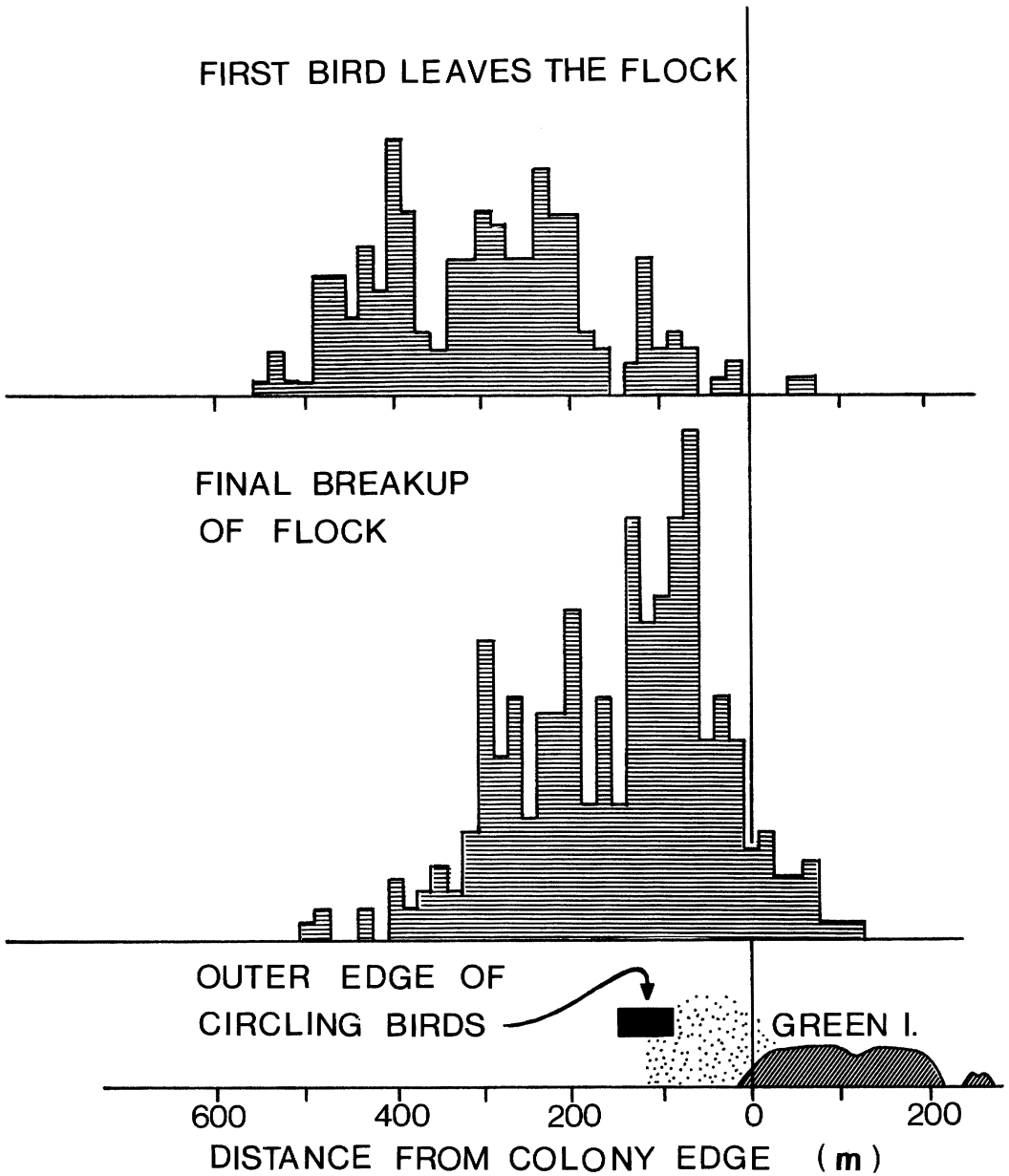| 600 | 400 | 200 | 0 | 200 |

DISTANCE FROM COLONY EDGE (m)

Figure 5. Breakup of 375 incoming flocks of 4 or more Common Murres approaching Green Island, showing the distribution of points at which the first bird left the flock and at which the flock was no longer recognizable (final breakup). The range of measurements of the outer edge of the dense circling swarm of murres around the colony is also shown. All distances were estimated by converting angles measured with a goniometer mounted on a spotting scope into linear distances at 2 km range. Observations were made on 10 days in 1985.

colonies randomly, but often departed in small groups. Birkhead (1985) cited this as circumstantial evidence that information exchange occurred at these colonies. There was, however, no information on which birds were leaders and which followers, or whether birds which left together stayed together until

they reached food patches. Grouped departures of seabirds can occur even where there is no evidence of information exchange (Andersson et al. 1981). Departures of murres from Gull Island were clumped, but this occurred at time scales (>1 min) which precluded following behavior, and the probable

cause was either environmental (e.g., tides Slater 1977) or linked to daily peaks in foraging effort (Burger and Piatt 1990).

