FORAGING-FLOCK RECRUITMENT AT A BLACK-BILLED GULL COLONY: IMPLICATIONS FOR THE INFORMATION CENTER HYPOTHESIS

ROGER M. EVANS

Department of Zoology, University of Manitoba, Winnipeg, Manitoba, Canada R3T 2N2

ABSTRACT.—The extent to which a flock leader advertises its departure from a colony and recruits flock mates is an important issue of the Information Center hypothesis. At a colony of Black-billed Gulls (*Larus bulleri*), I found that attractive calls were given by some leaders, that leaders called more often than followers, and that calling leaders recruited followers more often than silent leaders. Playback experiments demonstrated that these "contact" calls were attractive. The results indicate that some benefits, most likely related to group foraging, result from flock membership when the gulls are away from the colony. Benefits of group foraging away from the colony provide a more likely mechanism for explaining food-related selection pressures favoring a colonial foraging system than do the presumed benefits derived from the more complex, information-transfer mechanism envisaged by the Information Center hypothesis. *Received 11 December 1980, accepted 1 July 1981.*

ACCORDING to the Information Center hypothesis described by Ward and Zahavi (1973), certain avian assemblages, such as communal roosts and breeding colonies, evolved primarily because they function as information centers where birds that have been unsuccessful in locating a good food patch can benefit by following other, more successful birds to the latters' food. The hypothesis is considered to apply mainly to birds that utilize food distributed in unpredictable but temporarily rich patches. Data consistent with the Information Center hypothesis have been obtained in studies of the Red-billed Dioch [Quelea] (*Quelea quelea*) (Ward 1965), the Great Blue Heron (*Ardea herodias*) (Krebs 1974, 1978), and the Bank Swallow (*Riparia riparia*) (Emlen and Demong 1975).

The central concept of the Information Center hypothesis involves *information transfer* between or among birds at the roost or colony. Of particular relevance are signals whereby a potential leader might identify itself to followers. Although information transfer of the sort envisaged by the Information Center hypothesis could occur in the absence of specialized signals devoted to that function (Bertram 1978, Waltz in press), the extent to which a leader advertises its departure remains highly relevant to the hypothesis (Ward and Zahavi 1973). In this report, I examine some of the contexts and evolutionary implications of information transfer as it pertains to signals that could function as a means of flock recruitment at a colony and describe observations and experiments designed to assess the occurrence and probable function of these signals in Black-billed Gulls (*Larus bulleri*).

Black-billed Gulls nest in dense inland colonies in New Zealand (Stead 1932, Beer 1966, Evans 1970). They typically forage in flocks and utilize unpredictable but often temporarily rich food patches. Food items include fish, as well as worms and other small invertebrates that are exposed on open pasture land after rains or turned up on fields by farm implements (Dawson 1958, pers. obs.).

SOME CONTEXTS FOR INFORMATION TRANSFER AT COLONIES

Parasitic relationship.—A parasitic relationship would arise if followers that did not know where food was ("ignorant" birds) were able to victimize leaders that did know where food was ("knowledgeable" birds) by following them to their food patches, even though such information transfer were of no advantage to the leader (cf. Krebs 1978, Waltz in press). This situation could arise if a colony evolved and were maintained for reasons unrelated to information transfer, for example, if the colony provided protection against predators (Lack 1968). Possible costs to the leader might include those associated with leading potential competitors to the leader's food source. Even

if such costs to the leaders were negligible, it is expected that knowledgeable leaders would not be selected to expend time and/or energy in advertising their departures. The occurrence of calls or other conspicuous recruitment displays by leaders would not be predicted in a parasitic system. Attempts by leaders to slink away quietly and inconspicuously would be more likely (Bertram 1978).

