(ISBN: 0-943610-41-9)

# PATTERN, MECHANISM, AND ADAPTIVE SIGNIFICANCE OF TERRITORIALITY IN HERRING GULLS (*Larus argentatus*)

BY

JOANNA BURGER
Department of Biological Sciences
and Bureau of Biological Research
Rutgers University
Piscataway, New Jersey

ORNITHOLOGICAL MONOGRAPHS NO. 34

PUBLISHED BY
THE AMERICAN ORNITHOLOGISTS' UNION
WASHINGTON, D.C.
1984

# PATTERN, MECHANISM, AND ADAPTIVE SIGNIFICANCE OF TERRITORIALITY IN HERRING GULLS

## (*Larus argentatus*)

## ORNITHOLOGICAL MONOGRAPHS

This series, published by the American Ornithologists' Union, has been established for major papers too long for inclusion in the Union's journal, *The Auk.* Publication has been made possible through the generosity of the late Mrs. Carll Tucker and the Marcia Brady Tucker Foundation, Inc.

Correspondence concerning manuscripts for publication in the series should be addressed to the Editor, Dr. Mercedes S. Foster, USFWS/NHB-378, National Museum of Natural History, Washington, D.C. 20560.

Copies of *Ornithological Monographs* may be ordered from the Assistant to the Treasurer of the AOU, Frank R. Moore, Department of Biology, University of Southern Mississippi, Southern Station Box 5018, Hattiesburg, Mississippi 39406. (See price list on back and inside back covers.)

Ornithological Monographs, No. 34, xii + 92 pp.

Editor of AOU Monographs, Mercedes S. Foster

Special Reviewers for this issue, Joseph R. Jehl, Jr., Hubbs-Sea World Research Institute, San Diego, California; J. P. Myers, Academy of Natural Sciences, Philadelphia, Pennsylvania; Raymond Pierotti, Department of Zoology, University of California, Berkeley, California

Author, Joanna Burger, Department of Biological Sciences, and Bureau of Biological Research, Rutgers University, Piscataway, New Jersey 08854

First received, 24 January 1983; accepted, 9 June 1983; final revision completed, 3 February 1984

Issued August 21, 1984

Price $9.00 prepaid ($7.00 to AOU members).

Library of Congress Catalogue Card Number 84-71928

Printed by the Allen Press, Inc., Lawrence, Kansas 66044

ISBN: 0-943610-41-9

# PATTERN, MECHANISM, AND ADAPTIVE SIGNIFICANCE OF TERRITORIALITY IN HERRING GULLS (*Larus argentatus*)

BY

JOANNA BURGER
Department of Biological Sciences
and Bureau of Biological Research
Rutgers University
Piscataway, New Jersey

ORNITHOLOGICAL MONOGRAPHS NO. 34
PUBLISHED BY
THE AMERICAN ORNITHOLOGISTS' UNION
WASHINGTON, D.C.
1984

To
H. B. Tordoff

# TABLE OF CONTENTS

# LIST OF FIGURES

# LIST OF TABLES

# INTRODUCTION

In many avian species territorial behavior is a conspicuous and important component of the animal's overall fitness. Territory was defined as any defended space (Nice 1933; Noble 1939; Tinbergen 1952, 1956, 1957; Hinde 1956), although authors have argued for definitions involving aggressive defense of resources (Brown and Orians 1970; Wilson 1971), exclusive use of an area (Pitelka 1959; Schoener 1968), spacing patterns that differ from random (Davies 1978), and dominance relationships (Emlen 1957).

Territoriality has been extensively studied since Howard's (1920) early descriptions (Mayr 1935; Armstrong 1947). Most models for the evolution of territorial behavior assume that natural selection favors a particular territory size that maximizes reproductive success (Brown 1964). However, fitness is difficult to measure directly, and authors usually examine factors that are assumed to reflect fitness. In practice, ecologists use time-energy budgets to assess the costs of territoriality (e.g., Pyke 1979). Brown (1964) proposed that territory defense is correlated directly with the energy required to defend particular resources. Verner (1977) suggested that birds may also maximize their fitnesses by defending superterritories, which contain more resources than are required for reproduction, and, thereby, preventing other conspecifics from breeding. He assumed that the time required for territorial defense is a function of the mean distance between all possible points in the territory, and that larger territories require the expenditure of more energy for defense (MacLean and Seastedt 1979).

The primary questions surrounding territoriality deal with the pattern (size, shape), mechanism (behavior, time, and energy expenditures), and adaptive significance (reproductive success) of territorial behavior (Patterson 1980). Models proposed to explain the evolution of territoriality have often assumed that amount of aggression and territory size are directly correlated (Verner 1977), and that territory size affects reproductive success (Parker and Knowlton 1980). Field data concerning these assumptions are fragmentary or non-existent for most species. In this study I examine the pattern, mechanism, and adaptive significance of territorial behavior in Herring Gulls (*Larus argentatus*). I examine variations in size of territory, type and quantity of aggressive behavior in defense of territories, reproductive success, and the relationship between territory size, aggression, and reproductive success; I develop hypotheses concerning the relationships among them. Although some of these relationships have been examined previously in gulls (see below), not all aspects have been examined in any one species. I follow Emlen's (1957) definition of a territory as an area occupied by a bird, and in which it is usually dominant over conspecific intruders.

Herring Gulls are ideal for a study of territoriality because they are abundant, large, colonial, and show sufficient size dimorphism to allow experienced observers to sex members of a pair by sight. The territorial behavior of several gull species has been examined (Tinbergen 1952, 1956; Burger and Beer 1975; Hunt and Hunt 1975, 1976; Hutson 1977; Ewald et al. 1980). Herring Gulls have nesting territories (Type D of Nice 1941) in which all breeding activities such as copulation, incubation, and chick care occur. Herring Gulls sometimes defend a separate, small, pairing territory early in the season (Tinbergen 1956), but in this paper "territory" refers to their nesting territories unless otherwise specified.

## TERRITORY SIZE, AGGRESSION, AND REPRODUCTIVE SUCCESS

### TERRITORY SIZE

Determinations of the size and shape of territories are hampered by the difficulty of defining precise boundaries. In most studies, territory size has been measured for only a short period of time during part of the reproductive cycle rather than from daily observations throughout the cycle. Early investigators thought that territory size was fixed throughout the season (Kluyver and Tinbergen 1953). Huxley (1934) proposed that territories are like rubber discs; they can be expanded and contracted as conditions dictate, but there is a minimum size that provides adequate resources for reproduction (nesting territories) or for efficient foraging (foraging territories). More recent studies have shown, however, that territory size varies as a function of age of the defenders (Dhondt and Huble 1968; Ralph and Pearson 1971), time of day (Stenger and Falls 1959; Weeden 1965), environmental constraints (Hand et al. 1981), and stage of the breeding cycle (Stenger and Falls 1959; Stefanski 1967; Falls 1969; Veen 1977; Burger 1981a). In gulls, territory size is often estimated by measuring the distance to the closest neighbor or by observing the location of displays and fights with neighbors (Patterson 1965; Hunt and Hunt 1976; Hutson 1977). Territory size is largest early in the cycle in Southern Black-backed Gull (= Kelp Gull, *L. dominicanus*; Fordham 1964a) and Black-headed Gull (*L. ridibundus*; Hutson 1977), at hatching in Western Gull (*L. occidentalis*; Hunt and Hunt 1975; Pierotti 1981), or later in the season in Great Black-backed Gull (*L. marinus*; Verbeek 1979). Hunt and Hunt (1976) noted that in Glaucous-winged Gulls (*L. glaucescens*), territory size increased for 56 percent of the pairs, decreased for 17 percent, and remained constant throughout the season for the rest (27%) of the pairs. Thus, among gulls, territory size varies seasonally; it also varies with habitat (e.g., Ewald et al. 1980).

Variation in the timing of maximum territory size in gulls suggests that the specific function of territoriality may differ among gull species at different times of the nesting cycle. Presumably, territory size should be large early in the reproductive cycle when gulls are establishing territories, settling boundaries between neighbors, preventing territory-seeking pairs from usurping areas, and protecting mates from extrapair copulations. If the pressure from intruders continues, then territory size may remain constant as birds vigorously defend their borders. If pressure from intruders subsides, then territory size may increase. If pressures of predation or cannibalism are high, territory size may increase during the chick phase to provide space for chicks to wander without being killed by neighbors.

In some gull species or colonies, cannibalism is one of the major causes of egg and chick mortality (Ward 1906; Parsons 1971; Hunt and Hunt 1976; Burger 1979a, 1980a). To prevent losses of eggs, gulls should reduce the size of the area they defend because the primary mode of protection is through incubation. To prevent losses in the chick phase, however, parents should increase territory size to provide adequate loafing space for chicks. Because cannibalism is prevalent in Herring Gulls (Parsons 1971), I hypothesized that territory size should be greater in the chick phase than during incubation. Likewise, because territory size may reflect intruder pressure, I predicted that the smallest territories should occur in the prime nesting areas where many gulls seek to nest (Ewald et al. 1980). I define prime nesting areas as those occupied earliest in the season in the best habitat (bushes, Burger and Shisler 1978a, b).

### AGGRESSIVE BEHAVIOR

One aspect of reproductive investment that can be measured is aggressive behavior in defense of a territory. The mechanism of spacing in birds results partly from aggressive behavior directed at intruders, whether they are neighbors or strangers (Tinbergen 1956; Davies1978; Ewald et al. 1980; Burger 1981b; Krebs 1982). The outcome of such aggression is a territory of a certain size that justifies the cost of its acquisition in terms of increased reproductive success. Variations in agonistic behavior and the quantitative analysis of aggression have received minimal attention (Itzkowitz 1979). The problem lies in determining the area defended. Territory boundaries must be delineated before the percent of intruders attacked can be computed for that territory; yet, attack behavior is used to define territorial boundaries. The obvious circularity creates methodological problems. I use the term aggression to mean behavior directed at an intruder (either neighbor or non-neighbor) that usually results in the departure of the intruder or prevents forfeiture of space by the resident (Van Rhijn 1981). Indeed, territory owners usually defeat intruders (Krebs 1982).

In gulls and terns the importance of aggression was recognized early (Tinbergen 1959, 1960), and considerable attention has been devoted to descriptions of aggressive displays and aggression rates (Stout and Brass 1969; Stout et al. 1969; Beer 1976, 1980; Galusha and Stout 1977; Hayward et al. 1977; Amlaner and Stout 1978).

Aggression varies during the breeding cycle in gulls and terns. Territorial aggression rates are highest during the pre-incubation phase in Arctic Tern (*Sterna paradisaea*; Lemmetyinen 1971), Laughing Gull (*Larus atricilla*; Burger and Beer 1975), Black-headed Gull (Hutson 1977), and Lesser Black-backed (*L. fuscus*; MacRoberts and MacRoberts 1972a, b) and Southern Black-backed Gulls (Fordham 1964a). In Great Black-backed Gulls, aggression increases as the season progresses (Verbeek 1979). In other species, rates of aggression are highest at hatching (Sandwich Tern, *Sterna sandvicensis*; Lemmetyinen 1971). Similarly, in Laughing Gulls overt fighting increases slightly during the chick phase (Burger 1976). In some species, the peaks in rates of aggression occur at different points in the reproductive cycle in different colonies. For example, the rates of aggression of Common Terns (*Sterna hirundo*) can be highest early in the reproductive cycle (Lemmetyinen 1971), or at hatching (Veen 1977). Gulls not only show seasonal changes in rates of aggression, but also daily changes (Fetterolf 1979; Conover and Miller 1980).

