HOW IMPORTANT ARE BIRD COLONIES AS INFORMATION CENTERS?

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ABSTRACT.—Proponents of the Information Center hypothesis suggest that colonially breeding birds learn the location of good feeding sites by following successful birds from a colony, that such information exchange was critical to the evolution of coloniality, and that colonies acting as Information Centers are important for birds in all colonial taxa. The evidence supporting this hypothesis, however, is indirect and could result from behaviors other than information exchange. Further, information exchange may not be as important as other mechanisms whereby birds may more effectively exploit their food resources by nesting colonially. *Received 20 March 1981, accepted 31 August 1981.*

NOTING that some Quelea (*Quelea quelea*) followed more "purposeful" birds from a communal roost, Ward (1965) hypothesized that followers had foraged unsuccessfully and that they now followed successful (i.e. the more "purposeful") birds from a roost to good feeding sites. Subsequently, Ward and Zahavi (1973) expanded this Information Center hypothesis to include colonies of breeding birds and considered such information exchange[1] to be important in the evolution of coloniality.

The purpose of this paper is not to disprove the Information Center hypothesis, but to question its supportive evidence and universal importance among colonial birds. Therefore, I first discuss several methods by which birds may locate good feeding sites and then analyze the evidence for intraspecific information exchange, intra- and intercolony variability in intraspecific information exchange, and interspecific information exchange. Finally, I examine the possibility that information exchange was important in the evolution of coloniality, and consider the restricted situations where information exchange could be useful.

MECHANISMS FOR LOCATING FEEDING SITES

All sites.—Some colonial birds may need to locate new feeding sites infrequently because they have feeding territories (e.g. waterfowl, Palmer 1976; Great Blue Herons [*Ardea herodias*], Bayer 1978; terns, McNicholl 1979, Taylor 1979), or they generally may return to predictably available sites. Such sites include rip tide lines (Hoffman et al. 1981), water convergences or divergences (Brown 1980), tidally available areas (e.g. see Bayer 1978), or ice fronts (Brown 1980).

Probably most colonial birds, however, need to locate new feeding sites often because old sites become depleted or unavailable. These birds can discover feeding sites through independent hunting or through four types of socially facilitated searching.

The first socially facilitated type involves birds at a colony or other areas cueing to feeding flocks. A feeding flock signals a good feeding site where food is available; otherwise, the feeding flock would either disperse or become a resting or foraging flock (Gould 1974, Hoffman et al. 1981). Cueing to feeding flocks is known among seabirds (Sealy 1973, Baird and Moe 1978, Hoffman et al. 1981), ardeids (Krebs 1974, Kushlan 1977, Caldwell 1981), and Phainopeplas (*Phainopepla nitens*) (Walsberg 1977). Second, birds at foraging areas, roosts, or a colony can cue to the direction in which birds are flying either en masse (Hoffman et al. 1981) or "purposefully" (Simmons 1972). Another socially facilitated type occurs at roosts or a colony, where birds can cue to the direction from which other birds are returning to the colony (see Ward and Zahavi 1973). Fourth, birds can follow other birds from roosts or a colony to the previous feeding site of the leader(s). This is the Information Center hypothesis (see Ward and Zahavi 1973).

Thus, information exchange is only one of

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[1] Information exchange refers only to birds learning good feeding sites by using the colony as an Information Center.

several mechanisms whereby colonial birds may locate good feeding sites. There are no data, however, to determine the relative importance of each mechanism.

Ephemeral sites.—Information exchange has been suggested to be very important for locating ephemeral food (Ward and Zahavi 1973; Krebs 1974, 1978). Information exchange, however, would not be as rapid in locating ephemeral sites as the various types of cueing. This is so because the lag time between the first discovery of a site and the discovery of the site by other birds would be less for birds cueing to the finders or to birds flying to or from the site than for birds using information exchange.