Reciprocal altruism.—Information transfer could occur at a colony in a context of reciprocal altruism if a bird A leads another bird B to food on one trip, and bird B reciprocates and leads bird A to a food patch on some later trip (Krebs 1978). As pointed out by several investigators (Trivers 1971, Maynard Smith 1978, Davies and Krebs 1978, Vehrencamp 1979), however, systems based on reciprocal altruism are usually open to invasion by "cheaters." A cheater in the present situation can be defined as a bird that follows others to their food but does not lead others to any rich patches it might find itself. As in the parasitic situation, leaders in a system based on reciprocal altruism could face costs associated with leading competitors to the food supply and would not be predicted to expend time or energy in advertising their departures with calls or other recruitment displays.

Cooperation between selfish leaders and followers.—A system in which knowledgeable leaders and ignorant followers all benefit is a third context in which information transfer at colonies could occur. This situation could arise whenever leaders would benefit directly from the company of flock members away from the colony site, for example, if flocking en route to the foraging grounds or while foraging were beneficial as an antipredator adaptation (Bertram 1978), or if group foraging were beneficial (Rand 1954, Fisher 1958). When these away-from-colony benefits of flocking occur, leaders and followers should all benefit by leaving in a flock. If leaving as a member of a flock is beneficial, leaders should be selected to recruit followers. This prediction is opposite to that derived from the previous two situations (parasitism and reciprocal altruism).

Tests of Predictions

The main predictions derived from the above theoretical considerations deal with the extent to which a potential flock leader should be selected to render itself conspicuous or inconspicuous to others when it leaves the colony on a foraging trip. Whenever a bird flies away from a colony, its actions necessarily provide information in the form of visual cues to any observers that might be watching. Vocalizations, in contrast, need not be given and, when present, can be taken as evidence for the emission of ritualized signals subject to positive selection pressures (Smith 1977) of the sort expected from a bird selected to make itself conspicuous, but not from one that is selected to be inconspicuous. Gulls, including the Black-billed Gull, are highly vocal, and preliminary observations indicated that loud calls are sometimes associated with foraging flocks. The occurrence of calls and their function when emitted were used to test the above predictions.

Some foragers call when leaving the colony.—Black-billed Gulls departing from breeding colonies and roosts commonly emitted loud calls as they left. Similar calls were heard from flocks en route to or from a feeding site and again upon arrival at a roost, colony, or foraging site. Calling was also common in flocks flying over the river prior to colony establishment (see Beer 1966 for similar observations). In all of these contexts, the loud, single-note calls appeared to function as "contact" calls (Smith 1977), broadcasting the current location of the caller to others in the vicinity.

These observations suffice to demonstrate that at least some foragers call as they leave a colony. The mere existence of loud calls, however, does not necessarily prove that they function to attract and recruit others into a departing foraging flock. Three sets of data relevant to the possible functional role of these loud contact calls in recruiting flock mates were obtained at a large breeding colony on the Ashley River, as outlined below.

Leaders call more than followers.—Black-billed Gulls leaving a colony to obtain food normally depart in long, straggling flocks that commonly coalesce into more dense units as they move away. Intervals between flocks range from several seconds to several minutes and are usually sufficient to permit a clear distinction between successive flocks. In these studies, I used only flocks that could be distinguished as separate units. By sitting in a blind at the edge of the colony directly under the currently prevailing flight path taken by departing foragers, I could

record the number of instances in which flock leaders did or did not emit loud calls as they passed by within hearing range. The same data were then obtained for subsequent members of the departing flock (followers). Of 163 flock leaders, 65 (40%) emitted calls as they departed, while only 75 (17%) of a total of 443 followers called ($\chi^2 = 33.5$, $P < 0.0001$).

Leaders that call gain followers more often.—As indicated above, not all leaders called. I made use of this fact to test the hypothesis that those leaders that did call gained followers more often than those that did not. Of the 65 leaders that called, 51 (78%) gained recruits. Only 40 (41%) of the 98 that did not call gained recruits ($\chi^2 = 20.96$, $P < 0.001$).