Rates of aggression are also correlated with other factors (age and sex of defender and intruder, density, vegetation). Several authors noted that male gulls contribute more to defense than do females (Tinbergen 1960; Pierotti 1981), and are present on the territory for more time (Vermeer 1963). Pierotti (1981) found variability in the relative proportion of time males and females spend on the territory as a function of year and colony, as well as stage in the reproductive cycle. Black-headed Gulls respond differently to neighbors and non-neighbors (Patterson 1965). Similarly, Hutson (1977) showed that the distance from the nest at which the intruder is attacked in Black-headed Gulls varies as a function of sex of the intruder, location on the colony (central vs. peripheral), and nest density. The response of Laughing Gulls to intruders also depends on the age of the intruder (Burger and Beer 1975). The presence of vegetation, which decreases visibility of intruders, also may affect rates of aggression (Burger 1977a, b).

Ewald et al. (1980) emphasized the importance of examining intrusion rates in Western Gulls. They found that as territory size increased, the time spent per act of aggression increased. This finding partially corroborates Tullock's (1979) assumption that the greater the area, the greater the cost of territorial defense. However, Ewald et al. (1980) studied a low density colony of Western Gulls. Butler and Trivelpiece (1981) found the opposite; Great Black-backed Gulls in high density areas (with small territories) engaged in significantly more bouts of agonistic interactions.

In summary, aspects of territorial behavior have been extensively examined in gulls. Patterns and rates of aggression vary as a function of season, time of day, habitat, nest density, nature of intruder (age, sex), intrusion pressure, and location of the nest at the center or periphery of the colony.

## REPRODUCTIVE SUCCESS

The obvious measure of fitness is lifetime reproductive success (Lack 1954, 1968; Williams 1966; Ricklefs 1977). It is difficult to compute total reproductive success for long-lived seabirds that nest on remote islands. It is possible, however, to measure reproductive success of several pairs nesting in a colony for one or several years, and to evaluate the benefits of territoriality or aggressive behavior, it is essential to determine reproductie success.

Measuring reproductive success is difficult because success varies yearly and can be modified significantly by the presence of investigators (Manuwal 1978; Nisbet 1978; Schreiber 1979; Burger 1981c). Reproductive success has often been correlated with a number of variables including habitat and nest sites (see Montevecchi 1978), age and experience of the parents (Coulson 1966; Ryder 1980), date of egg-laying (Burger 1981d), and location in the colony (Coulson 1968).

The primary causes of lowered reproductive success in most seabirds are predation (including cannibalism and kleptoparasitism), starvation, and weather-related problems (reviewed in Parsons 1971; Davis 1975; Burger 1981d, in press; Hand et al. 1981). However, a few species of seabirds are vulnerable to oil slicks, fish nets, and exploitation by man (Manuwal 1978). The dispersion of nests within a colony seems to be a compromise between nesting so far apart that eggs or young are not detected by predators (Cullen 1960; Tinbergen 1967; Tinbergen et al. 1967; Krebs 1973), and nesting close enough to allow defense by the group (Lack 1954; Crook 1964; Kruuk 1964; Pulliam 1973).

Weather-related events can drastically lower reproductive success. Species that nest in unstable habitats (e.g., sandbars, marshes), such as Black-billed Gull (*L. bulleri*; Beer 1966; Evans 1982), Franklin's Gull (*Larus pipixcan*; Burger 1974a), Brown-hooded Gull (*L. maculipennis*; Burger 1974b), Laughing Gull (Montevecchi 1978; Burger and Shisler 1980), and Common Tern (Burger and Lesser 1978, 1979) are subject to flooding due to tides or heavy rains. Heat stress and extended exposure to rain or hail also cause mortality of young gulls and terns (Austin 1933; Power 1964; Harris and Plumb 1965; Nisbet 1975). Starvation is an important cause of chick mortality, but it is not clear if it results from insufficient parental care (Ryder 1980), inability of particular chicks to compete with nestmates for food (Lack 1968; Coulter 1977; Hahn 1981), or low food supplies (Lack 1954; Ashmole 1963, 1971).

## Territory Size, Rates of Aggression, and Reproductive Success

Often, theoretical models of optimum territory size are based on the assumptions (1) that a direct relationship exists between territory size and rates of aggression (i.e., that the time and energy required to defend territories is correlated directly with territory size or resource value), and (2) that territory size and aggression are correlated with reproductive success (i.e., that birds with larger territories or those that are more aggressive have higher reproductive success than less aggressive birds with smaller territories, see Verner 1977). There is, however, little field data to support these two assumptions.

In 1938 Darling reported that Lesser Black-backed Gulls on larger territories had higher reproductive success than those nesting on smaller territories. Fordham (1964a, b) reported that egg loss (and, thus, reproductive success) related to nest density (an indication of territory size) in Southern Black-backed Gulls. Although Hunt and Hunt (1976) found that Glaucous-winged Gulls on larger territories had higher reproductive success in one year, they did not find this the second year. Similarly, Patterson (1965) and Vermeer (1963) found no relationship between nest density and reproductive success in Black-headed Gulls and Glaucous-winged Gulls.

Thus, the relationship between territory size and reproductive success in gulls has not been clearly determined. One point of confusion is that size per se is not always a good indicator of quality, particularly for territories used for food gathering. Size may be correlated with quality when one compares a group of contiguous territories at the same time, but not when one compares distant territories or territories in the same location across years.

## Theoretical Considerations and Predictions

I assumed that territory size, levels of aggression, and reproductive success in Herring Gulls would vary. Indeed, Tinbergen (1956, 1960), Harris (1964), and Brown (1967a, b) noted such variations. Theoretically, the relationship between territory size and aggression could vary depending on environmental and social conditions, although many authors (e.g., Verner 1977) assume that larger territories require more overt aggression (Fig. 1A). I suggest that even if such a relationship exists, territory size should have a lower limit (Huxley's rubber disc model, 1934) beyond which birds cease to defend a space insufficient for reproduction (Fig. 1B). The relationship between aggression and territory size may be curvilinear with aggression increasing disproportionately to the increase in territory size (Fig. 1D). Presumably, an increase in area results in an increase in intruders, accounting for the increase in aggression.

Intruder pressure may depend upon the density of intruders. When the intruders are neighbors (usually interacting only at borders), rather than strangers (landing anywhere within the territory), the rates of aggression may be highest on small territories, where neighbors are close to the nest site (Fig. 1C). Strangers attempting to establish territories may be more apt to land on large territories where there

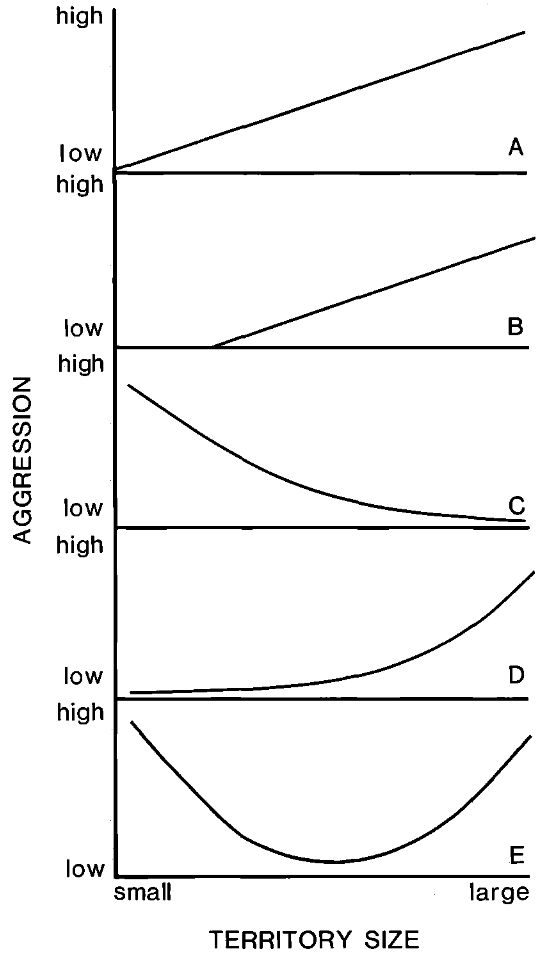

FIG. 1. Schematic representation of possible relationships between territory size and rates of aggression. Rates of aggression could increase (A, B, D) or decrease (C) as territory size increases, or could be related curvilinearly to territory size (E). Although authors have generally proposed a positive relationship between the two factors (A), presumably a minimum territory size exists below which birds cease to defend their areas (B).

are open spaces unoccupied by gulls, and neighbors may be more apt to fight when they are closer together, as they would be on small territories. Therefore, for Herring Gulls, I hypothesized that the owners of large territories would engage in frequent encounters with strangers (attempting to establish territories) and that those on small territories would engage in frequent encounters with neighbors. Thus, I predicted a curvilinear relationship with rates of aggression highest on small and large territories, and lowest on intermediate-sized territories (Fig. 1E, but see King 1973).

Biologists sometimes assume that gulls on large territories are more successful than gulls on small ones (Fig. 2A, but see Davies 1978, 1980; Myers et al. 1981), a finding reported for Glaucous-winged Gulls under some conditions (Hunt and

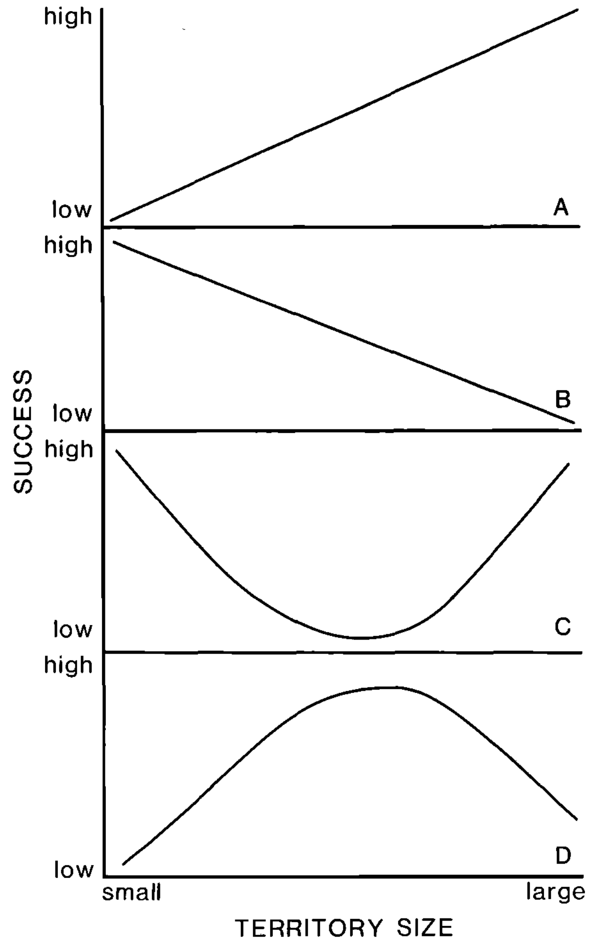

FIG. 2. Schematic representation of possible relationships between territory size and reproductive success. Reproductive success could increase (A) or decrease (B) as territory size increases, or it could be related curvilinearly with territory size (C, D).

