

THE EFFECTS OF TIMING OF BREEDING, DISPERSION OF NESTS, AND HABITAT SELECTION ON NESTING SUCCESS OF COLONIAL WATERBIRDS

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INTRODUCTION

This paper examines the effects of three major factors on reproductive success in colonially nesting waterbirds. Although most of the research focuses on the family Laridae, appropriate information regarding other families will be cited as well.

The definition of nesting success depends upon the focus of the investigator, but usually it includes some measure of fecundity, *e.g.* the size and numbers of eggs in a clutch, and production rate, *e.g.* hatching, fledging, or post-fledging success. Often several different measures of success are used, sometimes concurrently, making comparisons between studies as well as determination of the contribution of any particular variable on relative reproductive fitness difficult.

We often treat biological problems as if they were univariate, whereas in most settings a number of variables often operate simultaneously. Teasing them apart requires either relatively sophisticated statistical techniques, controlled experiments, or both. Furthermore, while we seek cause-and-effect relationships, identifying causes may be impossible. Explanations are often no more than extended descriptions. Attempting to discern ultimate causes by focusing on primary levels (Krebs, 1978) may lead to contradictory conclusions. For example, predation and food distribution are often used to explain various aspects of social organization, but Patterson (1965) and Krebs (1971) used predation to explain both colonial and dispersed nesting schemes.

The selection of a methodological approach to problem solving poses its own difficulties. The comparative approach can generate a large amount of data as well as ideas and hypotheses, but it does not necessarily explain relationships among variables. Few comparative studies offer "controlled" observations. Connell (1975) discusses "natural experiments" in which systematic observations may substitute for controls, but data from most comparative studies are correlational rather than empirical and of a limited heuristic value. Further, the use of taxonomic units for comparisons raises the question of the independence of observation among closely related groups, as well as the validity of conclusions based upon comparisons between units whose taxonomic and hence biological relationships are matters of debate.

On the other hand, the experimental approach attacks functional problems in a more straightforward way, but it can end up being relatively artificial as well as limited when results are extrapolated to the natural setting. Further, the increasingly serious question of the experimenter's own manipulations interfering with and possibly biasing interpretation of the reproductive phenomenon under investigation (*e.g.* Gillett *et al.*, 1975, Robert and Ralph, 1975) must be adequately addressed.

TIMING OF BREEDING

Lack (1968) suggested that patterns of nesting dispersal are adaptations, evolved through natural selection, that enable species to raise the greatest number of young. Social stimula-

tion, food, and predation are all factors that may influence the timing of breeding. Since Darling (1938) suggested that stimuli from nearby courting and nesting individuals enhance reproductive synchrony of mated pairs as well as the entire colony, the survival value of colonial nesting and the significance of breeding synchrony have received considerable attention. Darling hypothesized that in large colonies of gulls, and perhaps of other birds, laying started earlier and birds completed their clutches more quickly than in small colonies.

Darling also found that predators such as Great Black-backed Gulls (*Larus marinus*) and Gray Herons (*Ardea cinerea*) took a steady toll of young Herring Gull (*L. argentatus*) chicks. He suggested that the shorter the nestling period, the less the resultant mortality due to predation. Given a constant low rate of predation, birds that begin breeding during the peak period would be less likely to lose their nests and young than birds that nest earlier or later. The probability will be less for individuals breeding in highly synchronized colonies than for individuals nesting in less synchronized colonies.

MacRoberts and MacRoberts (1972) summarized the impact of Darling's hypothesis on subsequent research and readdressed the question: Is there a correlation between the degree of synchrony and the amount of stimulation received from conspecifics engaged in reproductive displays? They maintain that the results of much research have been equivocal.

For example, according to MacRoberts and MacRoberts, both Coulson and White (1960) and Horn (1970) found that the onset of breeding in the Black-legged Kittiwake (*Rissa tridactyla*) and Brewer's Blackbird (*Euphagus cyanocephalus*) was correlated with density. This was interpreted as partly the effect of social stimulation. However, Orians (1961) for the Red-winged and Tricolored Blackbird (*Agelaius phoeniceus* and *A. tricolor*), as well as Vermeer (1963) and Widemann (1956) for Black-headed and Glaucous-winged Gulls (*L. ridibundus* and *L. glaucescens*), found no evidence for density-correlated synchrony. Furthermore, as colony size or density increases

the spread of laying has been found to be unrelated, or to increase rather than decrease (Coulson and White, 1960; Vermeer, 1963; Robertson, 1973; MacRoberts and MacRoberts 1972). Moreover, Coulson and White (1956, 1958, 1960) and Coulson (1968) argue that the differences in the onset of breeding in the kittiwake are attributable, at least in part, to differences in age, breeding experience, and physical conditions.

Parsons (1975) noted that most published studies report a decline in nesting success as a function of time of season. Such declines have been observed in the Herring Gull (Paynter, 1949; Paludan, 1952; Kadlec and Drury, 1968; Erwin, 1971; Morris and Haymes, 1977); the Glaucous-winged Gull, the California Gull (*L. californicus*), and the Ring-billed Gull (*L. delawarensis*) (Vermeer, 1963, 1970); the Razorbill (*Alca torda*) (Plumb, 1965); the Shag (*Phalacrocorax aristotelis*) (Snow, 1960); the Black Noddy (*Anous tenuirostris*) (Ashmole 1962); and the Sooty Tern (*Sterna fuscata*) (Ashmole, 1963).

