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GULL RESEARCH IN THE 1980s: SYMPOSIUM OVERVIEW

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Symposia are now a regular feature of the annual meetings of scientific organizations. Two approaches are available for selecting themes for symposia. The subject may be a concept, such as the mechanisms of bird orientation, and researchers working on an array of species present results tied together by the unifying conceptual thread. The other option is to use a taxon as the common denominator and have the investigators discuss a variety of concepts as they apply to one or more closely related species. Both types of symposia have their advantages. The organizers of the 1985 First Joint Meeting of the Pacific Seabird Group (PSG) and the Colonial Waterbird Group (CWG) considered it an appropriate time to review the status of gull research in the 1980s. Presented herein are 11 papers and 10 abstracts reflecting current larid research and the approaches investigators are taking.

Gulls stand out as appropriate subjects for consideration at a scientific meeting because of their relationship with man in the past, present and, more than likely, in the future. During the nineteenth century egging activities, the feather trade, reduction in fish populations, use of nearshore islands for livestock grazing and other human endeavors lowered gull populations in North America (Graham 1975). Protection in the form of state, national and international legislation early in the twentieth century resulted in gradual population increases until about midway through this century. Then there was a continent-wide explosion in the population of several gull species (e.g., Drury and Kadlec 1974, Ludwig 1974). Environmental changes that probably made these population changes possible included the introduction of forage fishes (smelt and alewives) in the Great Lakes, the operation of large landfills throughout the winter ranges of North American gulls, construction of dredge-spoil islands, and the construction of new resting habitat (numerous ponds and reservoirs) throughout the ranges of some species.

In the 1980s, gull populations have become large or concentrated enough to result in conflicts with man. The increase in competition between gulls and man has added a practical component to gull research. In order to develop management strategies that are resource sensitive while also providing for man's environmental requirements, we must possess an in-depth understanding of the species involved, including their breeding biology, habitat requirements, food habits, and long-term responses to environmental change. The papers presented in this symposium contribute significantly to the development of a data base that is essential for resource managers. In addition, many of the papers address more theoretical aspects of behavioral ecology for which gulls are ideal subjects because of their colonial nesting habits and their tendency to use nest sites accessible to investigators.

Gulls as a group also have served as the subjects of basic research that has contributed to the formulation of many major biological concepts. Such studies have expanded our understanding of motivational systems (Tinbergen 1953, Baerends and Drent 1970), evolutionary behavior (Moynihan 1958a & b, Beer 1975), physiology (Tucker 1972, Howell et al. 1974), foraging behavior (Andersson et al. 1981, Curtis et al. 1985, Greig 1984, Patton 1986), territoriality (Burger 1984), interspecific associations (Gotmark and Andersson 1980, Barnard and Thompson 1985), life history strategies (see Burger et al. 1980), and a number of other subjects. Because several gull species have been thoroughly studied, it is now possible to design interesting comparative studies dealing with ecology and behavior. Even with all the attention gulls have received from investigators, many unanswered questions remain. The papers and abstracts presented in this volume provide an outstanding indication of the directions gull research is taking and suggest approaches for further inquiry.

Twenty-one species of gulls breed in North America and three other species regularly visit the continent (Farrand 1983). Of the five genera involved, *Larus* includes the largest number of species (19). Both species of *Rissa* occur here and *Rhodostethia, Xema* and *Pagophila* each are represented by one species. Several species range widely over arctic waters or are nearly pelagic in the North Atlantic and Pacific oceans. Six of the 21 breeding species tend to nest in inland locations whereas 15 species are primarily coastal nesters. During the nonbreeding period, considerable overlap occurs in the ranges of the nonarctic species. The breeding ranges, however, are more distinct and only occasionally do more than two or three species share colony sites (Southern 1980, American Ornithologists' Union 1983).

Several species of gulls are good research sub-

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jects because their colonies are relatively accessible and they nest in large numbers which allow investigators to obtain statistically important samples. During the last two decades alone, hundreds of papers have been published about gull migration and orientation, seasonal distribution, breeding biology, sex ratios, ecology, food habits and population size. Of the 21 species breeding in North America, 6 have received most of the research attention: Laughing Gull, *L. atricilla*; Ring-billed gull, *L. delawarensis*; California Gull, *L. californicus*; Herring Gull, *L. argentatus*; Western Gull, *L. occidentalis*; and Glaucous-winged Gull, *L. glaucescens.* Others such as the kittiwakes (*Rissa* spp.), have been studied thoroughly in the Old World. Considerably less is known about others (e.g., Franklin's Gull, *L. pipixcan*; Bonaparte's Gull, *L. philadelphia*; Mew Gull, *L. canus*; Iceland Gull, *L. glaucoides*; Ross' Gull, *Rhodostethia rosea*; Sabine's Gull, *Xema sabini*; and Ivory Gull, *Pagophila eburnea*).