Hunt 1976). The opposite could occur (Fig. 2B) if gulls on large territories spent all their time fighting and neglected their chicks (aggressive neglect; Hutchinson and MacArthur 1959; Ripley 1961; Dow 1979). One could argue that success would be highest on very small territories (if aggression due to neighbors were low) and on very large territories (if neighbors were so far away they were ignored, and if non-neighbor intruders were few), and would be lowest on intermediate-sized territories with frequent non-neighbor intruders and neighbors that were close enough to attack frequently (Fig. 2C). However, I hypothesize that eggs and chicks on very large territories may be neglected because parents are defending against strangers (non-neighbor intruders), whereas those on small territories may be neglected because parents are defending against neighbors (Fig. 2D). For example, on a small territory, a neighbor moving about within its own territory could induce territorial defense due to the close proximity of nest sites. Further, chicks on small territories may be more likely to wander on to a neighbor's territory while their parents are defending the territory against other intruders (Hunt and Hunt 1975, 1976). These hypotheses lead to the prediction also made by Davies (1978: fig. 11.2) that, for Herring Gulls, reproductive success should be highest on intermediate-sized territories (Fig. 2D).

Another possibility is that reproductive success and territory size are not related. Patterson (1965) found no relationship between nest density (an indication of territory size) and reproductive success in Black-headed Gulls, and Vermeer (1963) found no differences in fledging success of Glaucous-winged Gulls breeding at two different densities. At any given nesting density territory sizes of the nesting gulls vary. I suggest that in the above cases fledging success for pairs holding large versus small territories may have differed within each study area, but such differences cannot be detected by comparing mean fledging success between areas.

One assumption frequently made about territorial behavior is that the most aggressive individuals have the highest reproductive success (Fig. 3A). Considerations of aggressive neglect suggest the opposite relationship; birds that are less aggressive should have higher reproductive success (Fig. 3C). I hypothesized that Herring Gulls exhibiting low levels of aggression would be unable to defend territories large enough to successfully fledge young, or would fail to defend their chicks, whereas those exhibiting high levels of aggression would be unsuccessful because they would devote excessive time and energy to defense at the expense of guarding or feeding their chicks. Thus, I predicted that Herring Gulls engaged in intermediate levels of aggression would have the highest reproductive success (Fig. 1B).

In this study I gathered data on territory size and shape, aggressive behavior, and reproductive success. I test four major hypotheses. They are, (1) that territory size, rates of aggression, and reproductive success vary in Herring Gulls, (2) that gulls with intermediate-sized territories exhibit the lowest levels of aggression, (3) that gulls with intermediate-sized territories have the highest reproductive success, and (4) that gulls with intermediate levels of aggression have the highest reproductive success. In the following sections I discuss methods, territory size, aggressive behavior, reproductive success, and the relationships among territory size, aggressive behavior, and reproductive success. To some extent there will be unavoidable parallels in the discussions of territory size and of aggression, but as the relationship between these is a major topic of this paper, they must be discussed separately first.

## METHODS

### STUDY SPECIES

The Herring Gull (wt. = ca. 900–1,400 g) has a Holarctic distribution. The species requires four years to achieve fully adult plumage (Dwight 1925), although in many colonies younger birds may breed (Burger and Gochfeld 1981a). The species formerly bred mainly above 50°N latitude (Dwight 1925:193), but dramatic range extensions occurring in the twentieth century have been documented for both North America (Paynter 1949; Drury and Kadlec 1974) and Europe (Harris 1970).

The Herring Gull, like most gulls, shows a small but readily perceptible sexual

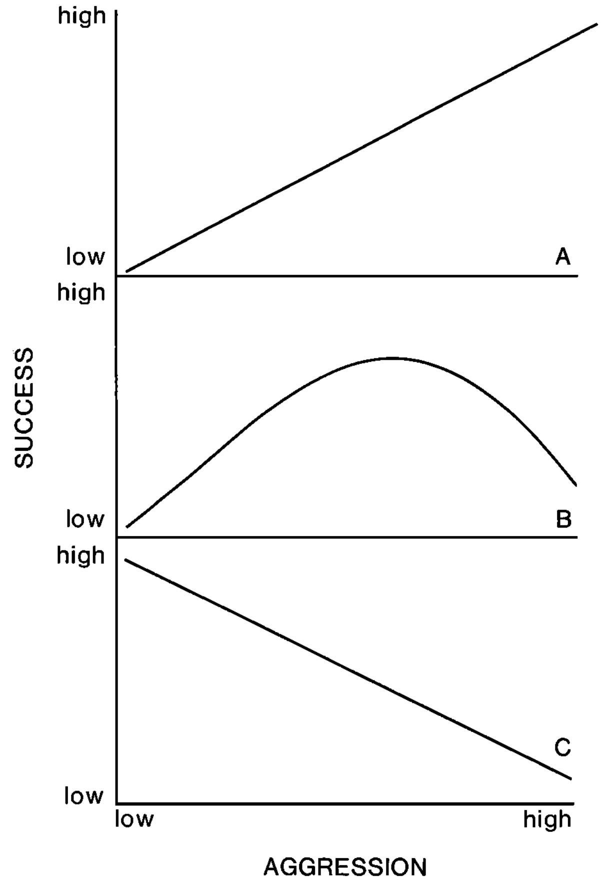

FIG. 3. Schematic representation of possible relationships between rates of aggression and reproductive success. Reproductive success could be highest in birds that are most aggressive (A), least aggressive (C), or exhibit intermediate levels of aggression (B). Very aggressive birds may have low success because they neglect eggs and chicks while they are aggressive, whereas non-aggressive birds may fail to defend a territory or chicks adequately.

size dimorphism (Bianki 1967; Ingolfsson 1969; Shugart 1977; Fox et al. 1981; Pierotti 1981). Males of the American race (*L. a. smithsonianus*) have wings 5 percent longer, culmens 14 percent longer, and bills 13 percent deeper than females. Male *smithsonianus* from Ontario, Canada, average 1,166 g, compared with 943 g for females (Fox et al. 1981). In most pairs the size dimorphism is readily apparent in the field upon close scrutiny.

Herring Gulls nest on the ground, often among dense vegetation, on rocks or cliff faces, and, rarely, even in trees (Bent 1921:103). Solitary nesting occurs in some arctic regions (Jehl and Smith 1970), although colonies exceeding a thousand pairs are characteristic of most populations (Paynter 1949). The modal clutch size in almost all populations is three (Paynter 1949), and supernormal clutches of more than 5 eggs are now recognized as being characteristic of unusual pairs, particularly those comprised of two females (Hunt and Hunt 1977; Conover et al. 1979; Ryder and Somppi 1979; Hunt 1980). Two contiguous nests bearing the eggs of two females mated to a single male have been found in some Great Lakes colonies (Shugart and Southern 1977; Fitch 1979; Shugart 1980).

Bent (1921) reported incubation periods of 24 to 28 days, a range that covers the values obtained in the present study. Both sexes share in incubation and feed the young, and one bird usually remains on territory at least until the third or fourth week of the chick phase (Dutcher and Bailey 1903). Infanticide and cannibalism are the most prominent forms of "predation" in some Herring Gull colonies, and have been emphasized as major selection pressures by many recent authors. Therefore, young gulls face a risk when they wander into a neighboring territory (Ward 1906; Parsons 1971). Details of colony and nest site selection for gulls studied in New Jersey are provided in Burger (1977a, b, 1979a, b, c) and Burger and Shisler (1978a, b). Detailed discussion of incubation behavior and physiology are provided by Baerends and Drent (1970), who did not, however, separate data for male and female behavior.

Herring Gulls are opportunistic feeders, frequently scavenging along beaches and foraging on garbage, which obscures the fact that usually most of their food is obtained from natural sources (Hunt and Hunt 1973), with dumps playing a role in sustaining inexperienced young or in allowing adults to winter farther north than in the past.

## STUDY AREAS

I studied Herring Gulls in 1976, 1977, and 1978 on Clam Island, New Jersey, in 1977 and in 1978 on Carvel Island, New Jersey, in 1979 and 1980 at Meadow Island and Captree (Long Island), New York, and in 1980 on Appledore Island (Isles of Shoals), Maine.

Clam Island is a 54 ha salt marsh island in Barnegat Bay, Ocean County, New Jersey (39°45′N, 74°08′W). Several channels cut the island into four major islets. Predominant vegetation is comprised of *Spartina alterniflora* (62%), *S. patens* (30%), and bushes (*Iva* and *Baccharis,* 8%) with a maximum height of 1.5 m. Ponds cover 25% of the island, although this varies with storm tides and rains. Clam Island contains a nesting colony of 600 to 800 pairs of Herring Gulls (depending on the year), 6 to 12 pairs of Great Black-backed Gulls, and 3,000 to 5,000 pairs of Laughing Gulls that nest in the *S. alterniflora* in lower sections of the marsh. The Herring Gulls nest in the high elevation areas with *S. patens* and bushes (about 30% of Clam Island), and so avoid the frequent flood tides.

Five habitat types, classified on the basis of vegetation cover, and used by Herring Gulls, can be recognized on Clam Island. Further, some solitary-nesting gulls nest in open grass. The grass in all Herring Gull nesting habitats is *Spartina patens.* Habitat types were determined for the 5 m around each nest by percent cover estimates. The habitat categories are: (1) Dense Bushes: 50% bush cover; (2) Intermediate Bushes: 20–49% bush cover; (3) Clumped Bushes: 5–19% bush cover; (4) Sparse Bushes: 5% bush cover; (5) Open Grass: no bushes.

Carvel Island (Barnegat Bay, New Jersey) is a 1.8 ha island covered 40 percent by bushes, and 60 percent with *S. alterniflora* and *S. patens.* The colony contains about 100 pairs of Herring Gulls, 6 pairs of Great Black-backed Gulls, 80 pairs of Common Terns, and 16 pairs of Black Skimmers (*Rynchops niger*).

Both Herring Gull colonies in New York are located in sand dunes on the barrier beaches of Long Island. The vegetation is mainly Beach Grass (*Ammophila breviligulata*) fringed by low shrubs (*Rhus toxicodendron, Prunus nigra*). Meadow Island (40°36′N, 73°33′W) is 70 percent open sand, whereas Captree (40°39′N, 73°16′W) is 20 percent open sand. Both colonies are in high inter-dune areas that are free from any threat of tidal flooding. The Meadow Island colony (ca. 2 ha) contains 500 pairs of nesting Herring Gulls and 5 pairs of Great Black-backed Gulls, whereas Captree (ca. 15 ha) contains 1,200 pairs of Herring Gulls and 100 pairs of Great Black-backed Gulls.