Other studies have documented other patterns, reaffirming the conception that multiple variables may operate simultaneously to determine nesting success. For example, Brown (1967) found that Herring Gulls and Lesser Black-backed Gulls (*L. fuscus*) breeding in midseason were the most successful. Similar results were generally found by Kadlec *et al.* (1969) and Erwin (1971) for Herring Gulls in the northeastern U.S., as well by Kruuk (1964) and Patterson (1965) for Black-headed Gulls in England. In a limited number of instances, moreover, late-breeding birds are found to have greater success. Such results have been reported by Harris (1969) for European Oystercatchers (*Haematopus ostralegus*) and Erwin (1971) for Great Black-backed Gulls. Occasionally some studies fail to document any differences in nesting success as a function of season, as for example the studies of Nelson (1966) for the Gannet (*Morus bassanus*) and Harris (1970) for the Swallow-tailed Gull (*Creagrurus furcatus*).

Parsons (1975) extended the breeding season of Herring Gulls by large-scale egg removal,

which resulted in many re-layings. He concluded that clutch size diminution as a function of time was the most important factor contributing to lowered production of chicks during the season.

While various studies have shown a decline in nesting success with laying date, date of hatching as related to post-fledging survival is less well documented (Parsons *et al.*, 1976). A high rate of mortality occurs just after fledging in many bird species, but such deaths often take place during post-breeding dispersal and migration; investigation of such mortality requires extensive banding.

Nisbet and Drury (1972) obtained evidence that early-hatching Herring Gull chicks have markedly lower post-hatching mortality. Similar survival patterns were reported for Franklin's Gulls (*L. pipixcan*) by Burger (1972). Harris (1969) found no such correlation in the European Oystercatcher, although Perrins (1966) noted that the late-hatching Manx Shearwaters (*Puffinus puffinus*) were less likely to return to the natal colony in subsequent years. Fretwell (1969) suggested that any survival advantage may be due to dominance of older young over later-hatching birds, possibly in the winter season. Conversely, Parsons *et al.* (1976) found that in Scottish Herring Gulls late hatching was no disadvantage.

For many species most nestling mortality occurs in the first few days following hatching (Nisbet and Drury, 1972; others). Some of this early mortality may be related to the size and possibly the quality of eggs, as well as certain qualitative differences among adults. Ryder (1975) examined the effects of time of egg-laying and egg size in relation to age of adult Ring-billed Gulls. Previously, studies had shown that older birds laid larger eggs than younger birds; *e.g.*, in Shags (Coulson *et al.*, 1969), Black-legged Kittiwakes (Coulson, 1963), Gannets (Nelson, 1966), and Short-tailed Shearwaters (*Puffinus tenuirostris*) (Serventy, 1967). In Ring-billed Gulls, Ryder (1975) found seasonal variation in laying date and a reduction in average clutch size among pairs to be a function of age and experience. Pairs composed of two mature birds started clutches earlier and

laid larger eggs. Furthermore, eggs laid by mature birds had much higher hatching success than those laid by pairs in which at least one bird was less than fully mature.

Food availability may influence timing of breeding (Baker, 1938) and subsequent reproductive success. Perrins (1970) suggested that for some species of birds, the timing of laying is the result of an interaction between the evolutionary advantage of early breeding and the physiological state of the female. There is strong selection for early breeding, but a minimum threshold of food abundance must be exceeded for egg production. In such cases, the availability of food acts as a proximate factor (Hilden, 1965), delaying the commencement of breeding until the female is physiologically ready.

A fluctuating food supply could affect not only the timing of nest initiation, but certain aspects of chick survival as well. For example, Nisbet and Cohen (1975), for Common and Roseate Terns (*Sterna hirundo* and *S. dougallii*), suggest that synchronous hatching is an important factor affecting the survival prospects of younger chicks within a brood. Hatching intervals tend to lengthen during the season because adults start incubating the first egg in a clutch progressively earlier as the season advances. If food supplies dwindle late in the breeding season, the prospects for raising two or more young may decrease; lengthening of hatching intervals permits larger (*i.e.* first hatched) chicks within a brood to compete more successfully for food, an extension of Lack's (1966, 1968) explanation for asynchronous hatching.

Predation also affects timing of nest initiation and chick survival. Robertson (1973) found that early-nesting Red-winged Blackbirds were consistently more successful than late-nesting ones; predation pressure increased as the season advanced. Nisbet (1975) suggested that in circumstances where food requirements of a predator are relatively constant, a larger fraction of available prey might be taken when few of them are present as, for example, at either the beginning or the end of the breeding season. Such an effect had already been demonstrated

by Ashmole (1963) for predation by feral cats on Sooty Terns, by Patterson (1965) for predation by Carrion Crows (*Corvus corone*) on eggs and chicks of Black-headed Gulls, and by Parsons (1971) for intraspecific predation (cannibalism) by Herring Gulls on chicks. Further, predators specializing on chicks might inflict the most damage at the beginning of the season, when earliest-hatched birds are small and more are needed to satiate the predator. Nisbet (1975) argues that this is the case in one Common Tern colony; in this instance, predation selected against very early-breeding birds.