Bent's (1947) "Life Histories" illustrates the nature of gull research prior to the middle of this century. Shortly thereafter, Tinbergen's (1953) classic study of the Herring Gull stimulated numerous ethological studies and field experiments. Moynihan (1958a & b) described the visual and auditory displays of several larid species and provided the types of information considered necessary for an ethogram. Such studies provided us with significant descriptive information but they also caused us to de-emphasize the importance of individual differences in behavior. The fixed action pattern concept of Lorenz (see translations, 1970) left the impression that much of bird behavior was inflexible. We now know that more plasticity exists in the performance of gull displays and the components of other behaviors than earlier investigators proclaimed. For example, gull chicks can stimulate adults to feed them by pecking at portions of the the bill other than the salient spot or ring that adults possess. Also, as parental care progresses during the nesting season, experienced parents may attempt to feed without any begging by the chick (Henderson 1975; pers. obs.). Experienced parents and chicks show more variability in the behaviors associated with parental care than do novice parents and their chicks. These raw materials for behavioral change are awaiting the influences of selective pressures and they should be catalogued by investigators (e.g., Hand 1979). Documenting the variability in behavior, rather than ignoring it in favor of the sample mean, may provide us with insight into the rate at which shifts in behavioral tendencies may occur.

Gull researchers have contributed to at least three recent findings that have influenced the way that avian field research is conducted. Researcher sensitivity to these factors will result in more accurate data collection and analysis, and conclusions that more correctly describe how a given species is performing. (1) Gull investigators are becoming increasingly cognizant of the importance of long-term studies (e.g., Mills 1973, Coulson and Thomas 1985), which take into account what happens throughout a particular breeding season as well as throughout the lifespan of individual gulls. This is particularly applicable in the case of studies dealing with population trends, reproductive success and habitat selection. (2) The project designs and methods used by many researchers clearly show that they are now cognizant of the effects of investigator-caused disturbance in gull colonies (Hunt 1972, Robert and Ralph 1975, Hand 1980, Fetterolf 1983). Ignoring these effects when designing or conducting a study can seriously bias the data collected, particularly in studies measuring chick survivorship, parental care, aggressiveness and territoriality. (3) Methods of marking gulls may influence the accuracy of data collected and seriously bias the outcome of a study. For example, Southern and Southern (1985) showed that wing markers detrimentally influence the breeding behavior of Ring-billed Gulls. Use of this marking method during studies dealing with mate fidelity, longevity, site tenacity or other studies requiring unimpeded return to the site of marking should be avoided. It is no longer possible for investigators to discount the possibility that their experimental methods may influence the behavior of their research subjects. Ways of avoiding such complications must be developed during the planning stages rather than attempting to work around them statistically during the analysis stage.

The topics covered by this volume are some of those having the greatest importance to larid researchers today. The papers and abstracts are grouped into five subject areas: life histories, behavior, foraging, habitat selection and hybridization. Information of these types is accumulating gradually for most gull species. Particular ones are more thoroughly studied than others but sufficient data exist for a comparative approach possibly relating the similarities and differences to morphological characteristics, ecological variables associated with differing geographical ranges, and the effects of sympatry. The recent work of Hoffman (1984) is an outstanding example of the value of the comparative approach. Components of life history and ecological characteristics of species are more difficult to describe quantitatively than skeletal features; however, someone needs to accept the challenge and synthesize the behavioral and ecological data for gulls, particularly sympatric species. Burger (1980) stands out as a major contributor of

species-specific data as well as a synthesizer of interspecific strategies.

The 11 full-length papers in this volume are a significant contribution to gull biology. The abstracts describe studies we will learn more about in the months to come as the associated papers are published. Following are some of my reactions to these papers. The abstracts are not discussed because of space limitations and the inability of the reader to refer to the full paper for details.