Contact calls are attractive.—The results described above suggest that contact calls emitted by leaders function to recruit followers. To test this hypothesis further, I recorded a series of contact calls by birds departing from a colony and then played them back at a different colony. A Uher 4000 Report tape recorder, augmented for playback with a 12-V amplifier and an external, remotely placed 8-ohm speaker, was used. For the playback experiments, I placed the loudspeaker approximately 50 m from the colony, in a direction away from that being used by most departing foragers at that time. I then noted the number of birds that flew over toward the loudspeaker during a series of 10 2-min playback intervals and compared this with the number that flew in the same direction in the immediately preceding 2-min periods. An average of 3.3 birds per 2 min flew toward the speaker during the playback periods, compared with 0.8 birds per 2 min during the immediately preceding, silent, control periods ($T = 2.5$, $P < 0.01$, Wilcoxon matched pairs test). These results do not provide evidence that the contact calls tested are necessarily more or less effective than other calls or displays of Black-billed Gulls, but they do provide evidence that the calls given by departing foragers are attractive to others and, hence, could act to recruit flock mates.

DISCUSSION

The main finding of this study was that when flocks of Black-billed Gulls leave a colony, the first bird out (defined as the leader) often advertises its departure by emitting loud calls that attract and recruit other foragers (followers) into the flock. This result is entirely consistent with the interpretation that flock leaders derive some average benefit from having others with them when they leave the colony, because it presumably would be very easy for them to forego calling if recruiting others were not advantageous. The results provide no support for the alternative possibilities that followers were parasitizing leaders that were at the colony for some other adaptive reason or were participating in a system maintained solely by reciprocal altruism.

It remains possible that a mixture of parasitism, reciprocal altruism, and selfish cooperation occurred at the colonies. For example, colonies may confer some antipredator or other as yet unidentified benefits, which could favor a degree of parasitic following of knowledgeable leaders. This could still be compatible with the emission of loud calls by leaders if the benefits of leaving in flocks were sufficient to more than offset any costs to leaders that might otherwise derive from being parasitically followed. Benefits from flocking could also presumably maintain a degree of reciprocation between leaders and followers, because the leaders on any one day could be followers another day. The results are thus entirely compatible with a mixture of these three evolutionary strategies, but only if the benefits of flocking away from the colony are sufficient to more than offset potential costs of calling and leading, thereby maintaining the evolutionary stability of the system.

Although the results suggest that flock leaders obtained some benefit from flocking away from the colony, they do not permit a distinction between different types of potential benefits, for example those derived from protection from predators while foraging or those derived from more effective group foraging apart from predator effects. Consideration of potential predator pressures and the foraging methods of Black-billed Gulls are required to assess the relative merits of these two potential benefits of flocking.

Defense from predators could be a relevant advantage of flocking in Black-billed Gulls, but such an interpretation is weakened appreciably by the historical lack of large mammalian or other quadruped predators in New Zealand (reviewed in Beer 1966). Large avian predators are also rare (Falla et al. 1970). The predator defense hypothesis is also weakened for Black-

bills because of their reduced levels of mobbing or other antipredator behavior compared with their northern hemisphere relatives (Beer 1966, pers. obs.). Benefit in the form of protection from predators cannot be ruled out but remains highly unconvincing for Black-billed Gulls.

Benefits from group foraging are a more plausible form of away-from-colony benefit for Black-billed Gulls. Elsewhere (Evans in prep), I describe instances where Black-billed Gulls locate current food sites by cueing in on other foragers ("local enhancement," Thorpe 1963). Local enhancement as a mechanism for food finding is well documented and of widespread occurrence in gulls and other large, conspicuous birds (Rand 1954; Sealy 1973; Scott 1973; Krebs 1974, 1978; Kushlan 1977; Porter 1981). Instances in which foraging flocks landed selectively among birds already at a foraging site were observed repeatedly on the study area. Local enhancement also occurred among flock members already at terrestrial sites and in flocks foraging over water (see Stead 1932, for further documentation of local enhancement in Black-billed Gulls). Group foraging could also be a benefit when it results in a more efficient search of a localized area (Cody 1974). Other possible on-site benefits of group foraging have been identified in birds (Rand 1954), but I was unable to detect any evidence of their occurrence in Black-billed Gulls.