Intraspecific predation may equal interspecific predation in importance as a determinant of temporal differences in nesting success. For Herring Gulls (Paynter, 1949) and for Ring-billed and California Gulls (Vermeer, 1970), greatest nesting success was found among early nesters where killing of chicks by conspecifics was at least equal to the mortality caused by other predators. For Lesser Black-backed Gulls, Davis and Dunn (1976) observed a marked decline in nesting success as the season advanced where the main cause of egg and chick loss was intraspecific predation.

To elucidate the determinants of success, at least at high densities, Hunt and Hunt (1976) modeled the optimal timing of hatching for chick survival by minimizing the probability of chick loss to neighbors and predators (Fig. 1). Adult aggressiveness and defense of territory increases at the time of hatching, so the probability of chick loss to neighbors is low early in the season when few pairs have young. The risk to chicks increases rapidly as hatching commences, and remains high for the remainder of the season. On the other hand, the highest rate of loss of chicks to predation is found early in the season, and decreases as hatching advances. Hunt and Hunt predict an optimal breeding time when $[1 - (1 - N)(1 - P)]$ is at minimum, where N is the probability of being eaten by a neighbor and P is the probability of being taken by a predator.

DISPERSION OF NESTS

Dispersion refers to nest placement within

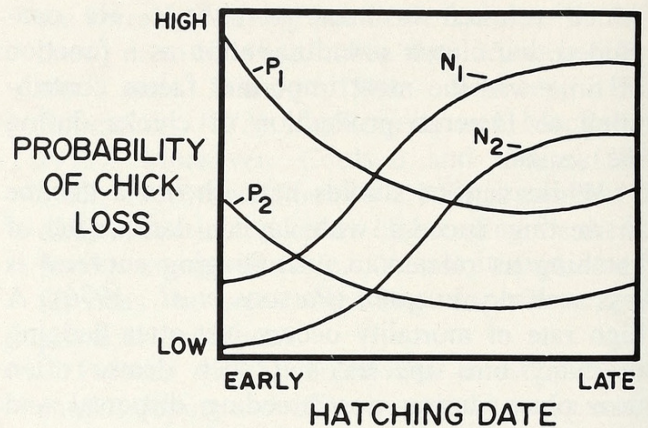


Figure 1. A model of optimal hatching date in which timing for maximum chick survival is predicted by probability of chick loss to predators and to neighbors. P_1 = loss due to heavy predation pressure; P_2 = loss due to light predation pressure; N_1 = loss due to very dangerous neighbors; N_2 = loss due to moderately dangerous neighbors. (From Hunt and Hunt 1976, © 1976, Ecological Society of America.)

the colony, which, in turn, relates to associations between a nest occupant and its neighbors as well as to the density of nests within the colony. Nest density relates in one way or another to territory size.

In 1952, Darling hypothesized that an important function of territory is the provision of periphery, an edge where there is another bird of the same species also occupying a territory. Noting the work of Williamson (1949) on the Great Skua (*Catharacta skua*), Darling suggested a need for a minimal level of mutual stimulation among nesting pairs, not obtainable by solitary or widely scattered nesting birds.

Tinbergen (1952, 1956), writing on the significance of territory in gulls, suggested and later demonstrated (Tinbergen *et al.*, 1967) that spacing of nests is a corollary of procryptic coloration. Territorial fighting is a means of promoting the dispersal of cryptically colored nests. The actual location of nests in a colony depends on a balance between the advantages of dispersal and the advantages of clustering (Cullen, 1957; Kruuk, 1964). Clustering allows the possibility of mobbing a predator, although there may be a lower limit for colony size enabling effective mobbing (Burger, 1974b).

That breeding success is a function of

colony size has been demonstrated in Black-headed Gulls (Patterson, 1965) and Northern Fulmars (*Fulmarus glacialis*) (Fisher, 1952), Gannets (Fisher and Vevers, 1944; Nelson, 1966), Herring Gulls (Darling, 1938, but see Haartman, 1945), Yellow-headed Blackbirds (*Xanthocephalus xanthocephalus*) (Fautin, 1941), Red-winged Blackbirds (Robertson, 1973), and Tricolored Blackbirds (Orians 1961, Payne 1969). Hoogland and Sherman (1976) state that, within Black-headed Gull colonies (Patterson, 1965) and Red-winged Blackbird colonies (Robertson, 1973) at least, much of the increased breeding success in larger colonies results from decreased predation per nest. Nisbet (1975) discussed evidence leading to the same conclusion in tern colonies.

Tenaza (1971) suggested that the average number of young produced per breeding pair should vary as a function of colony size; in Adélie Penguins (*Pygoscelis adeliae*) peripheral nesters seemed to raise fewer young compared with central nesters. He maintained that the increased probability of predation for peripheral nesters, occurring as a function of their relative proportion to the number of central nesters in small versus large colonies, is a simple alternative to the Darling effect for explaining the relatively lower breeding success of small colonies of seabirds as compared with large ones.