The lead paper by Walter V. Reid examines factors that may limit clutch size in the Glaucous-winged Gull. As with most *Larus* gulls, the clutch size of this species usually is limited to 3 eggs, with 4 or more eggs being relatively infrequent, or associated with female-female pairs (Conover 1984). Several hypotheses have been presented to account for the high frequency of 3-egg clutches. The energetic cost of egg formation has been offered as one explanation for egg and clutch size in gulls (e.g., Boersma and Ryder 1983). Measuring weight gains or foraging success of individual gulls after they reach the breeding range may not be the best approach for examining this possibility, although it is regularly used. More important may be the body condition of females when they arrive on the breeding grounds. Not infrequently, gulls spend relatively little time foraging during the early stages of the nesting cycle (i.e., prelaying; pers. obs.). It appears, therefore, that fat reserves may not only contribute to survival at this time but may provide some of the energy required for egg production by early nesters. Ryder (pers. comm.) is investigating whether or not this may be the case for Ring-billed Gulls.

Reid suggested that the incubation capacity of gulls may impose an upper limit on clutch size. No evidence exists, however, to show that possession of only 3 brood patches prevents gulls from successfully incubating more than 3 eggs (Vermeer 1963, Coulter 1973), although Coulter (this symposium) showed that hatching success is highest for 3-egg clutches. The brood-rearing capability of parent gulls has been suggested as another factor possibly responsible for limiting clutch size (Haymes and Morris 1977), although some gulls are capable of rearing more than three young (e.g., Coulter, this symposium). In spite of this, average reproductive success seldom exceeds 1.5 chicks per pair (Blokpoel and Tessier 1986) and may be considerably lower. It is likely that no single factor is responsible for the prevalence of 3-egg clutches in gulls. The multiple hypothesis approach of Winkler (1985) shows the advantages of a broader perspective to questions such as this.

Reid also calls attention to the small c-egg (third laid) commonly reported for gulls and suggests that it may not represent an adaptation for brood reduction. Instead he considers it a non-adaptive consequence of energy shortages during laying. He also points out that asynchronous hatching in gulls may be an adaptation for maximal growth rather than an adaptation for food stress. The pattern of hatching in some gull species such as the Ring-bill, however, is variable with some clutches hatching all 3 eggs on the same day but hatching in others is spread over 2–6 days (Clark and Wilson 1981; Southern, in prep.). Reid's explanation, therefore, is not generally applicable to all gull species.

D. Michael Fry, C. Kuehler Toone, Steven M. Speich and R. John Peard examine the factors affecting skewed sex ratios in gulls, a subject that has received considerable attention during the last decade. Sex ratios skewed toward females are thought to result female-female pairs (Hunt and Hunt 1977, Ryder 1978, Ryder and Somppi 1979, Conover 1984). This phenomenon is indicated by the occurrence of supernormal clutches (SNC) and indexed by the SNC percentage within a colony. Causes of skewed sex ratios may be multifaceted as the authors describe. The finding that there is a decrease in the number of male gulls and an increase in the number of SNCs in areas polluted with organochlorines is extremely interesting. Once again we are reminded that all behavioral, morphological and physiological conditions we identify when examining large samples of organisms, as is possible in gull colonies, are not necessarily adaptive (Gould and Lewontin 1979, Hand 1979). Some, such as female-female pairing, may not be indicative of a new mode of parental care that can be expected to sweep through gull colonies, although some investigators seemed to imply this in the past (e.g., Hunt and Hunt 1977).

Egg predation by conspecifics is not uncommon when pair members are nesting asynchronously from most of the colony or when they are casual about attentiveness (pers. obs.). This is especially true of gulls with small nesting territories. Attentive behavior by both sexes of parents during incubation and early stages of chick development appears to be an effective defense against this form of predation (L. A. Hanners MS; Shugart and Fitch, abstract this symposium). Individual differences occur, however, in the performance of parental care by gulls and this may contribute to differential brood success. Ralph D. Morris examines time-partitioning of clutch and brood care activities as measures of parental quality in Herring Gulls. His findings confirm that pairs displaying the greatest synchrony in parental care produce the most young.

The subject of survivorship and mortality is

fundamental to understanding the dynamics of avian populations and associated life history strategies. According to Larry B. Spear, Harry R. Carter, Teresa M. Penniman, Jay F. Penniman and David G. Ainley, only four studies provide reliable information on survival rates in adult gulls. These authors also report finding no quantitative estimates of the various causes of mortality that affect gull age or sex composition. Their paper points to one of the areas of gull research that requires further attention by investigators. Especially needed are reliable techniques for predicting changes in gull populations on a regional basis and for cataloging the factors which limit population growth of these successful generalists.