For information exchange to be practical to find ephemeral feeding sites, a feeding site must last at least as long as the sum of the following: the time for the site to be located, the time spent foraging at the site, the flight time from the site to the colony, the time spent at the colony and resting areas, and the flight time from the colony back to the feeding site by the bird (now a leader). Unfortunately, there is a lack of pertinent data to establish precisely the sum of these times, or whether or not these sums commonly are longer than the duration of most ephemeral feeding sites. Only Evans (in press) has examined feeding site-colony distances and feeding site durations. The feeding sites in his study would have lasted long enough to be found through information exchange, but it is doubtful that information exchange could be used to locate ephemeral sites in all colonial taxa throughout the breeding season (see below).

Round-trip flight times may make information exchange an impractical mechanism for birds to use in finding ephemeral sites distant from the colony. Although many taxa typically feed within 6 km of the colony (e.g. in ardeids, Custer and Osborn 1978, Thompson 1978; larids, Evans in press; alcids, Cody 1973, Evans 1981; hirundinids, Emlen 1954, Snapp 1976; icterids, Horn 1968, Wiley and Wiley 1980), many seabirds may often feed 100 km or more from the colony (Ashmole and Ashmole 1967, Feare 1976, Nelson 1978). Based on flight speeds given in Meinertzhagen (1955), birds that typically feed within 6 km of the colony fly about 40 km/h and have round-trip times of less than 8 min, but birds that can fly 100 km or more from the colony could fly about 80 km/h and spend 266 min or more in a round-trip flight. Thus, ephemeral sites 100 km from the colony lasting less than 4 h could not be located through information exchange.

Depending on nesting stage, birds of some taxa may spend considerable time at the colony, and thus would not be able to return or lead others to ephemeral feeding sites. During the incubation or brooding stages, the bird returning from a good feeding site remains at the nest for a shift that may last a day or more in many seabirds (Kendeigh 1952; Palmer 1962; Ashmole and Ashmole 1967; Nelson 1975, 1978; Boersma 1976) or less than an hour in many colonial passerines (Kendeigh 1952). After the end of the brooding nest stage, parents in a few taxa (Gannets [*Morus bassanus*], Nelson 1978; some large gulls, Hunt 1972, Butler and Trivelpiece 1981, Pierotti 1981; Parasitic Jaegers [*Stercorarius parasiticus*], Andersson and Gotmark 1980) share guardian shifts that may be several hours long throughout the rest of the breeding season, although this may vary somewhat within a species between colonies (Hunt 1972) or with breeding densities (Butler and Trivelpiece 1981).

EVIDENCE FOR INFORMATION EXCHANGE AT THE COLONY

Here I discuss bird return frequencies to the colony to determine how often various colonial birds have the potential to use a colony for information exchange. I also examine several interpretations other than information exchange for birds "waiting" in a colony, departing a colony "purposefully" or in "flocks," or departing in the same direction as other birds.

Return frequency.—For information exchange to occur, birds that will become leaders (voluntarily or otherwise) must return to a colony and later depart to their previous feeding site. Birds of all taxa do not have similar return frequencies, so taxa would not have equal potential rates of using information exchange. For example, taxa have diverse shift lengths (and hence return frequencies) during the incubation or brooding stages of nesting (see above). Further, parents in taxa with precocial young take their young away from the colony shortly after hatching and do not return; in these taxa, information exchange would thus be of minimal, if any, importance. Colonial taxa with precocial young include grebes (Palmer 1962), waterfowl (Palmer 1976), avocets (Hamilton 1975), pratincoles and sandgrouse (Nice 1962), and some murrelets (Sealy 1976). For parents with altricial young, typical return rates may differ between taxa after the brooding or guarding stages are over. For instance, seabirds may spend a day or more away from the colony before returning to feed their young (Palmer 1962, Ashmole and Ashmole 1967, Nelson 1978), but passerines may make many trips in a hour (Kendeigh 1952, Payne 1969, Wiley and Wiley 1980).

Within a taxon, colony return frequencies depend on feeding site-colony distances; as these distances increase, the return frequencies decrease (Ashmole and Ashmole 1967, Nelson 1978). Thus, infrequent returns as well as long flight times (see above) could result in birds having difficulty in locating distant ephemeral sites through information exchange.