A number of studies have reviewed particular effects of nest location on breeding success. Burger (1974a) reviewed the literature and found that most studies show optimal breeding success for gulls, at central locations within the colony. Hoogland and Sherman (1976) reviewed evidence that central nests experience less predation than peripheral nests. Among the species for which such differential success was found to hold were: Adélie Penguins (Eklund, 1961; Taylor, 1962; Reid, 1964; Penny, 1968), Black-headed Gulls (Kruuk, 1964; Patterson, 1965), Pinyon Jays (*Gymnorhinus cyanocephalus*) (Balda and Bateman, 1972) and White Pelicans (*Pelecanus erythrorhynchos*) (Schaller, 1964). That central nests are more successful than peripheral nests in ways at least indirectly related to decreased predation has been demonstrated in Brewer's Blackbirds (Horn, 1968),

Cattle Egrets (*Ardeola ibis*) (Siegfried, 1972), Cliff Swallows (*Petrochelidon pyrrhonota*) (Emlen, 1952), and Bank Swallows (*Riparia riparia*) (Emlen, 1971).

Fit and less fit individuals may not be randomly distributed within breeding colonies. In Black-legged Kittiwakes, Coulson (1968) noted larger clutch size, higher hatching success, and more young fledged per pair in the center of the colony as compared to the edge. The differences in reproductive rate between the center and the edge seemed to be the direct result of variation in the quality of breeding birds. Central males lived longer, were recruited at a slightly heavier weight, and were more productive on an annual basis (Coulson, 1971). Age may have been responsible for some of these differences. Tenaza (1971), for the Adélie Penguin, noted that the mean number of eggs produced per nest decreased from central to peripheral to isolated nests. Further, central nests were of superior quality in terms of nest structure. In Franklin's Gulls (Burger, 1974a) center and edge were less definable, and reproductive success was better on the edge than in the center of the colony. Burger speculated that this seeming inconsistency with other studies was the result of better accessibility of nest sites and display areas at edge locations, which in turn provided greater social stimulation.

Differences in the quality of adults might be expected to result in qualitative differences in eggs or young (Coulson *et al.*, 1969). Ryder *et al.* (1977) noted that Ring-billed Gull eggs hatched more frequently in the center than at the periphery of the colony, but when the authors tested eggs from such areas in regard to relative nutrient and energy content, no differences in regard to quantities of proteins, carbohydrates, and lipids (at least in the yolks) were found. Similarly, Ryder and Somppi (1977) found no significant differences between central and peripheral nests in Ring-billed Gull embryonic development and size.

The effects of nest density on reproductive timing has been the association most often studied, although the distinction between colony size and density of breeding birds has not always been clearly maintained. Goethe

(1937) and Paynter (1949) were among the first to observe that eggs tend to hatch earlier in more densely populated portions of gull colonies. Coulson and White (1956, 1958) found that Black-legged Kittiwakes returned earlier to colonies in which breeding occurred early and that individuals returning to colonies early also usually bred early. In 1960 they showed there was a correlation between nest density and time of return to a colony; birds returned earlier to those areas where nest density was high.

Darling (1938) suggested that the greater the number of birds in the colony, the greater the synchronization of birds breeding within the colony. Thus breeding should be both earlier and of shorter duration in larger colonies. Conversely, Coulson and White (1960) showed that for kittiwakes the spread of breeding time was greatest in dense colonies. Similarly, MacRoberts and MacRoberts (1972), looking at social stimulation as a factor in the reproduction of Lesser Black-backed and Herring Gulls, were unable to support the Darling hypothesis. Social stimulation of reproductive events leading to breeding synchrony was not observed, nor was the timing of laying found to be correlated with nesting density. Also, no difference was found between spacing patterns of pairs nesting early versus late in the season.

Colony density has been suggested to influence not only colony synchrony but also reproductive success. Harris (1964) maintained that in the Black-legged Kittiwake there was no reason to suppose that size of the colony over an initial threshold value should bear any relationship to the productivity of the colony. Further, he noted that although a connection between mortality and breeding density is theoretically possible, it is very difficult to measure breeding density in cliff-nesting gulls.

In a landmark study of the Black-headed Gull, Patterson (1965) noted that an apparent correlation between density and success disappeared when partial correlation analysis removed the effect of year of investigation. Hence, there was no substantive relationship between nest density and breeding success. Although predation was the most important cause of egg and chick losses, Patterson noted that the spacing of nests differed from that expected

on the basis of Tinbergen's (1952, 1956) hypothesis of dispersion among cryptic prey in order to minimize the formation of specific search images among predators. As the eggs of Black-headed Gulls are somewhat cryptic, Patterson had expected greater spacing of nests. Tinbergen *et al.* (1967) later suggested that Black-headed Gulls may profit from crowding through more effective attacks on predators. Brown (1967) also suggested that for Herring and Lesser Black-backed Gulls, increased density may contribute to earlier and possibly more efficient breeding through reduced losses of late eggs and chicks.

