LARID SITE TENACITY AND GROUP ADHERENCE IN RELATION TO HABITAT

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While conducting extensive banding studies of the Cape Cod, Massachusetts colonies of Common Terns (*Sterna hirundo*), O. L. Austin, Sr. developed an overall theory concerning the roles of various interacting factors in controlling the numbers and colony distribution in his region (Austin 1940, 1942, 1944, 1945, 1946, 1947, 1949, 1951; Austin and Austin 1956). The Austins' colonies were situated in relatively but not completely stable habitats that usually allowed successful nesting, but were susceptible to occasional flooding or predation. They found that individual terns tended to return to the same colony site or even nest site year after year, a tendency that increased with age of the bird. Similarly individuals showed an age-increasing tendency to nest with the same neighbors year after year, even when the colony or subcolony had to shift from the usual colony site. These tendencies to nest repeatedly on or close to the same site and among the same neighbors are termed site tenacity and group adherence respectively. Thus, as a tern grew older, it had a greater tendency to nest in both familiar physical surroundings (site tenacity) and familiar social surroundings (group adherence).

In general site tenacity undoubtedly has selective advantage in reducing susceptibility to predation and other damaging factors by familiarizing the bird with its surroundings and by allowing it to return to sites of previously successful nestings. This reduction of danger by familiarity of surroundings is frequently included among the functions of territoriality (Hinde 1956, Klopfer 1969). In slowly changing habitats, site tenacity may also help in pioneering new habitats (see Hilden 1965: 65 ff). Too great a development of site tenacity would be disadvantageous if it promoted the continued use of poor sites or of sites that changed rapidly or deteriorated. Thus the degree of site tenacity developed in a population may reflect the stability of nesting habitat, stable here used in the sense that many generations could be raised in the same location with little if any increase in danger to the offspring.

Group adherence may appear largely fortuitous in a colony of high site tenacity, but does appear to be a separate attribute. This is indicated by the fact that when the Austins' colony sites became temporarily unsuitable, the members reappeared elsewhere in a group as a subcolony of a larger colony, rather than randomly dispersed within one nearby colony. Presumably this group adherence is based on individual recognition, known to occur in larids (Davies and Carrick 1962, Beer 1969, Evans 1970). Group adherence may have selective advantage in reducing stress by the familiarity of neighbors, which in turn would be expected to promote rapid pioneering of newly suitable habitat by colonial nesting populations. In habitats of regularly fluctuating water levels and thus fluctuating suitability of sites, a reduced form of site tenacity combined with strong group adherence would promote rapid reuse of previously suitable (and thus familiar) sites. Similarly rapid pioneering of newly suitable sites within such fluctuating habitats would be important (see Weller and Spatcher 1965: 27).

These considerations suggest the following set of hypotheses: (1) nest site tenacity is particularly well-developed in highly stable habitats, but reduced in habitats of low stability; (2) in the latter habitats, group adherence is enhanced; (3) in intermediate situations both of these attributes may be important. The validity of these hypotheses are considered below.

Stable habitats.—In such highly stable habitats as cliffs, colonies of Black-legged Kittiwakes (*Rissa tridactyla*), other gulls, and many alcids tend to persist for many years, with new colonies or even new sites in old colonies often building up gradually and slowly (e.g. Coulson and White 1956, 1958, 1960; Uspenski 1958; Tuck 1960; and many others). Experiments by Salomonsen (1939) involving removal of eggs from Herring Gull (*Larus argentatus*) nests showed that grass-nesting birds were more likely to desert than those that nested on cliffs. Although Salomonsen attributed this to the greater effort required to build nests on cliffs, an alternate view might be that the cliff nesters, with a more stable habitat, have a greater degree of site tenacity, and are thus less likely to desert the site. Rocks in tundra lakes with little fluctuation in water levels also provide highly stable nesting sites, and are used year after year for nesting, as evidenced by the bulky nests of Herring Gulls at Churchill, Manitoba (pers. obs.) and of Glaucous Gulls (*L. hyperboreus*) at various arctic locations (Snyder 1957: 205; Taylor pers. comm.). This continued use of cliffs and rocks in tundra ponds suggests a high degree of nest site tenacity in larids (and other species) nesting in highly stable habitats. The role of group adherence in such habitats is difficult to assess, but that group adherence does at least sometimes operate is suggested by the filling of crowded cliffs often before much, if any, colonization of apparently suitable cliffs elsewhere (see Uspenski 1958, Tuck 1960). Perhaps it plays a role in founding new colonies when old colony sites become saturated.