On the basis of return rates, information exchange probably would be most frequent in taxa with birds that have short shifts at the nest, altricial young, and short feeding site-colony distances. Information exchange, however, may still enable some infrequently returning individuals to find a good feeding site occasionally, but these birds probably use other mechanisms more commonly to locate good feeding sites, especially ephemeral ones. Even if used infrequently, information exchange may be important to save some parents (or their offspring) from starvation (Ward and Zahavi 1973). But if it occurs infrequently, then the more common mechanisms of locating feeding sites must be considered as being relatively more important than information exchange, and the importance of information exchange alone in the exploitation of food resources by infrequently returning birds could be minimal.

Waiting at colony.—Ward and Zahavi (1973) and Krebs (1974, 1978) suggested that unsuccessful foragers may wait in a colony and then follow a successful bird to its previously good site. But waiting at the colony *per se* is not evidence for the Information Center hypothesis, because waiting birds may be either just resting, as suggested by Pratt (1980), or providing necessary care for young such as guarding them against predators or neighbors.

"Purposefulness" and success.—If information exchange occurs, unsuccessful individuals at or near the colony follow "purposeful," presumably successful birds to the previous feeding site of the "purposeful" bird (Ward and Zahavi 1973; Krebs 1974, 1978). Such following may occur after two types of colony departing sequences (Ward and Zahavi 1973, Custer and Osborn 1978). In the "successful bird first out" type, a "purposeful" bird departs and then an unsuccessful individual departs and follows it. In the "unsuccessful bird first out" type, an unsuccessful individual departs, waits near the colony while flying or perching, and then follows a "purposeful" bird that has just departed. "Purposeful" birds may be identified by having short colony waiting times and/or departures from a colony that are oriented unhesitantly in one direction (Ward and Zahavi 1973).

Information exchange may be difficult to document or disprove as an explanation for birds following others from a colony, because correctly relating bird feeding success to "purposefulness" may be impractical for researchers (and birds?). Theoretically, unsuccessful birds may be identified as returning to the colony with less food to feed their young than other parents (Krebs 1978), but this may not be true in practice. For instance, some parents may bring back less food not because of feeding failure but because their young require less food than young of other parents. This could occur between parents with different numbers of young or with broods that differ widely in age (Norderhaug 1970, Richdale 1963). Second, a successfully feeding bird may arrive at the nest with little food because it was kleptoparasitized before it could feed its young. Kleptoparasitism at or near the colony is common among some colonial birds, especially seabirds (see Brockmann and Barnard 1979). Lastly, a successful parent feeding near the colony may bring smaller amounts of food than a distantly feeding parent because the amount of food brought back may increase with feeding site-colony distance (see Orians and Pearson 1977).

"Purposeful" birds also may not be good leaders for unsuccessful birds to follow profitably. For example, a "purposeful" bird actually may have been unsuccessful, and by leaving the colony "purposefully" it could maximize its chance of finding a good feeding site quickly by searching independently or by cueing to feeding flocks or bird flight directions. Second, a "purposeful" bird may not be going to its previous feeding site but to a roost (Burke and Brown 1970, Nelson 1975) or bathing area (Brown 1958). There it may remain for

TABLE 1. Taxa in which colony arrivals or departures have been observed in flocks.