Interspecific interactions are associated with characteristics of nest spacing and location and may affect nesting success. For example, Erwin (1971) and McGill (1977) have documented a decrease in overall nesting success of Herring Gulls when nesting in close proximity to Great Black-backed Gulls as compared to nesting near conspecifics. McGill showed that in areas where the two species were nesting neighbors, Great Black-backed Gulls had fewer young survive to fledging than did Herring Gulls. Similar interactions have been noted among herons. Burger (1978) presented evidence that in New Jersey, Snowy Egrets (*Egretta thula*) suffer poorer success when breeding near Cattle Egrets than when they nest alone. Similar negative associations among Cattle Egrets and Little Blue Herons (*Florida caerulea*) were reported by Dusi (1968) and Werschkul (1977).

Christian and Davis (1964) suggested that for some mammals, crowding results in the advent of behavioral pathologies, including cannibalism. Intra-colony killing of eggs or young has been observed in many birds, *e.g.* Herring Gulls (Paludan, 1952; Brown, 1967), Glaucous-winged Gulls (Vermeer, 1963), and Black-headed Gulls (Weidmann, 1956). In some cases, the amount of mortality specifically attributed to cannibalism can be striking; Parsons (1971) reported that cannibalism accounted for approximately 23% of mortality of young in one colony of Herring Gulls.

General intraspecific aggression, quite apart from cannibalism, may also affect success. Buckley and Buckley (1972) noted that although high density was probably an anti-pred-

ator device for Royal Terns (*Sterna maxima*), eggs in unsuccessful nests failed because the parents were too often involved in bickering with close neighbors. Their results were compatible with those of Ansingh *et al.* (1960) and Dircksen (1932), who demonstrated that unhatched eggs in Royal Terns were significantly closer to other eggs than those that hatched.

Hunt and Hunt (1975) found Western Gull (*L. occidentalis*) chick survival was negatively correlated with the distance to the nearest neighbors' nests. There was no correlation between survival and either territory size or time of hatching. In a later study, Hunt and Hunt (1976) found that survival of chicks was significantly associated with territory size, but only for those years in which food availability was limited.

In neither year did inter-nest distance relate to chick survival, possibly because nests in large territories were frequently close to the territory boundary rather than the center, or because chicks left their nests shortly after hatching and thereafter used most of their territory. In years of low food availability, chicks that hatched early in the season on large territories had better survival rates than chicks hatched late in the season on small territories. In the year of high food availability, timing of breeding and territory size had little effect on survival.

Parsons (1976) compared nesting density and breeding success in the Herring Gull. The relationship between clutch size and nesting density was unclear in his study, but pairs nesting at the modal colony density had the greatest hatching and fledging success and reared the most chicks per pair of fledging. In addition, birds that spaced their nests the most uniformly were the most successful, possibly as a consequence of territorial behavior.

Birkhead (1977) studied the relationship of breeding success with nest density in Common Murres (*Uria aalge*). Breeding success—the number of pairs raising a chick to fledging—was greatest in dense groups within the colony and also appeared to be associated with spread of laying within groups. Birkhead maintained that dense groups nested over a shorter period of time and thus were less vulnerable to predation.

Furthermore, birds in dense groups spent more time sleeping and less time in alarm-related behaviors compared with birds nesting in sparse groups. The increased nervousness as well as less tenacious incubation in sparse groups may have facilitated attacks by predators, *i.e.* gulls. In dense groups, murres could deter gulls by lunging at them, but not so in sparse groups. Krebs (1978) reiterated that failure of communal mobbing accounts for greater vulnerability of less protected nests.

Hunt and Hunt (1976) suggested that past attempts to relate gull chick survival either to inter-nest distance (Fordham, 1970) or to average nest density (*e.g.* Vermeer, 1963; Patterson, 1965; Fordham, 1970; Parsons, 1971; Dexheimer and Southern, 1974) have failed to show consistent and significant relationships because most such studies inadequately measure actual territory size (which also may change as a function of time of season) and thus further poorly differentiate the quality of individual territories. For example, in areas with the same density of nests, it is possible to have very different distributions of territory size. It may be necessary to examine territory size directly to understand the role of spacing within gull colonies.

Hunt and Hunt attempted to model optimal territory size (Fig. 2), given the potentially conflicting requirements of providing sufficient room for chicks to avoid being molested by neighbors and sufficient clumping for effective group defense against predators. Chick loss to aggressive neighbors was predicted to be greatest on small territories and to decrease as area increases up to an asymptote, beyond which further increase in territory size will not affect chick loss. The position of the asymptote will vary with terrain, availability of hiding places, aggressiveness of neighboring adults, and the tendency of chicks to move away from their nests as well as how well and how often the chicks are fed (Hunt and McCloon, 1975). When nests are clumped, defense of chicks either by mobbing or swamping of predators should be most effective. However, protection derived from coloration should be more effective if nests and chicks are widely spaced. The optimal chick territory size was predicted when