The gull colony on Appledore Island (16 km E Maine coastline, 42°59′N, 70°37′W) occupies a variety of habitats including cliffs, rock outcroppings, grassy knolls, and low bushes (*Prunus* sp., *Rhus toxicodendron*). Approximately 2,000 pairs of Herring and 800 pairs of Great Black-backed Gulls nest on Appledore Island. Although the species nest together in some areas, they generally nest in monospecific groups over most of the island (Burger 1983). Black-backed Gulls nest on open grassy areas, and Herring Gulls nest on rocky shores and under bushes.

## GENERAL METHODS

Observations were made on Clam Island from 15 March to 20 August in 1976, 1977, and 1978. Two field assistants working full time obtained estimates of territory size and monitored reproductive success on samples of 256 to 442 nests per year. I spent 60 to 84 hrs per week observing from a blind, monitoring aggressive behavior, mapping fluctuations in territory size, and measuring reproductive success on 14 to 15 individually marked pairs each year. This dual approach allowed me to make detailed observations on individually marked birds while collecting data on territoriality and reproductive success on a sufficient number of gulls to allow statistical analysis.

### BEHAVIORAL OBSERVATIONS OF INDIVIDUAL PAIRS

From 1976 to 1978 I made behavioral observations on birds occupying three study plots located in the center of the colony, in an intermediate bush habitat. I chose areas in prime, preferred habitat (Burger and Shisler 1978a), expecting them to contain the oldest, most experienced, and successful gulls (Ryder 1980).

Behavioral observations were usually conducted from 06:00 to 20:00 each day, four to six days per week during the nesting period for a total of approximately 3,682 hrs on Clam Island. To avoid undue disturbance one field assistant walked me to the blind, then departed, and returned to retrieve me at the end of the day, since gulls settle down more quickly when someone is seen to leave the blind and gullery. I always entered the blind from the rear, and no one ever walked in my observation area except to color-mark adults and young. The number of pairs observed each year is shown in Table 1.

During the pre-incubation period, I determined sex on the basis of size dimorphism. Thereafter, all gulls were dyed for individual identification, and sexed by measurements, body size, and copulation position (only if the same bird was on top at least three times). Pierotti (1981) reported that female gulls never mount males. I color-marked adults by suspending a small cup of dye above the nest. When the bird returned to incubate, I pulled a string attached to the cup, tipping it and pouring dye over the sitting bird. The dye did not fall on the eggs. By using

## TABLE 1
NUMBERS OF HERRING GULLS OBSERVED IN THIS STUDY

| | 1976 | 1977 | 1978 | 1979 | 1980 |
|---|---|---|---|---|---|
| Clam Island, New Jersey | | | | | |
| Behavioral observations | | | | | |
| Pairs by my blind | 14 | 15 | 14 | — | — |
| Pairs in intermediate bush habitat | 12 | 12 | 8 | — | — |
| Pairs in grass (in colony) | 12 | 12 | 8 | — | — |
| Pairs in grass (nesting solitarily) | 12 | 12 | 6 | — | — |
| Ecological and success data | | | | | |
| Nests followed[1] | 256 | 382 | 442 | — | — |
| Carvel Island, New Jersey | | | | | |
| Nests followed[1] | 98 | 101 | — | — | — |
| Captree, New York | | | | | |
| Pairs by my blind | — | — | — | 15 | 12 |
| Meadow Island, New York | | | | | |
| Pairs by my blind | — | — | — | 15 | 12 |
| Appledore Island, Maine | | | | | |
| Pairs by my blind | — | — | — | — | 18 |

[1] Includes only nests for which complete data were obtained (ca. 60% of the nests each year).

several colors I could easily identify individuals by their splash patterns. This procedure resulted in minimal disturbance to the birds, which immediately settled and were not distressed by being trapped or handled. The dye lasted until late August.

Because I wanted to identify neighbors, I color-marked all pairs in my study plot, and all of their nearest neighbors. I defined neighbors as gulls that shared a territory boundary. A non-neighbor was any gull that did not share a boundary. At the beginning of the incubation period each year I color-marked 15 pairs of gulls (plus their neighbors).

Upon first entering the blind, I recorded the date, time, and weather (rain, fog, temperature, cloud conditions). Thereafter, I recorded all aggressive interactions on timed sheets (half-hour intervals), noting the participants (individual defending, whether aggressor was a neighbor or not, individual and sex if the intruder was a neighbor, and sex if intruder was a non-neighbor), the aggressive behavior exhibited, distance the encounter was from the nest site, and outcome. Any agonistic behavior directed at another gull was considered to be an aggressive interaction, and included Long Calls, Walking or Flying Toward an intruder located on the ground, Grass Pulling or Choking directed at an intruder, aerial chases, overt attacks, and fights (see Moynihan 1955, 1956, 1958a, b, 1959a, b, 1962 for descriptions of displays). A defender won the encounter if the intruder left (as non-neighbors usually did). Encounters between neighbors either resulted in a win (in which case the former territory boundary may have shifted), or a draw (which frequently occurred at the accepted territory boundary).

*Territory size.*—I determined the distance the encounters were from nest sites by using stakes placed at 3 m intervals before the nesting season, and all encounters were plotted each day on maps containing the locations of all nests. I then drew a line around the points of defense for each pair (Burger 1980a). I also recorded the stage of the reproductive cycle of each pair on the maps, which were dated and used to determine territory boundaries. Boundaries between neighbors were easily defined because long Grass Pulling encounters frequently occurred at the same locations. A digitizing tablet was used to enter points directly into the computer for determination of the area of each territory. I determined territory size for pairs by stage in the reproductive cycle, as well as for the entire cycle. I correlated mean territory size from egg-laying to 30 days post-hatching with internest distances for the 43 pairs of gulls I observed around my blind.

Because the movements of chicks provide an indication of territory size requirements, I examined chick movements in 1977. I mapped the location of every adult and all chicks every 15 min to determine chick movement as a function of age. I observed the chicks until they were at least 40 days old. In this relatively undisturbed colony chicks remained on their territories during this period (Burger 1981a). I also estimated the distance chicks and parents were from the nest every 15 min throughout the day in the intermediate bush habitat (4–5 days/week), grass habitat (1 day/week), and sparse bush habitat (1 day/week) on Clam Island in 1977. When the field assistants checked nests, they recorded the locations of all chicks (distance and compass direction from the nest). Chick locations were also noted on Carvel Island in 1978. Chicks were assigned to habitats based on the locations of their parent's nests.

*Aggressive interactions.*—All aggressive interactions (Long Call, Walk Toward, ground chase, Choke, Grass Pull, displace, aerial chase, and fight) observed each day were recorded on data sheets that were divided by nest number, sex of the nest owner, and time of day. I recorded the type of interaction, the distance from the nest, and the outcome (see above). Whenever an intruder landed within 3 m of a nest without eliciting a response, I entered it as no response. Long Calls and Choking were considered aggressive only when given to an intruder. Overt aggression included Walking Toward (but not actually to) an intruder, Flying Toward it (ground chase), flying and landing where the intruder had been (displaced), flying after an intruder was already airborne (aerial chase), or actually making physical contact (fighting).

Daily aggression frequency (interactions/hr) was then determined for each bird by dividing the number of its interactions by the amount of time it was on territory. I then obtained a mean aggression frequency for each bird for the entire season, and for the incubation and chick stages separately. I also computed a combined rate of aggression for the pair at each nest during the incubation and chick phases by dividing all aggressive encounters for both sexes at that nest by the number of hours of observation. The above aggressive interactions were recorded for four to six days a week during each breeding season for three years on Clam Island.

To ascertain the effects of environmental and behavioral variables on rates of aggression, I collected data in 15 min sample periods (06:00–20:00) from early incubation to 65 days post-hatching in 1978 on Clam Island. These samples were taken every three to four days (N = 30 days). At the beginning of each sample period I recorded the date, time of day, tide time (0 = low tide, 6 = high tide), rain conditions (0 = no rain, 6 = heavy rain), and percent cloud cover. For each pair (n = 14) I recorded stage in the reproductive cycle. During the sample period, I recorded all instances of aggression between neighbors and aggressive encounters with non-neighbors; total aggression is the sum of the two. I used a stepwise multiple regression procedure (S.A.S. 1979) to generate a model that best explained the variance in the dependent measure. The procedure first selected the independent variable that contributed the highest $r^2$ (coefficient of determination) to the dependent variable, then selected another variable the addition of which produced the maximum increase in the $r^2$, and so on until a point was reached at which no further variable produced a significant increase (at the 0.05 level). For the resulting model the procedure gave the overall $r^2$, the $F$ value, and the level of significance. The $F$ and $P$ values were also given for each independent variable in the model. The contribution that each variable added to the model is calculated after eliminating any effect from colinearity with variables already in the model (S.A.S. 1982).

To determine the effect of habitat on aggressive behavior and chick movement I observed gulls in habitats with bushes and in open grass. Both study areas were in the center of the gull colony. These observations were conducted 8 to 12 hrs a day, two days per week in 1978. To reduce the likelihood of age differences in the pairs sampled, I observed only pairs whose egg and clutch sizes were similar to those of the gulls that nested in the central study plot. In gulls, egg size is related to age of the female (Coulson 1963; Davis 1975; Ryder 1980).

I also examined the territorial behavior of solitarily nesting pairs of gulls (those nesting at least 50 m from another pair, located at the edge of the colony) and compared it to that of birds nesting in the grass, and near bushes (within the center of the colony). To minimize age effects I selected solitary pairs whose egg and clutch sizes were similar to those of birds nesting in the grass and bushes.

In May and June of 1979 and 1980 I observed territorial behavior of Herring Gulls in dry land colonies in New York (325 hrs) and Maine (120 hrs) to ascertain whether the patterns observed in New Jersey colonies were typical. I usually observed from 06:00 to 18:00. I examined rates of aggression and types of defense behaviors used by territorial birds as a function of stage in the reproductive cycle.

## DATA COLLECTED ON THE ENTIRE COLONY AT CLAM ISLAND

The entire colony was gridded at 50 m intervals so that nests could be accurately located on maps (by triangulation from two grid markers). All areas of the colony 50 m or more from my blind were checked every other day, and all new nests, eggs, and chicks were marked. When a new clutch was found, the distance to its closest neighbor (from center to center of nest), the habitat (classified above), and the distance to the edge of the colony (nearest peripheral nest) were recorded. Internest distances were used as approximations of territory size for the nests followed in 1977 and 1978. Internest distance was recorded at the time of nest initiation (a scrape in the ground which later resulted in a nest), and the distances to the nearest, second, and third neighbor nests were measured in the middle of the nesting season when no new nests were being initiated. By definition, the second and third neighbors' nests were in different 45° segments from the closest neighbor. These three measurements together give an approximation of territory size. The number of nests within a 5 m and 10 m radius of each nest provided a measure of density.

Newly hatched chicks were banded and, thereafter, weighed daily, and their locations noted. We kept a master list of U.S. Fish and Wildlife Service band numbers which gave the nest number of each chick, and a list of nest numbers which gave the grid location of every nest. Nest checks were made until chicks were at least 40 days old to determine reproductive success. Most chicks were found at least once in every two or three nest checks. We frequently found dead chicks, or their bands (in regurgitated pellets near other gull nests).