	Flock[a]		
Taxon	Arrivals (%)	Departures (%)	Reference
Adelie Penguin (*Pygoscelis adeliae*)	X	X	Penney and Lowry 1967
White Pelican (*Pelecanus erythrorhynchos*)	56–68[b]	67–86[b]	O'Malley 1980
Great White Pelican (*P. onocrotalus*)	X	X	Brown and Urban 1969
Pink-backed Pelican (*P. rufescens*)	X	X	Din and Eltringham 1974
Red-footed Booby (*Sula sula*)	X	X	Verner 1965
Gannet (*Morus bassanus*)	X	?	Nelson 1978
Great Blue Heron (*Ardea herodias*)	9[c], 35[c]	5[c], 24[d], 34[c], 65[e]	Krebs 1974, Pratt 1980, Bayer 1981
Little Blue Heron (*Florida caerulea*)	X	0[f]	Custer and Osborn 1978
Cattle Egret (*Bulbulcus ibis*)	?	30[f]	Custer and Osborn 1978
Great Egret (*Casmerodius albus*)	?	3[f]	Custer and Osborn 1978
Snowy Egret (*Egretta thula*)	?	5[f], 29[f]	Ogden 1977, Custer and Osborn 1978
Louisiana Heron (*Hydranassa tricolor*)	?	5[f], 15[f]	Ogden 1977, Custer and Osborn 1978
Marabou Stork (*Leptoptilus crumeniferus*)	X	X	Din and Eltringham 1974
White Ibis (*Eudocimus albus*)	?	17[f]	Custer and Osborn 1978
Greater Flamingo (*Phoenicopterus ruber*)	X	X	Brown 1958
Eleonora's Falcon (*Falco eleonorae*)	?	X	Vaughn 1961
Parasitic Jaeger (*Stercorarius parasiticus*)	?	1[g]	Andersson and Gotmark 1980
Mew Gull (*Larus canus*)	?	16[g]	Andersson and Gotmark 1980
Arctic Tern (*Sterna paradisaea*)	?	37[g]	Andersson and Gotmark 1980
Alcids	X	X	Bedard 1969, Manuwal 1974, Aschcroft 1976
Swallows	X	X	Emlen 1954, Emlen and Demong 1975
Quelea (*Quelea quelea*)	X	X	Vesey-Fitzgerald 1958
Brewer's Blackbird (*Euphagus cyanocephalus*)	X	X	Horn 1968

[a] Where no percentage is given, X indicates that flocks were noted, ? indicates no data available. Where several percentages are given, each is for a different colony.

[b] Percentage of birds 0.5 min or less apart.

[c] Percentage of birds 1 min or less apart.

[d] Percentage of birds 4 min or less apart.

[e] Percentage of birds 5 min or less apart.

[f] Criteria not given as to when birds were classed as departing in flocks.

[g] Percentage of birds 150 m or less apart.

some time before going to feed (Burke and Brown 1970). Third, a "purposeful" bird may be going to a feeding territory (Bayer 1978, McNicholl 1979, Peifer 1979, Taylor 1979); in this case, followers would waste their time if they followed because they would be excluded from the feeding territory when they landed.

Flock departures.—Krebs (1974, 1978) suggested that flock departures from a colony are evidence of the "successful bird first out" type of information exchange. But birds in most taxa depart alone (Table 1), so information exchange may not be used frequently when birds depart. Further, birds departing more than 1 min apart are not a flock (Bayer 1981); thus, the proportion of birds departing in flocks is even less than that indicated by some researchers (see Table 1 footnotes).