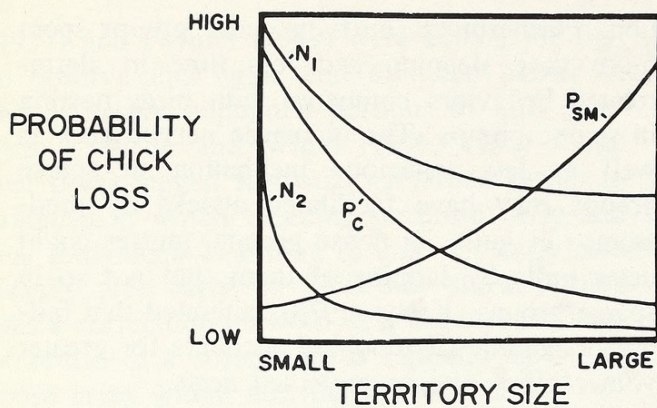


Figure 2. A model for optimal territory size in which territory size for highest chick survival is predicted by probability of chick loss to predators and to neighbors. N_1 = loss due to very dangerous neighbors; N_2 = loss due to relatively harmless neighbors; P_c = loss to predators due to failure of cryptic components of defense; P_{sm} = loss to predators due to failure of swamping or mobbing strategies of defense. (From Hunt and Hunt 1976, © 1976, Ecological Society of America.)

$[1 - (1 - N)(1 - P_{sm})(1 - P_c)]$ is at a minimum value, where P_{sm} is probability of loss to predation due to the failure of swamping or mobbing, P_c is the probability of loss of chicks due to the failure of cryptic components of defense, and N is the probability of loss of chicks to neighbors.

THE EFFECT OF HABITAT

Colony and nest sites are selected on the basis of both ultimate and proximate environmental characteristics. Ultimate factors include food, breeding site requirements imposed by structural and functional characteristics of the species, and shelter against weather and enemies. Proximate features comprise the more immediate stimuli of landscape and vegetation; terrain; areas for nesting, feeding, and drinking; and other animals (Hilden, 1965).

The influence of other birds, either conspecific or heterospecific, can be either positive or negative, as cited earlier in this paper. Interspecific competition for colony and nest site resources is generally found to result in increased specialization and reduced overlap among species' resource requirements. In the absence of interspecific competition, intra-

specific competition can determine the width of the habitat range of a species; optimal habitats may be exploited when populations are sparse but as population density increases, less favorable habitats also may be occupied, generally in their relative order of suitability (Kluyver and Tinbergen, 1953; Hilden, 1965).

Klopfer and Hailman (1965) hypothesized that the most important habitat variable orienting gulls to correct feeding, courting, and nesting habitat is the presence of other gulls, although other environmental cues are sampled as well. They maintained that the choice by early arrivals of one of the several possible sites determines the colony location for a particular year.

Studying nest site selection by Laughing Gulls, however, Borngiorno (1970) found that, if habitat were not changed, gulls nested within the same general breeding areas from year to year and in the same patterns in experimental quadrats. In contrast to Klopfer and Hailman's (1965) hypothesis, he concluded that Laughing Gulls first placed their nests in response to environmental features; further spacing depended on a bird's response to its neighbors.

Similarly, Burger (1974a) noted that Franklin's Gulls generally tended to return to display on colony sites of previous years. Such behavior has the selective advantage of reuniting members of a pair. Burger noted that cattail density and dispersion were environmental features most important for colony site selection. Nest sites were selected on the basis of minimal visibility to nearby nests. Similar results for nest-site orientation were later found for Black-headed Gulls (Burger, 1976). Of course, other variables are important as well; Burger and Shisler (1978) point out that nest-site selection is ultimately a compromise among various selection pressures of weather, cannibalism, predation, and other variables.

Prior breeding experience in an area may contribute significantly to the selection of one area over another for breeding (Klopfer and Hailman, 1965). Hilden (1965), reviewing the work of Austin (1940, 1945, 1949), stated that among Common Terns (*Sterna hirundo*) older birds returned faithfully to original nesting sites although vegetational changes over the years

gradually rendered the substrate unsuitable for younger birds.

Borngiorno (1970) reviewed general tenacity in colony-site selection among gulls. Laughing Gulls may completely abandon former nesting sites, but many larids occupy the same general site over successive years, *e.g.*, Herring Gulls (Tinbergen 1952, 1961; Drost, Focke, and Freitag, 1961; Ludwig, 1963), Ring-billed Gulls (Southern 1967, 1977), Black-headed Gulls (Svardson, 1958; Beer, 1961), Glaucous-winged Gulls (Vermeer, 1963), Laughing Gulls (Stone, 1937; Noble and Lehrman, 1940; Noble and Wurm, 1943), Sooty Terns (Robertson, 1964), and Royal Terns (Kale, Sciple, and Tompkins, 1965). Brewer and Harrison (1975) also noted the same general phenomenon, citing the work of Nice (1937) and Haartman (1949). Occasional exceptions occur in species whose habitats are unstable, *e.g.* Black-billed Gulls (*L. bulleri*) (Soper, 1959; Beer, 1966), Franklin's Gulls (Burger, 1974a), Brown-hooded Gulls (*L. maculipennis*) (Burger, 1974b), and Ring-billed Gulls (Southern, 1977). Erwin (1977) has calculated an index to colony-site change rates for Herring Gulls as well as other species.