An alternative to following behavior occurs in situations where birds at the colony can identify successful foragers and the direction from which they approach the colony (Greene 1987). This mechanism does not seem to apply to murres at nest sites, because they could not accurately assess the direction from which successful neighbors were coming. Incoming flocks tended to disperse when >100 m from the ledges, and there was usually a confusing swarm of circling, departing and incoming birds flying close to the nests sites. Most incoming birds altered their trajectories as they approached their nest ledges. Flight paths at sea were also altered in response to strong winds and the need to round points of land. Many birds landing on the ledges during the chick-rearing period were not active breeders and gave no indication of successful foraging. In short, the colony and the surrounding area within 100 m had a high noise:information ratio. The orientation and behavior of murres on the ledges suggested that they paid little attention to the arrivals and departures of conspecifics. Both on-duty and off-duty birds focused most of their attention on themselves (i.e., preening), their mate, chick, egg or near neighbors, and spent little time looking seaward.

The "Information-Halo" Hypothesis

A murre on the ocean near the colony would be able to detect the bearing of incoming conspecifics much more clearly than at the colony itself. During the chick-rearing period, when demands for food are greatest (Cairns et al. 1990), they could also readily assess the numbers of incoming birds carrying fish in their beaks. Two critical requirements for information exchange, the identity of successful individuals and the direction from which they approached (Greene 1987) would, therefore, be readily visible. Extending Gaston and Nettleship's (1981) idea, I propose that the area surrounding the colony, away from the swarm of circling birds, acts as an information halo.

My data provided only indirect evidence that the murres used this information to improve their foraging efficiency. Many successful foraging trips began with a stop-over in this area, and murres with chicks brought back meals after 69% of splashdown departures. The majority of these birds were not getting this prey within the 100-600 m zone: birds holding fish and those making prolonged dives typical of foraging (Bradstreet and Brown 1985) were rarely seen in this zone during the 4 years of observations. Most birds were preening, bathing or resting, and many left to forage elsewhere.

Birds that had been on the ledges for the longest time, i.e., those that would have the least information on where food patches were located, were the most likely to land in this zone rather than make direct departures to foraging areas. An alternative explanation is that murres which had made prolonged visits to the colony had an increasing need to bathe. Many had plumage soiled by feces after several hours at the nesting ledges, and bathing was common after splashdown departures. The requirement for bathing, however, need not exclude the requirement for information.

Outgoing murres could continue to monitor the direction of incoming flocks even after they left the area near the colony (Gaston and Nettleship 1981). Unless constrained by strong headwinds, incoming birds flew high, probably to facilitate navigation using landmarks, and were clearly visible to the low-flying outgoing birds. Strong winds, by forcing incoming flocks to fly low, might therefore reduce the effectiveness of in-flight information exchange, in addition to distorting the flight trajectories between colony and prey patch. An outgoing bird's ability to see and compare diverging paths of murres flying from widely scattered prey patches would rapidly diminish as it left the area near the colony. The optimal location for assessing incoming flight paths would be close to the colony, just beyond the circling swarm where incoming flocks break up. At the Witless Bay murre colonies this appeared to be 100-600 m offshore.

Others have recognized that areas located near colonies or roosts of gulls (Evans

and Welham 1985), geese (Ydenberg *et al.* 1983) and puffins (Ward and Zahavi 1973) might serve as information centers, even if the colony or roost did not. In some cases swallows circle around colonies before joining successful foragers (Brown 1988). Gaston and Nettleship (1981) noted that poor visibility, distant foraging sites and frequent changes in food patches made information exchange highly desirable in Thick-billed Murres at Prince Leopold Island, but this exchange did not appear to occur at the nest sites. Many outgoing birds splashed down within sight of the colony when initiating foraging trips, and low-flying outgoing murres oriented themselves with streams of high flying incoming murres. Outgoing birds often changed direction but incoming ones seldom did. Gaston and Nettleship (1981) noted that humans have long used streams of birds to navigate in foggy areas and birds were likely to do the same.

In studies of colonial birds, the ICH has attracted considerable attention, but not consistent support. Many field studies (e.g., Krebs 1974; Evans 1982; Brown 1986, 1988; Waltz 1987) and reviews (Bayer 1982, Wittenberger and Hunt 1985, Waltz 1982) focused primarily on following behavior, but this is not the only mechanism, and might not even be the dominant mechanism, whereby information exchange occurs. Some colonial birds learn about the availability, locality and type of prey just by watching incoming conspecifics (Greene 1987). A more flexible approach to possible mechanisms of information exchange might reveal additional processes, such as the presence of information halos proposed here. Exchange of information near the colony or while flying is most likely in species which carry prey visibly (e.g., alcids and raptors), but many other colonial species might benefit from information on the flight bearings of incoming flocks.

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