Flock departures alone are not evidence of information exchange, because flocks may result from several other factors. These other factors, however, may not be always exclusive of the occurrence of information exchange and even may increase the chance of information exchange to occur sometimes. The first factor is that these flocks may result simply because birds arrive at the colony in flocks, which occurs commonly among many colonial taxa (Table 1). Because birds that arrive together probably spend about the same amount of time at a colony, birds that arrive in flocks probably would depart in flocks also. Second, flocks may result from some birds being socially bonded to each other (i.e. some birds may remain together while foraging and arriving or departing the colony). Third, flocks may occur when the flight of one bird from the colony facilitates the departure of other birds that may or may not be socially bonded (e.g. Crook 1961, Davis 1975). Socially facilitated flights have not been demonstrated directly, but the data of Krebs (1974) and O'Malley (1980) indicate that departures are clumped significantly, which is consistent with social facilitation. Although flights resulting in information exchange would all be socially facilitated, all socially facilitated departures may not involve information exchange. Fourth, flocks may sometimes be an artifact of colony size, inasmuch as the probability of birds departing together independently at about the same time (and thus appearing to be a flock) increases with increasing colony size (Bayer 1981). Fifth, flocks may result from synchrony with time of day or tides. The time of day can influence departure rates by reducing predation (e.g. in petrels and auklets, Palmer 1962, Manuwal 1979), inducing thermal development that can allow birds to travel farther easier (e.g. in Great White Pelicans [*Pelecanus onocrotalus*], Brown and Urban 1969; or in Wood Storks [*Mycteria americana*], Clark 1979), or influencing prey abundance (e.g. some prey are available only in darkness or twilight, see Ashmole 1971, Brown 1980). Tides can influence prey availability and bird foraging cycles. This can result in the frequency of flock departures being correlated with tidal cycle in ardeids (Krebs 1974, Brandman 1976, Erwin and Ogden 1979, Bayer 1981) and terns (Baird and Moe 1978). Sixth, flocks may result from departing birds independently and simultaneously either orienting to the same external stimuli (e.g. feeding flocks) or being restricted to a few flight routes from the colony (e.g. in Red-footed Boobies [*Sula sula*], Verner 1965; ardeids, Krebs 1974, Ogden 1977, Thompson 1978, Pratt 1980; and Parasitic Jaegers, Andersson and Gotmark 1980). Birds flying along these routes may do so because they thereby use the most energetically economical routes between a colony and feeding areas. Lastly, group departures may result from some birds forming foraging flocks so that they can search more efficiently for new feeding sites than if they searched solitarily (Evans 1982).

Flock destination.—The only evidence necessary to support the Information Center hypothesis is that unsuccessful foragers follow successful birds from the colony to the site where the lead bird(s) had fed prior to arriving at the colony. Such data have not been reported yet, although some indirect evidence has been documented. In an aviary, De Groot (1980) demonstrated that Quelea sometimes may learn the location of new feeding sites through following each other. For free-living birds, the "unsuccessful bird first out" procedure has been reported in Cattle Egrets (*Bulbulcus ibis*) (Custer and Osborn 1978) and White Pelicans (*Pelecanus erythrorhynchus*) (O'Malley 1980), and the "successful bird first out" procedure has been described once in Brewer's Blackbirds (*Euphagus cyanocephalus*) (Horn 1968) and three times in Phainopeplas (Walsberg 1977). The reports for free-living birds have not been clear enough to document information exchange because the researchers did not determine whether or not the leader returned to its previous feeding site and any followers subsequently fed near the leader.

Information exchange should not be assumed if some birds at or near the colony appear to follow others, because birds in such "flocks" may have different destinations. Although there are no quantitative data on destinations of birds departing together, Pratt (1980) found that only 20% of the Great Blue Herons she observed departing in flocks even flew in the same direction as the preceding heron. Krebs (1974) reported that some Great Blue Herons followed others from a colony, but his herons generally flew to the shoreline before "deciding" (his wording) where to fly. Krebs did not determine if "following" continued after herons reached the shoreline. At the shoreline, these herons could survey the foraging grounds and cue to signals of good feeding sites. Thus, "following" from his colony to the shoreline probably resulted from a limited number of economical flight routes from the colony to a location where foraging areas could be appraised and not necessarily from information exchange at the colony.

Even if a "flock" departs a colony and then forages together at the same site, the colony may not have acted as an Information Center. There must be evidence that the only indication of the site was provided by a lead bird returning to a site where it had fed prior to its return to the colony. Otherwise, birds in the "flock" may have cued independently to the same signals of a good feeding site (e.g. a feeding flock) while they departed together. This would be especially possible where birds fly along a few flight routes from a colony before "deciding" where to go.

INTRACOLONY VARIABILITY IN INFORMATION EXCHANGE

Temporal and spatial position of the nesting parents within a colony have been suggested to have a profound influence on the amounts of information exchange that may occur. Here I examine differences in nesting success between early and late nesters, center and edge nesters, and neighbors and non-neighbors to determine if these differences only support the Information Center hypothesis, as has been suggested.