Brewer and Harrison (1975) suggested that for many species it seems likely that most individuals nest throughout their lives near the spot where they settled in their first year. McNicholl (1975) wrote that site tenacity generally has the selective advantage of reducing susceptibility to predation by familiarizing a bird with its surroundings as well as allowing it to return to sites where successful nesting previously took place. Of course, too strong a site tenacity could be disadvantageous if it promoted the continuous use of poor sites or those that have deteriorated (see the work of Austin, cited earlier). The degree of site tenacity within a population may reflect the stability of the habitat. McNicholl suggests that colony and nest-site tenacity is particularly well developed in highly stable habitats and reduced in unstable habitats. Group adherence—the association of several individuals from one year to the next—may be more important than site tenacity for species nesting in unstable habitats.

Variation of breeding success in relation to physical features of the environment is not well

known (Birkhead, 1977). The factors determining the optimal breeding habitat of a species have been investigated for only a few species, *e.g.*, the Gray Partridge (*Perdix perdix*) (Southwood and Cross, 1969) and the Common Puffin (*Fratercula arctica*) (Nettleship, 1972). To adequately describe the relationship between the nesting success of a species and its habitat, information about environmental conditions throughout its total geographic range as well as its breeding success in representative areas should be known (Nettleship, 1972). In fact, there have been relatively few such systematic studies of the relationship between habitat and productivity. Most published accounts have been largely anecdotal or at least of limited scope, where habitat-productivity relationships were described as part of a larger study (*e.g.* Snow, 1960; Beer, 1966; Nelson, 1966; Brown, 1967; Coulson, 1971). Nettleship (1972) noted that colonial seabirds should make excellent study subjects for studies relating breeding success to habitat features; they tend to breed in high numbers at relatively traditional colonies where nests are abundant and where the number of environmental variables is small and relatively constant.

At Great Island, Newfoundland, Nettleship found Common Puffin density negatively correlated with distance from cliff edge and positively correlated with the degree of slope; close to the cliff edge where the angle of the slope was steep, the breeding success of puffins was significantly higher than on level habitat. Characteristics of the eggs in both habitats were approximately the same and egg-laying dates were similar, but the annual variation in egg characteristics was greater on the level than on the slope habitat. The frequency of infertile eggs was lower on the slope. Fledging success was higher on the slope. Frequency of chick deaths in the nest and disappearance before fledging was higher on level habitat in both years. Fledging success was higher for earlier-hatched chicks in both habitats, but the total breeding success was higher on the slope habitat.

Nettleship concluded that the difference in breeding success in the two habitats was due to higher exposure of chicks and eggs to gull

predation on the level habitat. The primary cause of this differential exposure was that adults on slope habitats were less vulnerable to gull disturbance during incubation and gull robbery when feeding chicks. Breeding failures resulted from the interaction of food shortage and gull interference.

Burger (1977) recently investigated the comparative nesting success of Herring Gulls as they invaded previously unused *Spartina* salt marsh habitat in New Jersey. Gulls constructed larger and deeper nests in wetter as compared to drier areas. In wet areas, more complete repairs to damaged nests were effected. Hatching success was poorest in wet areas, much more successful in dry areas. Her results not only demonstrate a nice relationship between qualitative habitat differences and breeding success, but also indicate that the highly adaptable Herring Gull is making yet another successful shift into new areas because the species is able to give appropriate behavioral responses to previously unencountered habitat stimuli.

SUMMARY AND CONCLUSION

Various factors may account for observed declines in nesting success as the breeding season advances. For example, experienced birds can begin breeding earlier, can have larger clutches, and can be more successful in rearing young. Further, for some species food may be less abundant as time advances, resulting in less success among later-hatched young. Similarly, predation and intraspecific interference may increase nesting synchrony and nesting success, although not always at consistent periods within the season. Models have been proposed for the optimal timing of chick hatching by minimizing intraspecific and interspecific losses in gulls.

Breeding success often varies as a function of colony size. The increase in breeding success in larger colonies results from decreased predation per nest; there is a smaller proportion of vulnerable peripheral nests in larger colonies. Furthermore, fit and less fit individuals generally are not equally distributed within colonies. More experienced birds may acquire

more desirable locations. Also, newer and often smaller colonies may be established by younger, less reproductively fit individuals.

The distinction between colony size and density within those colonies has not always been maintained. Nonetheless, the effect of density on reproductive synchrony and nesting success has been the relationship most often studied. There has been little unequivocal support for Darling's hypothesis of earlier breeding and intra-colony synchrony in large and dense colonies. Likewise, clear evidence for greater breeding success with increased density has not been found consistently. In fact, increased density and interspecific nesting associations may enhance opportunities for negative interactions through predation, cannibalism, or simple interference. Models have also recently been proposed relating optimal territory size to the amount of space necessary to prevent molesting of chicks by neighbors while at the same time allowing for sufficient clumping of nests for effective group defense against predators. These models attempt to resolve inconsistencies among reported results as well as predict simple relationships among spacing parameters and certain aspects of gull breeding success.

Colony and nest sites are selected on the basis of a variety of proximate and ultimate environmental characteristics. Numerous studies recently have described, in considerable detail, proximate features of breeding habitat of many colonial birds. Many studies have used sophisticated statistical techniques to enhance descriptions, *e.g.*, principal component analysis. Such descriptive studies have contributed to an evolving understanding among avian biologists of the relationship between habitat stability and nest- and colony-site tenacity.