Gull populations have increased dramatically across the Northern Hemisphere during recent decades thereby providing opportunities for investigations of the causes and effects of such changes. Conditions responsible for these significant population changes are not restricted to a single region nor to a single species. Interesting biological questions are associated with these population changes and the resulting inter- and intra-specific conflicts. Arie L. Spaans, Alle A. N. de Wit and Marianne van Vlaardingen examined the effects of increased population size on Herring Gull breeding success in The Netherlands. Between 1968 and 1984, the increase in Herring Gull population size was more than five-fold. In the authors' study plots, the increase was three-fold with a corresponding decrease in the number of young fledged per pair. Interestingly, under these conditions, experienced breeders were producing most of the offspring and the breeding schedule had advanced 4–9 days since the 1960s. Gulls are breeding earlier in other parts of the world as well. For example, since 1975 the onset of hatching of Ring-billed Gulls at Rogers City, Michigan, has advanced 7–10 days with the first chicks now hatching in mid-May (Southern, in prep.). It is possible that the factors associated with this shift involve more than density-dependent phenomena, as suggested by Spaans and his co-workers for Herring Gulls. Possibly subtle changes in temperate zone climatic conditions are having a gradual affect. Other circumstances such as rising Great Lakes and ocean water levels may be a further reflection of such changes.

The subject of parental recognition of their young has received the attention of several investigators working with various species of gulls (e.g., Tinbergen 1953; Beer 1970, 1979; Miller and Emlen 1975). Intuitively it would seem that ground nesting colonial gulls with potentially mobile young should possess some method for distinguishing their young from those of nearby conspecifics. At least this would be the case if natural selection was occurring at only the individual level and the concept of inclusive fitness was applicable. Although earlier studies produced evidence supportive of these contentions, the results from recent ones, including those of Joseph G. Galusha and Ronald L. Carter presented here, indicate that recognition may not be well perfected in gulls and that adoptions or temporary care of young other than a parent's own may occur (Holley 1981, 1984; Spear et al. 1986). This raises some interesting evolutionary questions, including the significance of unintended cooperation in breeding gulls. In studies without investigator or other disturbances, chick mortality often is not a consequence of chicks invading neighboring territories. Some adults show varying levels of tolerance or acceptance of chicks other than their own. The result often is temporary or permanent adoption (Southern, in prep.). Selective advantages to acceptance of chicks by neighbors could exist, particularly in the case of gulls with small territories. Our skepticisms about group selection should not close our minds to such possibilities as the benefits may be at the individual level. The conclusion of Galusha and Carter that adult gulls do not recognize their chicks individually but accept or reject them on the basis of their behavior deserves careful attention by other investigators. Short-term and long-term adoptions also occur regularly in Ring-billed Gulls (pers. obs.). A possibility worthy of testing is that acceptance of "foreign" chicks, particularly by experienced pairs that have lost their own chicks, contributes to colony stability during a particular nesting cycle by keeping more adults at the colony. If social facilitation has any importance to breeding gulls, particularly those with small territories, assuring an optimally sized social assemblage may be selectively advantageous.

As information about gull species increases, it becomes increasingly important to synthesize the data and present an overview of what is typical as well as what is unique to individual species or groups of species. Joanna Burger presents a paper that accomplishes this goal using data she collected for 15 species of gulls in North America, Africa, Australia and Europe. Few investigators have had such vast experience with the world's gull species. Although an assortment of authors cited by Burger have discussed the age-related differences in feeding ability, she is the first to use uniformly collected data to examine foraging efficiency for a large number of widely distributed gull species. Her results solidify the theory that delayed maturation is likely to occur in cases where foraging difficulties exist.