Late nesters.—Ward and Zahavi (1973) and Emlen and Demong (1975) proposed that late nesters have fewer birds to follow from the colony, and they suggested that poor information exchange among late nesters is demonstrated by the higher proportion of runts and starved young for these birds. But there are other reasons than poor information exchange for the lower success of late nesters. For instance, late nesters may fail because some of the other socially facilitated mechanisms of locating good feeding sites have become inadequate. This would occur as a result of fewer birds arriving at the colony late in the breeding season; hence, there also would be fewer flight directions to which birds could cue. Second, late nesters may neglect or abandon young because they generally are inexperienced (see Ryder 1980). Third, late birds may have too little social stimulation from the few remaining nesters to continue caring for young (Lomont *in* Brown 1958). The final reason is that late-nesting parents in taxa with low annual adult mortality may increase their own survival and probably maximize their lifetime reproductive output by abandoning or neglecting late young. This would occur because the risks that late breeders would take in most years to rear young may not be worth the benefits (i.e. late-reared young have low post-fledging survival rates; Burger 1972, Nisbet and Drury 1972, Harris 1979). If they did not abandon or neglect their young, late breeders might have a reduced chance of surviving to or breeding in the following breeding season, perhaps because they might not have time to acquire adequate body reserves while food is seasonally abundant to sustain them through a moult, migration, and/or the winter.

Center and edge nesters.—Horn (1968), Ward and Zahavi (1973), and Krebs (1978) suggested that centrally nesting birds have more surrounding birds to use for information exchange. Proof of this, they suggested, is that young of central nesters grow faster and central nests are more productive than edge nests. These and other advantages of central nesting, however, may not have resulted from more efficient information exchange, but may be because edge nesters are inexperienced birds (Ryder 1980), are located in suboptimal habitats (Dexheimer and Southern 1974), are less effective in reducing predation (Burger 1981), and/or have less social stimulation to remain nesting.

Neighbors.—Krebs (1974) indicated that nesting neighbors could use each other for information exchange more effectively than non-neighbors because neighbors could see each other easily, and thus determine who had foraged successfully.

Krebs (1974) reported that Great Blue Heron neighbors often departed together, and Aschcroft (1976) found that Common Puffin (*Fratercula arctica*) chicks from neighboring nests had more similar rates of weight gain than chicks from the colony as a whole. Krebs suggested that these observations were evidence of information exchange. But they may result from neighbors being more synchronous in nesting than the colony as a whole (see subcolony review in Gochfeld 1980); thus, neighbors are more likely to be acting in concert in all activities than non-neighbors (Hailman 1975). Also, the synchrony of neighbors' departures may have resulted from socially facilitated flights (see Crook 1961, Davis 1975). Because neighbors are closer together, socially facilitated flights are more likely between neighbors than non-neighbors; such flights may or may not be involved with information exchange.

INTERCOLONY VARIABILITY IN INFORMATION EXCHANGE

Large colonies could be more effective Information Centers than small colonies because they contain more birds to search for good feeding sites and to follow from the colony. Ward and Zahavi (1973) and Erwin (1978) have suggested that an indication of greater information exchange in large colonies is their greater productivity per parent.

The relationship between productivity and colony size, however, may be unrelated to information exchange. For example, increased productivity may result simply because large colonies form only where foraging and nesting conditions are most conducive to raising young. Further, these birds may be more productive because they have lower predation rates (Burger 1981) and/or greater access to other socially facilitated mechanisms of locating feeding sites (i.e. the number of bird flight directions to which birds may cue increases with colony size). The failure of small colonies may result not from insufficient information exchange but from inadequate pairing processes (Hall 1970), a higher proportion of inexperienced breeders (Richdale 1951, Fisher 1954), or a lack of social stimulation (Darling 1938).