Chicks that moved from their nests when disturbed by nest checks either ran to a hiding place used previously, or found a new place. On each visit we plotted the location of each chick on maps, noting the shift in compass direction (in degrees) from its previous location (to test the hypotheses that chicks use the same hiding places repeatedly). I computed only the degree deviation in the direction of movement, and not the direction. Thus, values could range from 0° (moved in the same direction) to 180° (moved in the opposite direction). We always followed the same path through the colony, approaching each nest from the same direction each time. Data were obtained on a minimum of 10 shifts within each 3 day interval.

We found that the way we moved through the colony influenced disturbance. Rapid movement caused birds to flush up to 30 m away. When one moved slowly through the colony, gulls within 5 m flew overhead, gulls nesting 5 to 10 m away only stood on their nests or looked alert, and birds nesting more than 10 m away usually remained incubating.

### DETERMINATION OF REPRODUCTIVE SUCCESS

Reproductive success was determined only for gulls on Clam Island. For the birds around the blind, success was determined by observation of chicks when parents came to feed them. The field assistants checked all other areas of Clam Island for nests, eggs, and chicks every other day (1976–1978). Records were updated nightly so the content of each nest was known, including the hiding location and weight of each chick. At the end of the season we also captured chicks from the surrounding bay to determine if any chicks were unbanded (none was), and if missing chicks (not reported for several weeks) were alive (only 2 or 3 a year were located after having been missing for at least two weeks).

The fate of each egg was classified as hatched (a chick present), preyed on (evidence of peck holes or broken shells), addled (no apparent development, watery contents), or unknown (disappeared without any evidence). We followed all nests until the chicks were at least 40 days old. At 10 days of age all chicks were classified as alive, killed (peck marks, band attached to a leg only and found in the nest of a neighbor), starved (weight well below the mean weight of chicks that age, decreasing weight over the last few days), unknown (a dead body without evidence of starvation or attack), or missing (not found). At 20 and 30 days all chicks usually could be assigned to a category since missing chicks were too large to be able to hide successfully during nest checks and were visible if they had starved or been killed by neighbors. Missing chicks less than 20 days old were assumed to have been killed by predators (since they were still small enough to be eaten), whereas larger chicks were assumed to be fledged if they were seen at least once between 20 to 30 days of age. When chicks were never seen after 20 days of age, they were assumed to have been preyed on if their siblings were regularly located (broods tend to stay together).

I computed several measures of reproductive success, (1) mean clutch size:

number of eggs laid per nest; (2) hatching rate: number of eggs hatched per nest; (3) nest hatching success: percent of nests in which at least one egg hatched; (4) fledging rate: number of chicks alive per nest at stated ages; (5) fledging percent: two measures were computed, the percent of eggs laid that resulted in live chicks at a given age (20, 30 days), and the percent of hatched eggs that resulted in live chicks at a given age.

### PREDATION EXPERIMENTS

Observations from the blind in 1976 indicated that predation was one of the main causes of egg and chick mortality in undisturbed areas. In 1977, heavy flood tides washed out a large number of Herring Gull eggs on a nearby island, and I placed these eggs in dummy nests in different habitats to determine the effect of cover on predation rates. I made 12 artificial nests (3 eggs each) of *Zostera* in each of several habitats: dense bushes, intermediate bushes, clumped bushes, and open grass. From a blind I recorded the time until the first egg in each nest was eaten by a conspecific, noting if the predator was a neighbor or non-neighbor. In an area where I had color-marked both members of eight pairs, I conducted another experiment with artificial nests and eggs to determine whether both males and females were predators.

### COMPARISON OF TERRITORY SIZE, AGGRESSION, AND REPRODUCTIVE SUCCESS

For the Herring Gulls observed from the blind (Clam Island, 1976–1978) I determined reproductive success (hatching rate, fledging rate) by observing nests, parents, and chicks from the blind four to six days per week until the chicks were at least 40 days old. I then examined variations in reproductive success as a function of territory size, distances to the nests of nearest and second nearest neighbors, and defense behavior (active and passive). Methods of measurement of territory are given in Burger (1980a). Passive defense included the percent of time males and females incubated and the percent of time they were present on territory when not incubating or brooding. Active defense was measured as (1) the approach distance (distance from the nest that an intruder elicited a response), (2) the mean aggression frequencies of males and females during the incubation and chick phases, and (3) the combined rates of aggression of pairs at the nest.

Finally, stepwise multiple regression procedures were used to determine the factors contributing to the variance in the reproductive success of the 43 pairs of Herring Gulls observed on Clam Island (S.A.S. 1979). Factors considered included: date of initiation of egg-laying, mean internest distances (nearest, second, third), territory size (primary, secondary, and unique, see p. 17), amount of time male or female incubated or was present, amount of time both were present, levels of aggression, and approach distance.

Data on territory size and aggressive behavior are not available for the remainder of the nests on Clam Island. Nonetheless, data on internest distances and nest density can be used as indicators of territory size. Similarly, data on reproductive success of birds at these nests were available, although estimates may be slightly lower than the actual reproductive success because some young less than 20 days old that disappeared may actually have fledged. I used multiple regression techniques to determine the percent of variance in reproductive success attributable to factors such as date of egg-laying, habitat (amount of bush cover present), internest distance, and density. For these nests (382 in 1977, 442 in 1978) I examined several parameters of reproductive success including clutch size, number of eggs that were rotten, preyed on, or hatched, number of chicks that were preyed on, and number of chicks that were alive at 20 or 30 days of age.

### STATISTICAL PROCEDURES

Where appropriate, Chi-square Goodness of Fit ($\chi^2$) and Student's $t$ tests were used to determine differences between samples, and correlation coefficients (Pearson $r$ or the non-parametric Kendall tau) were calculated. Where the data were normally distributed and met other required assumptions, I used Analysis of Variance to determine differences among samples. Least Significant Intervals were used to determine which means were significantly different (Zar 1974; Nie et al. 1975). This procedure is useful as it provides a method of determining significant differences among several means. Unless otherwise stated, I give means ± one standard deviation in the text.

To determine the effects of environmental and behavioral variables on rates of aggression (see above), and the relationship of reproductive success to territory size and aggressive behavior, I used multiple regression techniques. A stepwise regression (S.A.S. 1979, 1982) was used to select variables for incorporation into a general linear models analysis (Draper and Smith 1981). Statistical procedures were performed on log transformed data where appropriate.

## SPATIAL PATTERN OF NESTING TERRITORIES

In this chapter I examine (1) differences in territory size for individual pairs as a function of type of intruder, season, habitat, location, and nest density, (2) the movements of undisturbed and disturbed chicks, to determine the territory requirements chicks place on their parents, and (3) the distance disturbed chicks wander from their nests before hiding or crouching. If the latter distance exceeds the mean radius of territories, then chicks are exposed to attacks by neighboring gulls.

Herring Gulls on Clam Island defend three types of nesting territories at the same time (Burger 1980a): a primary territory defended against neighbors (gulls sharing territory boundaries), a secondary territory defended against strangers (any gull not sharing a territory boundary), and a unique territory that is defended against all intruders. Primary territories are contiguous, and non-overlapping; secondary territories are larger than primary territories, often extending into the primary territories of their neighbors. Gulls chase intruders in their secondary territories (outside their primary territory) only when their neighbors do not chase the intruders. The unique territory is smallest; it is that space where a gull will chase all intruders even if it must stop incubating to do so. The three territory types were examined in Burger (1980a) for only one year, and the relationships between territory size and aggression or reproductive success were not considered.

### RESULTS

### TERRITORY SIZE

*Pairs observed from the blind.*—Territory size varied seasonally and among pairs. Significant differences occurred among pairs within and among reproductive stages and territory types (Table 2, ANOVA, $F = 49.3$, d.f. = 6, 771, $P < 0.001$),

TABLE 2

TERRITORY SIZES OF CLAM ISLAND HERRING GULLS AT DIFFERENT REPRODUCTIVE STAGES[1]

| | Pre-incubation | Incubation | Chick phase |
|---|---|---|---|
| Primary territory | | | |
| 1976 | 49 ± 18 | 28 ± 4 | 61 ± 15 |
| 1977 | 53 ± 12 | 32 ± 3 | 73 ± 14 |
| 1978 | 46 ± 11 | 33 ± 4 | 78 ± 18 |
| Range 1976–1978 | 12–82 | 8–61 | 32–116 |
| CV | 27.80 | 11.93 | 22.28 |
| Secondary territory | | | |
| 1976 | 91 ± 12 | 62 ± 10 | 105 ± 21 |
| 1977 | 104 ± 8 | 70 ± 4 | 118 ± 18 |
| 1978 | 96 ± 18 | 55 ± 13 | 111 ± 17 |
| Range 1976–1978 | 42–160 | 32–76 | 48–191 |
| CV | 13.20 | 15.20 | 16.90 |
| Unique territory | | | |
| 1976 | 18 ± 3 | 21 ± 5 | 43 ± 16 |
| 1977 | 20 ± 4 | 22 ± 4 | 52 ± 18 |
| 1978 | 23 ± 6 | 19 ± 3 | 48 ± 17 |
| Range 1976–1978 | 6–42 | 8–32 | 14–58 |
| CV | 20.90 | 19.30 | 35.81 |

[1] Values are means ± one standard deviation, in $m^2$; sample sizes are 1976, 14; 1977, 15; 1978, 14. CV = coefficient of variation.

but not among years (*F* test). In all three years, the primary and secondary territories were smallest during incubation and largest during the chick phase. The unique territory was similar in size during the pre-laying and incubation phases, and larger during the chick phase.

Mean territory sizes for the entire reproductive season were computed by summing all data for each pair (Table 3). Because territory size changes during the reproductive cycle (Table 2), the variance of the mean across the entire reproductive cycle is greater than those for the means during each stage (Tables 2, 3).

The internest distances to the nearest and second neighbors at the end of the season were significantly correlated with the average size of the primary territory for the entire season for all three years (except nearest neighbor in 1977, Table 4). In 1978 the primary territory size was more highly correlated with the internest distance of the nearest neighbor, while in 1976 and 1977 it was more highly correlated with the internest distance to the second neighbor. No significant relationship existed between either the secondary or the unique territory size and internest distances. Although internest distance is usually calculated at the end of incubation, I measured it at egg-laying to reflect territory size at the time when the gull's primary activity is territory defense rather than incubation.