Evaluation of differential reproductive success in relation to physical and other biological features of the environment has not kept pace with descriptive habitat studies. There is poor documentation of reproductive success in relation to the environmental factors which define the optimal breeding habitat of a species. Characterization of optimal or even sub-optimal habitat has suffered because of the lack of sufficient comparative data from the range of en-

vironments in which a species breeds. Seabirds have been proposed as a group whose study could elucidate such relationships between environmental factors and reproductive success.

For conceptual clarity and because of the way results have been reported in the literature, the effects of timing of breeding, spacing of nests, and habitat selection have been treated separately. Such simplification, of course, does not exist in the biological world. Interactions among variables occur, often in a nonadditive fashion. For example, dispersion of nests probably varies and influences reproductive success in quite a different fashion in sub-optimal habitats as compared to optimal habitats. Unfortunately, most published results do not permit assessment of such interactions. In the future, our planning and attention should be focused upon studies that will permit such evaluations.

It is encouraging that many of the results cited in this review generally fit relatively straightforward models, such as those proposed by Hunt and Hunt (1976). Most interesting, however, are those studies whose results do not fit the models. Many of those studies were conducted over short periods of time. Conclusions based on such limited samples of reproductive performance and the factors that influence it may be spurious. Moreover, such short-term studies may fail completely to allow for an opportunity to discriminate among the interactions of environmental variables. To better understand long-lived organisms, such as many colonially nesting birds, studies must be conducted over many years, using more systematic methods of data collection than have been attempted previously. It is through such investigations that we will eventually succeed in more completely determining the empirical relationships among timing of breeding, dispersion of nests, and habitat characteristics, and their effects on reproductive success in colonially nesting birds.

ACKNOWLEDGMENTS

Joanna Burger, R. Michael Erwin, James L. Gullledge, and Charles R. Smith critically read the manuscript and made numerous helpful sug-

gestions. Ann M. Rogers and Gwen K. Beck aided in bibliographic tasks. My wife, Rena, typed most of the final as well as all the earlier drafts of the paper.

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COMMENTS

Burger: With respect to the cattails affecting the nesting behavior of Franklin's Gulls that you referred to, habitat variables were important and I was measuring them. The critical factor was that the social interactions were mediated by the vegetation. When you remove the cattails, there was an enormous increase in the amount of aggression. As cattails grew and reduced visibility, aggression decreased. Then removal of the cattails again resulted in increased aggression. Thus, it was the social factors, not the vegetation that were of primary importance.

McCrimmon: I am glad that you point out that multiple factors often interact.

Parkes: There has been an infinite number of studies of the effects on breeding success of seasonal food availability not only with respect to colonial birds, but everything from tropical fruit-eating passerines and hummingbirds to songbirds. There has been an infinite number of studies of effects of predation on breeding success. Do you know of any study that has tried

to bring these two things together? Obviously, there will be a period in which the predator needs more food to feed its own young. Have there been any attempts to isolate the principal predator on a colonial seabird to see whether there is a correlation between the life cycle of the predator and the prey?

McCrimmon: No, not to my knowledge. That's an excellent idea.

Coulter: Tim Birkhead did look at the rooks and the guillemots on Skomer Island, Wales. Ray Pierotti is looking at the gulls in terms of Nettle's puffin story from Newfoundland. Early work by M. P. Harris (*Ibis*, 1964) suggests a relationship between Great Black-backed Gulls and other breeding seabirds on Skokholm Island, Wales. Finally, Ian Spellerberg has been writing something on the skua-Adélie Penguin story, but I don't know whether it has come out yet; and Fritz Trillmich has an article on the skua-Adélie Penguin story in the 1978 *Auk*.

McCrimmon: Is the work by Birkhead in his dissertation in print?

Coulter: It came out in *Ornis Scand.*: Birdhead, T. R. 1974. (*Ornis Scand.* 5, 2: 71-81.)

McCrimmon: It is something I am not familiar with, and I couldn't get his dissertation in time to include in this review.

Gochfeld: I would like to emphasize one of the last points that Don was making. Most of us who have worked in the colonies year after year will find that there are a few years that fit the model perfectly and other years that show exactly the opposite. Inter-year variability in many of our breeding seabirds, as Don implied, is one of the most fascinating aspects of their biology.

McCrimmon: It is one of the most difficult to study and one that takes really long-term commitments.

Gochfeld: Evolution does look at these

long-term changes. It's not particularly concerned with May of 1978.

Vuillemier: I was somewhat disturbed at your distinction between proximate and ultimate factors, and it seems to me that if we use the term in the sense that Lack originally used it, all or most of the factors that you've discussed today I would call proximate.

McCrimmon: Yes, that's true.

Vuillemier: Now, do you believe in ultimate factors in that sense, or do you use a different definition than Lack?

McCrimmon: I think the point is that some variables can occur in both a proximate and an ultimate fashion.



McCrimmon, Donald A. 1980. "The effects of timing of breeding, dispersion of nests, and habitat selection on nesting success of colonial waterbirds." *Transactions of the Linnaean Society of New York* 9, 87–102.

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