Offshore feeding birds tend to have larger colonies than inshore feeders (Lack 1968, Ward and Zahavi 1973, Erwin 1978). Ward and Zahavi and Erwin proposed that this occurs because offshore feeders have more difficulty in locating food and thus require the greater potential for information exchange in larger colonies. But colony sizes may reflect spatial or temporal distributions of food relative to nesting site locations and minimization of feeding site-colony travel times to feed young (Horn 1968, Hamilton and Watt 1970). Thus, the generally smaller colonies of inshore feeders may result simply from the greater availability of nest sites nearer their foraging areas. Further, offshore feeders may not be as able as inshore birds to predict and choose a nesting site that will prove to be the optimal location to minimize travel time during the ensuing breeding season. This could result because the clumping of potential nest sites relative to the extent of foraging areas is greater for offshore than for inshore feeders, and the predictability of the seasonal distribution of good feeding sites for offshore feeders probably is much less than that for inshore feeders. Offshore feeders, then, may offset the disadvantage of occasional longer travel times by nesting in large colonies to minimize predation (see Lack 1968).

INTERSPECIFIC INFORMATION EXCHANGE

Ward and Zahavi (1973) and Krebs (1978) considered information exchange to be important in mixed-species colonies, but there is no supportive evidence for this. Only Custer and Osborn (1978) have examined interspecific departures from a mixed-species colony, and they observed only one instance of a departing interspecific flock. If interspecific information exchange were important, they probably would have seen more flocks.

INFORMATION EXCHANGE AND THE EVOLUTION OF COLONIALITY

It is doubtful that groups of breeding birds acting as Information Centers were important in the evolution of coloniality in all taxa, for three reasons. First, coloniality is a complex phenomenon (Lack 1968, Buckley and Buckley 1979, Gochfeld 1980) that probably evolved several times (Friedmann 1935) in response to several interacting factors other than just information exchange. These factors include nest site scarcity (Snapp 1976, Pleasants 1979), predation reduction (Lack 1968), and exploitation of food resources (Ward and Zahavi 1973; Krebs 1974, 1978). Efficient food exploitation through coloniality may be achieved by siting of nests (Horn 1968, Hamilton and Watt 1970) or through any of the socially facilitated mechanisms of locating feeding sites. Thus, information exchange is only one of several means whereby birds can use their food resources more effectively by nesting colonially.

Second, information exchange probably evolved after coloniality already had developed, because information exchange can occur only after birds already nest together. Otherwise, there would be no neighbors to follow. In contrast, some of the other socially facilitated mechanisms of locating good feeding sites do not depend on the prior existence of colonies. Thus, these other mechanisms may have been instrumental in the evolution of coloniality by enhancing bird carrying capacities and densities so that birds could forage economically while nesting increasingly closer together.

Third, information exchange is of doubtful importance in the evolution of coloniality in taxa with precocial young. In these taxa, parents do not return to the colony to feed young, so information exchange would be possible only during the incubation stage of nesting. Even then, the potential for information exchange may be remote, because birds in these taxa may not go away from the colony after an incubation shift (e.g. in colonial waterfowl; see Palmer 1976).

POTENTIALLY USEFUL SITUATIONS FOR INFORMATION EXCHANGE

Although information exchange is probably of much less general importance than has been suggested by proponents, information exchange may be useful to birds in some taxa under certain circumstances. Information exchange may be important in taxa such as passerines that return to the colony often (i.e. >1 return/h) and have short feeding site-colony distances. These birds would have frequent opportunities to follow others from the colony and to find a good feeding site before it disappears. Information exchange may be used also by females that feed nonterritorially while males feed territorially; females (but not males) would then need mechanisms such as information exchange to find new feeding sites. Such sexual differentiation in foraging dispersion, however, has been suggested in only one colonial taxon, Great Blue Herons (Brandman 1976). Lastly, information exchange could benefit flying young that still return to the colony to be fed (see Emlen and Demong 1975, Pratt 1980). These young may use information exchange to follow adults out of the colony, presumably to feeding sites where the young may become familiar with foraging techniques and feeding sites before they become entirely independent. Fledged young return in several taxa (e.g. ardeids, Palmer 1962; seabirds, Burger 1980), but in most taxa such information exchange would not be feasible because once young leave the colony they do not return (Kendeigh 1952, Burger 1980).

CONCLUSION

To confirm the Information Center hypothesis and its importance, proponents must document information exchange *directly* and show that information exchange at the colony is not rare.

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