*Birds from the rest of Clam Island.*—Because I did not have data on aggressive interactions of gulls that did not nest near my blind, I used internest distance as an indication of territory size. I examined internest distances as a function of date of egg-laying (Table 5). All data were gathered in the three preferred habitats (dense bushes, intermediate bushes, and clumped bushes) in central areas of the colony to avoid biases due to habitat and location (Patterson 1965; Brown 1967a; Dexheimer and Southern 1975). The internest distance of the nearest neighbor

TABLE 3

TERRITORY SIZE AND INTERNEST DISTANCES FOR PAIRS OF CLAM ISLAND HERRING GULLS

| | 1976 | 1977 | 1978 | 1976–1978 |
|---|---|---|---|---|
| Number of nests | 14 | 15 | 14 | 43 |
| Primary territory area (m²): | | | | |
| Range | 16.0–41.0 | 22.6–72.6 | 16.0–61.0 | 16.0–72.6 |
| X̄ ± s.d. | 34.8 ± 8.3 | 37.0 ± 15.9 | 46.5 ± 14.5 | 38.9 ± 14.8 |
| CV[1] | 23.85 | 43.01 | 31.23 | 38.12 |
| Internest distance (m) | | | | |
| Closest neighbor: | | | | |
| Range | 2.3–6.0 | 2.5–5.8 | 2.9–8.3 | 2.3–8.3 |
| X̄ ± s.d. | 4.4 ± 1.9 | 4.8 ± 1.5 | 5.6 ± 1.4 | 4.8 ± 1.7 |
| CV | 43.20 | 31.35 | 25.00 | 35.40 |
| Second neighbor: | | | | |
| Range | 4.2–8.0 | 3.8–11.0 | 4.6–9.5 | 3.8–11.0 |
| X̄ ± s.d. | 5.3 ± 2.1 | 6.1 ± 2.6 | 7.7 ± 1.5 | 6.2 ± 2.3 |
| CV | 39.62 | 42.6 | 19.5 | 37.1 |

[1] CV = coefficient of variation.

at the time of nest initiation was similar for the early and middle periods, but was less for late-nesting gulls.

At the end of the incubation period, when few new nests were being initiated, I examined internest distances of the nearest, second, and third neighbors (Table 5). For all three egg-initiation periods nesting gulls had neighbors nesting closer during incubation than at the beginning of the cycle, indicating that some pairs succeeded in inserting themselves among already-established pairs. Assuming that internest distance to the second closest neighbor reflects territory size (Table 4), territory size was generally similar at nest initiation and in late May for pairs that laid late in the season; territory size was smallest in late May for gulls that initiated egg-laying early in the season (Table 5).

Territory size in the whole Clam Island colony, as indicated by internest distance, also varied among habitats (Table 6). Only data from nests initiated between 20 April and 15 May were used, in order to eliminate differences due to date of egg-laying. At the time of nest initiation, as well as later in the season, the lowest internest distances between nearest neighbors were in the clumped bush habitat. This habitat also had the highest density of nesting gulls. The closest second neighbors, however, were in the dense bush habitat.

## CHICK MOVEMENT

When undisturbed, chicks walk about the territory and are sometimes called back to nest sites by attending parents. The distance chicks move from their nest sites when undisturbed should be indicative of the territory size parents must defend to successfully fledge chicks. By examining chick movement in different habitats and under different disturbance regimes, I determined the space requirements of chicks.

*Birds observed from the blind.*—At undisturbed nests, chicks and their parents

## TABLE 4
## RELATIONSHIP BETWEEN INTERNEST DISTANCES AND TERRITORY SIZES FOR HERRING GULLS[1]

| Internest distance to | Territory area<br>Primary | Secondary | Unique |
|---|---|---|---|
| 1976 (N = 14) | | | |
| Nearest neighbor | .73*** | .00 | .35 |
| Second neighbor | .78*** | .11 | .00 |
| 1977[2] (N = 15) | | | |
| Nearest neighbor | .17[2] | .05 | .40 |
| Second neighbor | .83***[2] | .35 | .07 |
| 1978 (N = 14) | | | |
| Nearest neighbor | .68*** | .04 | .32 |
| Second neighbor | .45* | .18 | .00 |
| 1976–1978 | | | |
| Nearest neighbor | .53** | .03 | .37 |
| Second neighbor | .68** | .22 | .02 |

[1] Clam Island; values are correlation coefficients and levels of significance (* = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$).
[2] From Burger 1980a.

remained within 4 m of their nests until the chicks were 35 days old (Fig. 4). For the entire period, the mean distance (1.2 m, s.d. = 0.84 m) between chicks and their nests was similar to the mean distance (1.31 m, s.d. = 0.80 m) between parents and the nest (two-way ANOVA on repeated measures with log transformed data $P > 0.05$). However, adults were significantly farther from the nests than chicks (two-tailed Sign Test, $z = 3.6$, $P < 0.0002$). Distances between the chicks and their nests (Kendall tau = +.85, N = 35 pairs, $P < 0.0001$), and between the parents and their nests (Kendall tau = +.62, N = 35 pairs, $P < 0.0001$) were correlated with ages of the chicks. Chicks and parents usually remained close

## TABLE 5
## INTERNEST DISTANCE AS A FUNCTION OF DATE OF EGG-LAYING FOR CLAM ISLAND HERRING GULLS[1]

| | Date of egg-laying<br>17–30 April | 1–14 May | After 15 May |
|---|---|---|---|
| Number of nests | 328 | 520 | 232 |
| Distance to nearest neighbor at nest initiation | 8.8 ± 15.9 | 8.4 ± 9.3 | 6.9 ± 5.4 |
| Distance to nearest neighbor in late May[2] | 4.5 ± 3.8 | 5.8 ± 5.7 | 6.2 ± 4.9 |
| Distance to second neighbor in late May | 7.8 ± 7.3 | 8.8 ± 8.7 | 10.4 ± 12.8 |
| Distance to third neighbor in late May | 10.7 ± 12.9 | 11.8 ± 12.2 | 12.3 ± 12.9 |
| Number of neighbors within 5 m | 1.2 ± 1.0 | 1.0 ± 1.1 | 0.9 ± 1.0 |
| Number of neighbors within 10 m | 4.5 ± 2.7 | 3.6 ± 2.7 | 3.3 ± 2.4 |

[1] Values given are means ± one standard deviation, in m.
[2] 31 May–3 June.

TABLE 6
INTERNEST DISTANCES AND NEST DENSITIES AS FUNCTIONS OF HABITAT TYPE FOR HERRING GULLS[1]

| | Dense bushes | Intermediate bushes | Clumped bushes | Sparse bushes | Grass |
|---|---|---|---|---|---|
| Number of nests | 212 | 412 | 264 | 125 | 67 |
| Internest distance (m) | | | | | |
| Nearest neighbor at nest initiation | 7.5 ± 14.2 | 7.1 ± 9.9 | 4.3 ± 1.9 | 7.4 ± 5.5 | 10.5 ± 8.5 |
| Nearest neighbor[2] | 3.4 ± 1.6 | 4.6 ± 2.7 | 2.7 ± 2.5 | 4.9 ± 5.2 | 8.6 ± 7.5 |
| Second neighbor[2] | 5.5 ± 2.3 | 7.5 ± 5.6 | 6.6 ± 0.9 | 8.8 ± 8.5 | 13.3 ± 13.7 |
| Third neighbor[2] | 7.1 ± 3.1 | 10.3 ± 12.9 | 7.6 ± 0.9 | 13.7 ± 16.3 | 16.8 ± 13.9 |
| Number of neighbors at nest initiation | | | | | |
| Within 5 m | 1.6 ± 1.1 | 1.2 ± 1.0 | 2.7 ± 1.2 | 0.7 ± 0.5 | 0.4 ± 0.7 |
| Within 10 m | 5.4 ± 2.5 | 4.4 ± 2.6 | 8.0 ± 2.7 | 3.8 ± 1.8 | 1.8 ± 1.5 |

[1] Includes nests initiated between 20 April and 15 May in 1976, 1977, and 1978 on Clam Island; values given are means ± standard deviation.

[2] Measured 31 May–2 June.

together, and the distances adults and chicks were from the nests were also correlated (Kendall tau = +.88, N = 35 pairs, $P < 0.0001$). The mean distance between chicks and their parents was usually very short ($\bar{X} = 0.7$ m, s.d. = 0.8 m, N = 350, 14 nests over 35 days). Parents were generally farther from the nest than were chicks 15–20 days old (Fig. 5, most points below the diagonal), but most 30 to 35 day-old chicks were farther from their nests than their parents (Fig. 5, most points above the diagonal). In habitats with fewer bushes, undisturbed chicks moved farther from their nests, but usually remained within 4.5 m even when they were 30 days old (Table 7).

*Birds observed from the rest of Clam Island.*—Chicks disturbed by field assistants walking slowly through the area moved farther from their nests than undisturbed chicks (Table 7). On Clam Island the mean distance chicks moved from their nests also differed significantly as a function of habitat (N = 272 distances; Median Test, $P < 0.01$). Chicks in intermediate bush cover remained closer to their nests than did those in grass, and chicks in open habitat ran farther from their nests when they were very young than did chicks in other habitats (Fig. 6). It is important for chicks in dense-nesting areas to remain near their nests because young chicks can get lost and are too small to defend themselves from attacks by neighbors whose territories they enter.

Chicks tended to shift directions (i.e., to find new hiding places) if disturbed when they were less than 8 days old ($\bar{X} = 65°$, s.d. = 8°), and when they were 15 to 21 days old ($\bar{X} = 70°$, s.d. = 21°), but 9 to 12 day old chicks usually ran in the same direction ($\bar{X} = 12°$, s.d. = 6°). After 21 days chicks very seldom shifted direction ($\bar{X} < 12°$). Overall, successive escape directions of chicks differed significantly from previous escape directions ($F = 7.54$, d.f. = 17, 153, $P < 0.01$, least significant interval = 4.1). Directions of movement from nests were evenly distributed with respect to compass direction and direction of our approach ($\chi^2$ tests).

*Birds observed on Carvel Island.*—To examine the effect of human disturbance

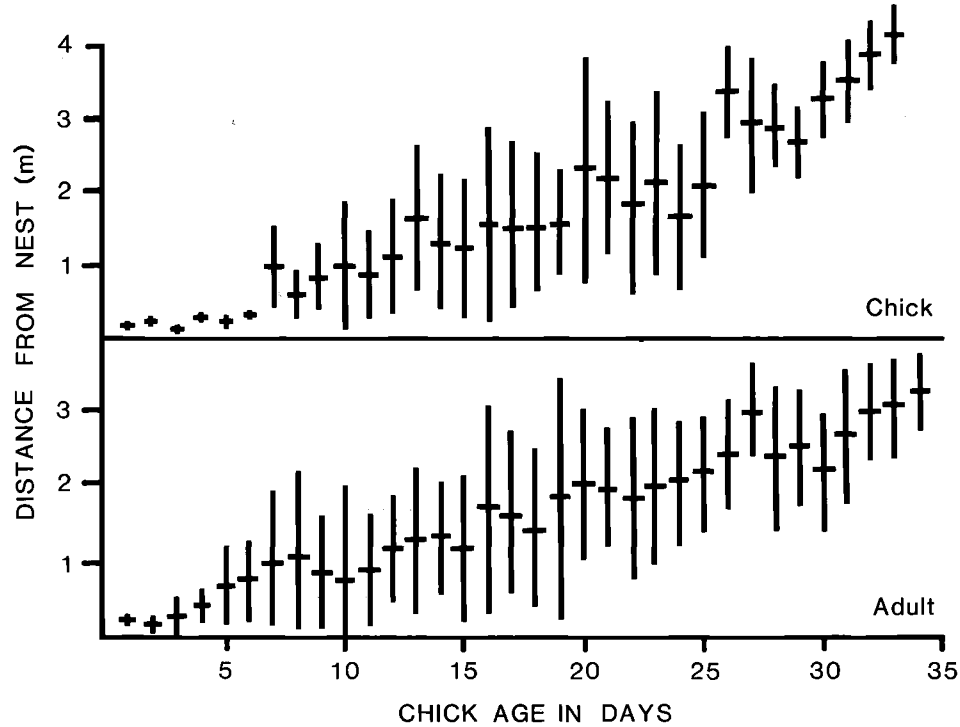

FIG. 4. Average distances parents and chicks (mean = horizontal line, ± one standard deviation = vertical line) moved from their nests under normal, undisturbed conditions (intermediate bush habitat, Clam Island, birds observed from blind, N = chicks from at least 10 nests in each age class).