Unstable habitats.—At the opposite extreme of habitat stability are open sand or mud beaches or banks, especially as bars in rivers. In such places site tenacity would be disadvantageous, as the sites rapidly become unsuitable or disappear altogether. That site tenacity is probably greatly reduced in species that nest in such habitats is suggested by the low tolerance of at least some of them to any encroachment by vegetation (Tomkins 1959; Kale et al. 1965). That group adherence may be well-developed in such species is suggested by the rapid appearance of whole colonies in new sites, and disappearance from others. Such rapid changes in colony locations have been reported for the Least Tern (*Sterna albifrons*), especially in river sand bar populations (e.g. Ganier 1930, Youngworth 1930, Hardy 1957, Tomkins 1959), Royal Tern (*Thalasseus maximus*) (e.g. Kale et al. 1965, Ogden 1970), and Sandwich Tern (*T. sandvicensis*) (Marples and Marples 1934: 203, 206–207; Géroudet 1965: 289). In one case (Stewart 1970) an entire colony of Least Terns suddenly appeared and nested on top of a building. Such rapid colonization of suitable colony sites would be particularly important in the Black-billed Gull (*Larus bulleri*) of New Zealand, whose temporary mud banks and bars rarely last more than one season or two (Beer 1966). Preston's (1962) observation of 100 pairs of Large-billed Terns (*Phaetusa simplex*) on a newly created sand bar in the Amazon River suggests that this little known species may similarly be capable of rapidly pioneering newly created but unstable habitat. Thus nest site tenacity is probably reduced or obliterated in species nesting in highly unstable habitats. The appearance of such species in colony sized numbers in new sites suggests that group adherence is important in helping them rapidly colonize newly suitable habitat.

Habitats of intermediate stability.—Habitats that fluctuate from one year to the next or over a period of a few years represent an intermediate situation in that many generations may be raised in or close to a given spot, but these may not be in consecutive years. In habitats of intermediate stability, the evidence suggests that a retention of nest site tenacity is combined with group adherence. Site tenacity may encourage use of abnormal nest sites in emergency situations, as evidenced by dry land nestings of Western Grebes (*Aechmophorus occidentalis*) and California (*Larus californicus*) and Ring-billed Gulls (*L. delawarensis*) during years of drought or flooding in Saskatchewan (Nero et al. 1958, Nero 1961), and the nesting of 350 pairs of Black-headed Gulls (*L. ridibundus*) in trees above their flooded colony site (Vine and Sergeant 1948).

Clearly such changes in nesting sites are not always possible, especially in places of frequent fluctuations in habitat. Two such fluctuating habitats are marshes, especially prairie marshes (Weller and Spatcher 1965, Hochbaum 1967), and shallow prairie lakes (Behle 1958, Houston 1962, Evans 1972). In prairie marshes fluctuations in water levels change the suitability of nesting locations over a period of years, but unlike the highly unstable sand and mud bars, the same locations may be suitable many years in succession or at a later date following an intervening period of unsuitable habitat.

Although precise nest site tenacity would be impossible in Forster's Tern (*Sterna forsteri*) (McNicholl 1971) and other marsh-dwelling larids that nest on floating debris, some form of colony site tenacity appears to remain, as these species continue to use the same colony sites as long as they remain suitable. In addition sites formerly used but temporarily unsuitable may be rapidly recolonized when they again become suitable. At one Delta, Manitoba colony (School Bay), Forster's Terns nested in 1967, but with low water levels in 1968 returned only briefly and did not nest. When the water level again became suitable in 1970, the terns again nested there (McNicholl 1971).

Similarly certain islands in large, shallow prairie lakes may be suitable in high water years for nesting gulls, White Pelicans (*Pelecanus erythrorhynchos*), and other birds, but may become attached to the mainland in other years, and thus susceptible to predation. Like the marsh-nesting species, larids and pelicans change colony sites in response to these changes in suitability, and rapidly recolonize previously used sites after periods of flooding or low water levels (Behle 1958, Evans 1972).

That these situations may lead to rapid pioneering of newly suitable habitat is attested to by the well-documented rapid appearance of Franklin's Gull (*Larus pipixcan*) colonies at new sites in marshes in the Northern Great Plains and Minnesota (e.g. Roberts 1900, 1932: 582; Bent 1921: 164, 166; Lawrence 1937, 1940; Du Mont 1938; Hatch pers. comm.). Similar rapid changes in colony locations, or at least sudden appearances of whole colonies have been reported for such marsh-breeding terns as Whiskered Terns (*Chlidonias hybrida*) (Fuggles-Couchman 1962), Black Terns (*C. niger*) (e.g. Rockwell 1911, Trautman 1939, Baggerman et al. 1950, pers. obs.), and Forster's Terns (Rockwell 1911, Van Rossem 1933, McNicholl 1971), and the sometimes marsh-nesting Gull-billed Tern (*Gelochelidon nilotica*) (Beckett 1966). Thus a high level of group adherence appears likely in these species.

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SUMMARY

Nest site tenacity appears to be strongly developed in larids in highly stable habitats. In highly unstable habitats, site tenacity is necessarily greatly reduced, and group adherence assists rapid pioneering of newly suitable habitat. In fluctuating marshes and prairie lakes, group adherence and reduced site tenacity allow rapid colonization of newly suitable habitat, while the maintenance of at least a weak form of site tenacity allows rapid recolonization of previously used sites.

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