Mixed vocal strategies.—Although the interpretation that selfish leaders and followers all benefit from group foraging away from the colony site appears to provide the best explanation for the presence of loud calls given by flock leaders at Black-billed Gull colonies, it is not immediately evident from the predictions and observations considered thus far why flock leaders should have exhibited a mixed vocal strategy, in which some called and others did not. Because fewer than half of the flock leaders actually called, evidently some complicating factor was acting. A simple, unmixed strategy whereby all leaders benefit from recruiting others into the flock predicts the occurrence of calls in virtually all cases.

One possible explanation for the mixed-calling strategy of leaders that has relevance for the Information Center hypothesis is that calling was dependent upon foraging success. If leaders that were successful on their most recent foraging trip called and unsuccessful birds did not, a powerful mechanism would exist for identifying the most successful birds. This asymmetry fits well with what one would expect from the leaders, because they are assumed to benefit by calling to recruit others into their flocks for purposes of group foraging away from the colony. This interpretation fails, however, to account adequately for the behavior of the silent leaders that are presumed not to know where food is located. These presumed ignorant leaders are the very birds that are expected to gain the most from group search for a new food patch or from other benefits of group foraging; hence, they should be even more strongly selected than the knowledgeable birds to emit calls or other conspicuous recruitment signals when they initiate a departure from the colony. The interpretation that knowledgeable leaders call while ignorant leaders do not is thus not a viable explanation for a mixed-calling strategy by leaders.

An alternative explanation for a mixed-calling strategy by leaders is the reverse of the above scenerio. Because birds that do not know where a current food patch is located should benefit the most by recruiting others into a departing flock, ignorant leaders might be more likely to call. Knowledgeable leaders, who already know where food is, might leave quietly. This interpretation, like the preceding one, provides a mechanism whereby knowledgeable and ignorant leaders could be readily distinguished. In this case, selective following of silent flock leaders would be favored by recruits requiring information about current food locations. This interpretation fails, however, because selective following of silent leaders is directly contradicted by the data, which show that vocal leaders were followed selectively.

What emerges from the above two scenarios is the conclusion that the only evolutionarily stable strategy (ESS) is for ignorant flock leaders to do exactly what knowledgeable flock leaders do, i.e. they should call with equal frequency when they leave the colony. If ignorant leaders call less than knowledgeable leaders, they will suffer a potential cost as a result of having fewer recruits with them for group foraging. If ignorant leaders call more frequently than knowledgeable leaders, they immediately set up a situation in which the following of silent birds is favored, and, again, the ignorant flock leaders will obtain fewer recruits than

they would if they called at the same rate as knowledgeable leaders. Thus, differential rates of calling by knowledgeable and ignorant flock leaders is not an ESS and is not a viable explanation for the observed mixed-calling strategy.

A definitive explanation for the mixed-calling strategy of flock leaders may not be possible from existing data. The following explanation is offered as one possible hypothesis. My interpretation is that the rate of calling upon leaving a colony or other assemblage will depend on the amount of calling immediately preceding the time of departure of the bird in question. Considered functionally, such a negative-feedback system would mean that a bird departing the colony soon after other calling birds had departed would be more likely to encounter flock mates en route to or at a foraging site than would a bird that left some time after others had gone. The latter bird is less likely to encounter previously departed birds and would, on average, gain relatively more by recruiting a flock of its own. It would therefore be more strongly selected to call. The same interpretation would predict that recruits call less frequently, on average, than do flock leaders. Recruits into a flock are most certain of having others with them to forage and are also most likely to have been exposed very recently to calls by the leader. The fact that recruits did call less than flock leaders thus provides some support for this interpretation. Nothing in this hypothesis prohibits variations in absolute calling frequency. For example, if food were very difficult to find, the absolute level of calling might well go up, but a differential in calling rates between different individuals, dependent on the amount of calling to which they were exposed in some preceding time interval, could still occur. Circumstantial evidence that absolute calling rates may vary was provided by observations at one colony that was abandoned soon after nest initiation. Calling was virtually incessant as birds wheeled about over the colony prior to abandonment, and an inspection of the region for several kilometers adjacent to the colony failed to reveal any evidence of foraging gulls. This interpretation is thus consistent with existing data for Black-billed Gulls but requires further testing.