I compared the distances chicks moved from nests on Clam Island (in sections checked 3–4 times/week) to the distances chicks moved on Carvel Island (checked once/week). I combined data in five-day intervals because of smaller sample sizes and less frequent sampling. The distances differed significantly as a function of habitat; chicks in bushy areas did not move as far as those in grass (N = 136 distances, Sign Test, $P < 0.01$, Fig. 7). In general, the less frequently chicks were disturbed, the closer they remained to the nest when disturbed (compare Figs. 6 and 7). Chicks disturbed once a week ran the same distance from their nests as the chicks from the nests near my blind that were not disturbed by nest checks on Clam Island (compare Figs. 4 and 7).

## DISCUSSION

### TERRITORY SIZE

Tinbergen (1956, 1960) noted that Herring Gull territories usually ranged from 5 to 23 m in diameter, with some nests as close to each other as 1 m. Fordham (1964a) reported that Southern Black-backed Gull territories ranged from 28 to 154 $m^2$, and by calculating territory size from his maps I obtained a mean territory size of 59 $m^2$. Hunt and Hunt (1976) calculated territory size during the chick stage in Glaucous-winged Gulls as 14.3 $m^2$ (range = 1.8–34 $m^2$, N = 41) in one year and 14.8 $m^2$ (range = 2.3–46.7, N = 104) in another. They did not examine

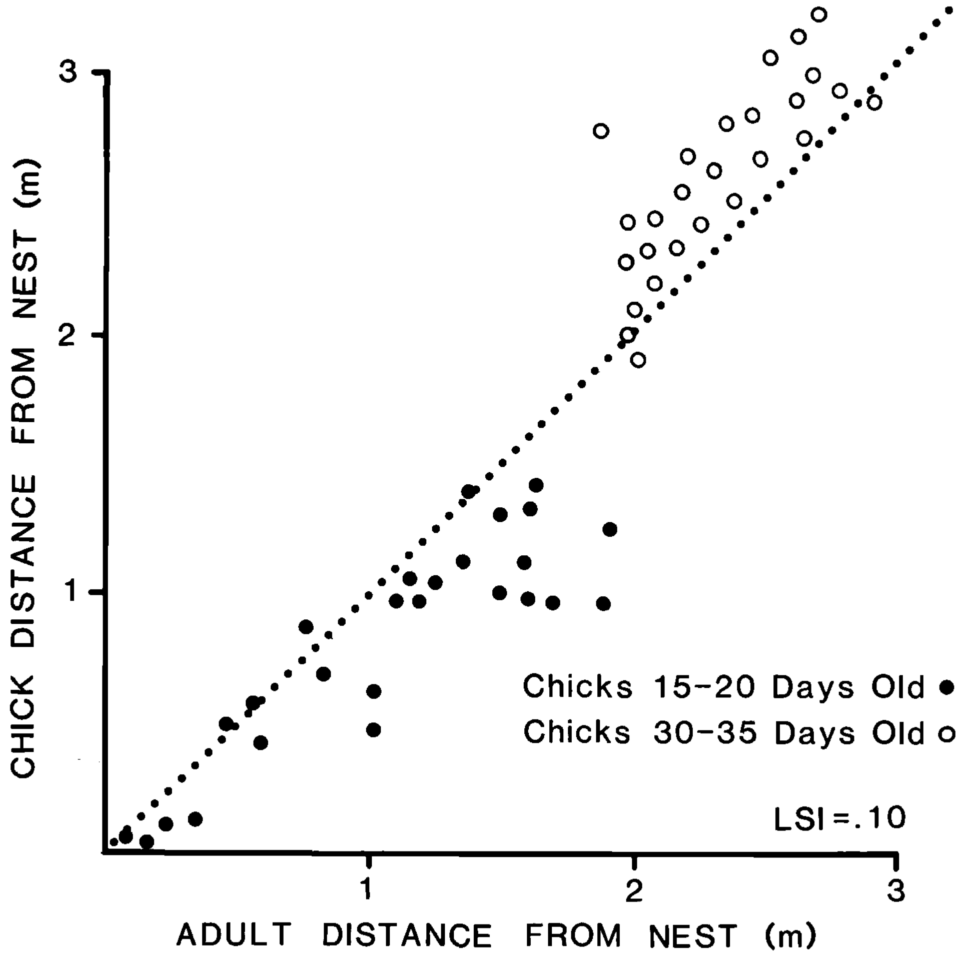

FIG. 5. Mean distances parents and chicks were from their nests for two age classes of chicks. Dotted line indicates chicks and parents were equidistant from their nests (intermediate bush habitat, Clam Island, birds observed from a blind). LSI = Least Significant Interval.

type of territory. More recently, Ewald et al. (1980) examined territory size in Western Gulls nesting at low densities and found it to vary from about 50 to more than 120 m$^2$. These data indicate wide variations in the sizes of gull territories even within one colony. In this study, mean territory size of all three types of territories varied as a function of date of clutch initiation, habitat, and stage in the reproductive cycle.

Habitat effects on territory size have been noted for Western Gulls; in areas with little cover close to clubs, gulls had small territories (Ewald et al. 1980). Territories of Clam Island Herring Gulls, however, were generally smaller in areas with greater cover. In both examples, the critical factor was intruder rate (see section on Aggressive Behavior and the Mechanism of Territoriality). On Clam Island dense cover areas were preferred and suffered high rates of intrusion,

TABLE 7

INTERNEST DISTANCES AND DISTANCES CHICKS WERE FOUND FROM NESTS AS A FUNCTION OF HABITAT[1]

| | Open grass | Sparse bushes | Intermediate bushes |
|---|---|---|---|
| Internest distance | | | |
| Number of nests | 67 | 125 | 412 |
| Nearest neighbor | 8.6 ± 7.5 | 4.9 ± 5.2 | 4.6 ± 2.7 |
| Second neighbor | 13.3 ± 13.7 | 8.8 ± 8.5 | 7.5 ± 5.6 |
| Distance from nest in undisturbed areas[2] | | | |
| Number of nests | 12 | 12 | 12 |
| 5–10 days of age | 2.3 ± 1.5 | 2.0 ± 0.8 | 0.8 ± 0.6 |
| 25–30 days of age | 4.5 ± 1.6 | 4.1 ± 1.2 | 2.5 ± 1.2 |
| Distance from nest in disturbed areas[3] | | | |
| Number of nests | 67 | 125 | 412 |
| 10 days of age | 8.1 ± 6.0 | 3.0 ± 1.5 | 2.0 ± 1.2 |
| 28 days of age | 13.0 ± 3.7 | 8.3 ± 2.0 | 6.8 ± 1.6 |

[1] Clam Island; values given are means ± one standard deviation, in m.
[2] Birds nesting near observation blind.
[3] Birds nesting on the rest of Clam Island; nests checked 3–4 times/week.

whereas in Ewald et al.'s (1980) study area, high intrusion rates occurred in low cover areas, near clubs.

Vegetation also affects nest placement. In Southern Black-backed Gulls (Burger and Gochfeld 1981b, c) and Herring Gulls (Brown 1967a; Burger and Shisler 1978a) nests are frequently located under dense vegetation. In the present study internest distances varied significantly by habitat, as a function of the location of the bushes in each habitat, and visibility from nest sites (see Burger 1977b). Internest distances were lowest in the clumped bush habitat because the vegetation was clumped. Two or three gulls would place their nests in each clump, extending their territories into open grass away from bushes. Thus, territories were not smaller in this habitat than in dense bush habitat. In the latter habitat nests were close together because low visibility eliminated conflicts between close neighbors.

For birds observed from the blind, territory sizes determined by observations of aggressive encounters and by using internest distances were related. Thus, for Clam Island it was possible to use internest distance as an index of territory size. In contrast, Hunt and Hunt (1976) did not find a correlation between territory size and nearest neighbor distance in Glaucous-winged Gulls. I suggest that a combination of the three closest internest distances (as discussed in Burger 1980a) may be the best index of territory size. Further, internest distances should be a better indicator of territory size in densely populated colonies where territories are small and a pair places its nest more centrally within its territory. Averaging the mean distances for the three closest neighbors (Table 6) gives an indication of average primary territory size. Using this measure, the mean territory sizes for birds nesting in each habitat increased in the following order: dense bushes, clumped bushes, intermediate bushes, sparse bushes, and open grass.

Nesting density may be another indicator of territory size, with birds in areas where nests are densest having the smallest territories. Density, however, may be an indication of the packing of territories rather than actual territory size. Some

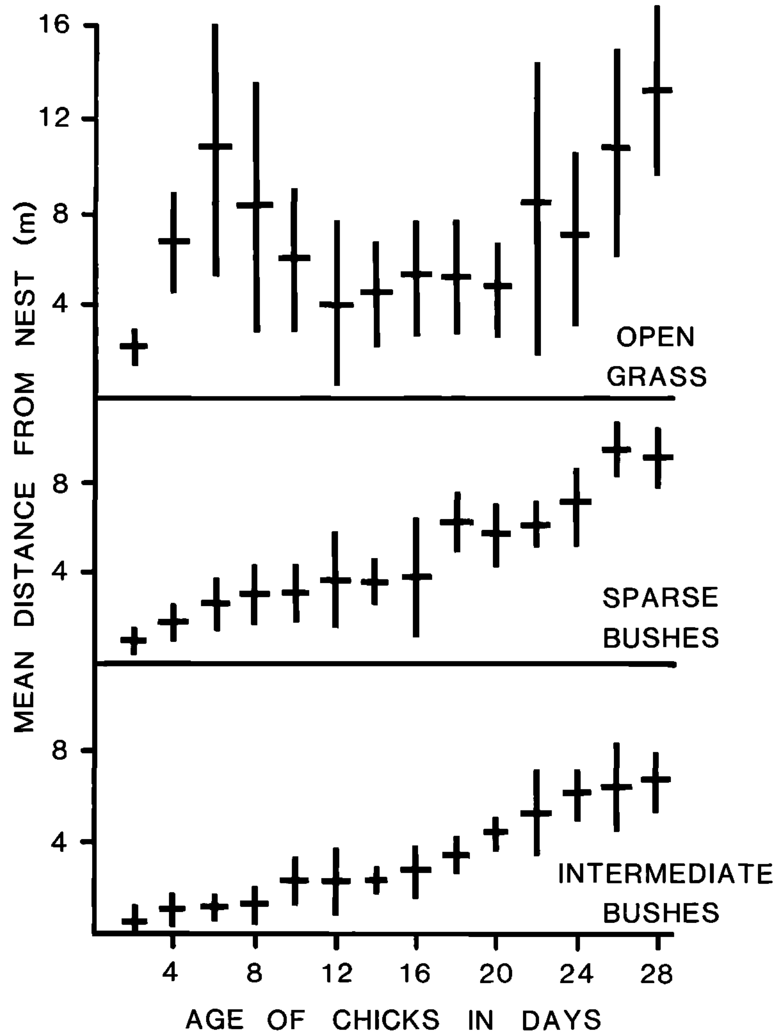

FIG. 6. Distances (mean = horizontal line, ± one standard deviation = vertical line) disturbed chicks on Clam Island moved from their nests as a function of habitat and age.

sections in the bush habitat were unused because the bushes were very dense and prevented gulls from flying from their nests easily. Such territories seemed to be abandoned after gulls spent considerable time walking through bushes to ascertain the cause of disturbances.