The responses of nesting gulls to nocturnal predators and the effects of predators on breeding success are subjects of broad interest to gull re-

searchers (L. Southern et al. 1982). Joseph R. Jehl and Charles Chase III discuss the foraging patterns and prey selection of predators, especially Great Horned Owls (*Bubo virginianus*) on California Gulls. As in other studies (e.g., Southern et al. 1985), the authors found that adult gulls left the colony during owl attacks. As a result, indirect chick losses were a regular occurrence. The hunting patterns of owls were regular and predictable. Adult losses were low but chick losses occasionally were great. This study provides further evidence that the "antipredator" behavior of gulls, particularly under nocturnal conditions, is little more than avoidance by leaving when predators are present. If adults make any attempt to protect their offspring at night, it is ineffective against most persistent nocturnal predators (see Southern et al. 1982 for a review). Jehl and Chase also provide important information about who gets killed and why, which has implications for habitat selection and colony siting. Because the impact of predators can be local but severe, sampling methods in large colonies must be considered carefully.

Considerable attention is being directed at the topics of habitat and nest-site selection by gulls. Kees Vermeer and Kevin DeVito compare the characteristics of sites selected by Mew Gulls and Glaucous-winged Gulls. Information about the Mew Gull is especially interesting as this species has been little studied in North America. On Vancouver Island about 80% of the Mew Gulls nested as solitary pairs. Nest sites frequently were on the tops of poles or other objects which were surrounded by water. The Glaucous-winged Gull, on the other hand, is primarily a colonial nester. Interspecific plasticity in nest site selection by both species was noted.

Habitat selection has received considerable attention from gull biologists, and justifiably so (Bongiorno 1970, Burger and Shisler 1978, Erwin et al. 1981, Montevecchi 1978). A common flaw in many such studies, however, is that the investigator assumes that the conditions under which gulls may be nesting when a study starts are the same as those that existed when individual gulls first occupied the site. Changes in cover type and density may occur within a breeding season because of plant growth and even more dramatic changes may occur over the lifespan of individual gulls. Since nest site tenacity is well documented in gulls (L. Southern, in prep.), as is mate fidelity, the probability exists that given nest sites will change over time because of plant succession or other variables. Long-term studies are necessary to distinguish between the effects of nest site selection and effects associated with plant succession or other time-related factors (i.e., time vs. tradition) on an individual's total reproductive output. It appears that gulls continue to use sites long after the habitats that existed when they selected them no longer are evident. In this volume, Raymond Pierotti examines the behavioral consequences of habitat selection in Herring Gulls. He compares the time budgets, rates of aggressive behavior and diets of gulls nesting in three different habitats in Newfoundland. His results demonstrate that habitat choice may influence the type and frequency of particular behaviors which, in turn, influence reproductive success. Studies such as this which address the variability within a population or species are extremely important. Variation appears to be the rule rather than the exception, particularly when we are dealing with gulls because so many exhibit high levels of plasticity in behavior. From the evolutionary standpoint, tomorrow's trends exist in today's variability. It is well documented that behavioral changes can occur over relatively short spans of time. Devoting more attention to such things as how variability in habitat preference influences the production of offspring may give us a better record of evolution in progress.

By studying hybridization in nature, it is possible to assess the evolutionary status of closely related populations (Moore 1977). If members of two populations successfully and freely interbreed whenever their ranges overlap, taxonomists should seriously consider classifying them as conspecifics (Hoffman et al. 1978). Hybridization occurs between many of the large *Larus* gulls (Tinbergen 1953, Ingolfsson 1970, Jehl 1971). In this volume, Aonar Ingolfsson, who is recognized for his long-term studies of gulls in the far north, presents information collected over 15 years about the extensive hybridization between the Herring and Glaucous gulls in Iceland. Herring Gull-like birds raised fewer young per nesting attempt that more Glaucous Gull-like individuals. Birds of intermediate appearance had a higher incidence of non-breeding than the others. It appears that the population in this area is not becoming more Glaucous Gull-like, possibly as a result of continuing immigration of pure Herring Gulls from Europe.

A variety of topics is discussed in this volume. I am confident that you, the reader, will find them stimulating as well as a significant contribution to the gull literature. Ernst Mayr (1984) vividly portrayed the contributions ornithologists have made to biology. It is clear that we are continuing to make progress. Our understanding of the appropriateness of techniques, the importance of long-term studies, and our attention to the effects our own activities may be having on the accuracy of our data, will enable gull biologists to make even greater contributions in the future.

This volume is the first joint publication of the

Pacific Seabird Group and the Colonial Waterbird Group and originated at their First Joint Meeting. We hope this achievement will stimulate further cooperation between two organizations which together can have profound influence on colonial waterbird and seabird conservation and management in this hemisphere and worldwide.

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