Selection pressures for colonial nesting.—Several ecological conditions that could select for nesting in colonies have been advanced (Mock 1980). Protection from predators at the colony site may be one important condition for some species (Lack 1968). In Black-billed Gulls, the predator-protection hypothesis is not convincing due to a paucity of potential predators (see above, Beer 1966). As discussed above, the occurrence of calls by flock leaders is also contrary to expectation if Black-billed Gull colonies exist primarily for protection from predators at the colony site.

The Information Center hypothesis itself constitutes another potential explanation for the evolution or maintenance of roosts or colonies (Ward and Zahavi 1973, Krebs 1978). According to this hypothesis, benefits derived from information transfer at the colony are adequate to account for the occurrence of such an assemblage. For this interpretation to be considered valid, other primary benefits at or away from the colony must be excluded as major evolutionary pressures involved in the evolution or maintenance of colonies. Some form of reciprocal altruism or a colony based on assistance to kin (e.g. Waltz in press) seems essential if information transfer at the colony is to be the primary evolutionary explanation for colonies. As discussed above, a system based on reciprocal altruism seems entirely inadequate, because it is open to cheaters and hence is not an ESS (see Waltz in press, for similar conclusions). That kin selection is a viable mechanism whereby information transfer of the sort envisaged by the Information Center hypothesis could select for colonies is a definite possibility but must remain in doubt until evidence for selective following of kin is obtained.

Colonies as assembly points for group foraging.—The results of this study suggest that a much simpler mechanism for the transfer of information about current food supplies could be involved in the evolution or maintenance of colonies than that required by the Information Center hypothesis. The finding that the pattern of calling by flock leaders at Black-billed Gull colonies is best interpreted as indicating that all flock members, leaders and followers alike, benefit from leaving in a flock suggests the simple alternative that colonies of this species function as assembly points where dispersed foragers can reunite for purposes of subsequent group feeding activities. Because the very nature of efficient search for patchy and unpredictable food clumps necessitates a degree of dispersal over the habitat, foragers

run the risk of becoming more and more widely dispersed as they move about searching for good food patches. To ensure that excessive dispersal does not occur (i.e. to maintain a population sufficiently large to ensure maximum net benefits of group foraging), I suggest that the periodic return of dispersed foragers to a central assembly point can be favored and, hence, can provide a selection pressure favoring the evolution or maintenance of roosts or colonies. In Black-billed Gulls, locating food patches by cueing in on others (local enhancement) seems to be a particularly likely benefit derived from flock foraging (see above). Significantly, local enhancement has also been noted in the same species for which the concept of Information Centers has been invoked (e.g. Ward 1965; Ward and Zahavi 1973; Krebs 1974, 1978).

It should be emphasized that the hypothesis that colonies could have evolved or are maintained as assembly points for subsequent group foraging does not preclude the occurrence of information transfer at the colony. The present interpretation offers an alternative way in which food-related benefits could select for colonies. Once formed, colonies could be exploited for information transfer in a manner consistent with the Information Center hypothesis. This interpretation means that information transfer at colonies, if it occurs (and that remains to be proven), is at most a secondary influence on the evolution of colony-based foraging systems such as that exhibited by Black-billed Gulls (cf. Wittenberger 1981).

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