In this study territory size varied during the reproductive cycle and was smallest during incubation. During the pre-incubation and chick phases, territories were large, but for different reasons. In the pre-incubation phase pairs prevented intruders from landing and establishing territories, whereas in the chick phase parents provided protected areas for chicks to move about. Large territories should occur during the chick phase in gulls where cannibalism or intense territorial aggression are factors. This seems to be the case in Great Black-backed Gulls

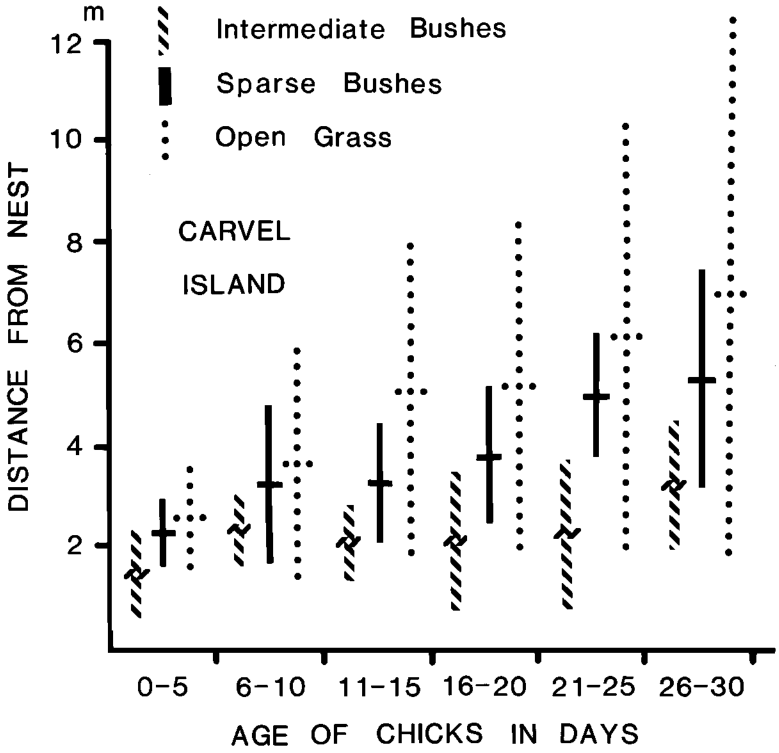

Fig. 7. Distances (mean = horizontal line, ± one standard deviation = vertical line) chicks in different habitats on Carvel Island moved from their nests when disturbed.

(Verbeek 1979), Glaucous-winged Gulls (Hunt and Hunt 1976), Western Gulls (Hunt and Hunt 1975), and Herring Gulls (this study). Such an increase in territory size does not appear to occur in the smaller hooded gulls (Moynihan 1959a) in which cannibalism is not prominent (Tinbergen 1956; Patterson 1965; Burger and Beer 1975; Burger 1979a).

## Chick Movement

One important function of territoriality in gulls is to provide a safe place for the young to develop. Thus, chicks should stay within the territory until they abandon the nest site. In some species (e.g., Caspian Terns, *Sterna caspia,* Shugart et al. 1981; Ring-billed Gulls, Evans 1970; Conver and Miller 1979; Black-billed Gulls, Beer 1966; and Sandwich Terns, Veen 1977) the chicks are led from the nests within a few days of hatching, although these early departures may be caused by human disturbance (Shugart et al. 1981; Burger 1981c; Gochfeld 1981). Nonetheless, in many species the chicks remain on the territory until they fledge. Herring Gulls on Clam Island regularly returned to the nest site until they were 70 to 85 days old (Burger 1980b, 1981a), although they were able to fly at 45 days.

Chick movement varied depending upon age of the chick, type of habitat, and amount of human disturbance. Undisturbed parents and young in bush habitat

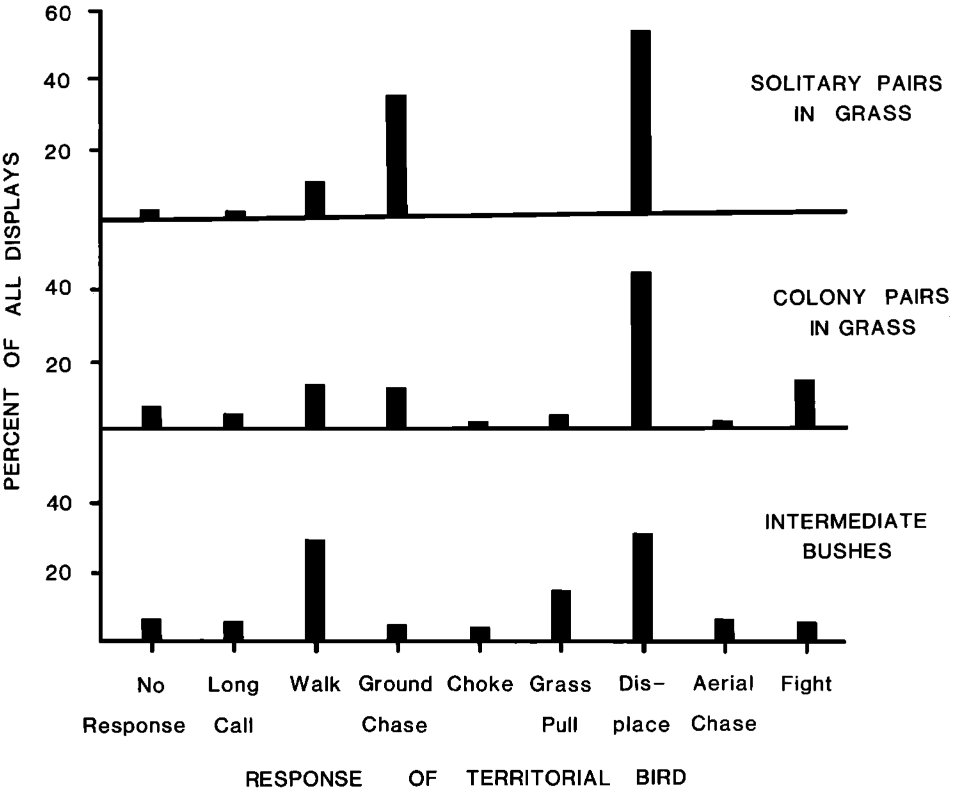

FIG. 8. Responses of territorial Herring Gulls on Clam Island to all intruders as a function of habitat (grass and intermediate bushes).

remained very close to the nest, normally less than half the distance to their closest neighbor's nest. Such chicks normally are not attacked by neighbors unless the neighbors are using chicks as a food source (Tinbergen 1960). Chicks that do wander may (Herring Gulls), or may not (Glaucous-winged Gull, Hunt and Hunt 1976), be defended by their parents. Glaucous-winged Gulls tend to wander farther from parents if their food-begging has been unsuccessful, increasing their risk of predation by neighbors (Hunt and McLoon 1975).

Territory size and the distance chicks wandered from nests increased with decreasing cover, whereas nest density decreased with decreasing cover on Clam Island. Cover is important in preventing predation (Brown 1967a; Burger 1974a; Hunt and Hunt 1975; 1976; Davis and Dunn 1976). Chicks that were disturbed wandered far from their nest sites, often going beyond neighboring nests, increasing the probability of the chick being killed. Chicks did not always return to the same hiding place, but frequently changed directions and ran farther than previously. Chicks often bypassed clumps of bushes to hide in other, similar clumps of bushes. The tendency to shift directions was very high in 3 to 6 day old chicks, just when they were beginning to leave the nest when disturbed (Deusing 1939). This may reflect their exploration of the territory; thereafter, they usually ran in the same

TABLE 8

RESPONSES OF TERRITORIAL HERRING GULLS AS A FUNCTION OF HABITAT AND TYPE OF INTRUDER[1]

| | | Intermediate bushes Type of intruder | | |
|---|---|---|---|---|
| | Grass | Neighbor | Non-neighbor | Immature |
| Long call | 5 | 8 | 15 | 0 |
| Walk toward | 16* | 26 | 23 | 50* |
| Choke | 3 | 4 | 0 | 0 |
| Grass pull | 7 | 23* | 0* | 0* |
| Ground chase | 12 | 4* | 12* | 6 |
| Displace | 33 | 29 | 38 | 33 |
| Aerial chase | 5 | 2 | 3 | 11* |
| Fight | 19* | 4* | 9* | 0* |
| No. encounters | 265 | 461 | 223 | 98 |

[1] Clam Island, 1977; values given are percents. Nest density was similar in the bush and grass habitats where data for this analysis were obtained. For the chi-square contingency table I used the raw data. Percentages were computed for the period including all of incubation and the chick stage until the chicks were 40 days old. * = displays given significantly more or less frequently than expected (expecteds based on overall occurrence of displays in bush habitat).

direction and hid in a familiar location. Chicks 15 to 21 days old also shifted directions. At this age they are sufficiently mature to seek new hiding places large enough to cover their bodies.

## AGGRESSIVE BEHAVIOR AND THE MECHANISM OF TERRITORIALITY

In this section I examine the aggressive behavior (displays, rates of aggression, intrusion pressure, and approach distance) of territorial Herring Gulls. I expected that the intensity and frequency of aggression, and the approach distance (distance from the nest at which an intruder will be attacked), would be high in the pre-incubation phase when pairs are establishing territories, low during incubation when the birds are incubating and protecting eggs, and high during the brooding phase when chicks are vulnerable. I was particularly interested in the relationship between rates of aggression (frequency of aggressive displays and encounters), approach distances, and intrusion pressure. Although previous authors have often assumed that territory size is related directly to aggressiveness (Verner 1977, but see Myers et al. 1981), I hypothesized that pairs holding intermediate-sized territories would be the least aggressive.

### RESULTS

### AGGRESSIVE DISPLAYS

A variety of aggressive behaviors were used by Herring Gulls to defend territories. The frequency with which different behaviors were employed varied by habitat ($\chi^2 = 287.7$, d.f. = 14, $P < 0.001$; N = 155 displays for birds from solitary pairs nesting in grass, 265 displays for colonial birds nesting in grass, and 684 displays for colonial birds nesting in intermediate bushes, 1976–1978; Fig. 8). In general, solitary nesting gulls either performed ground chases or displaced intruders landing nearby. Because birds from solitary pairs did not have close neighbors, their aggression was entirely directed toward non-neighbor intruders.

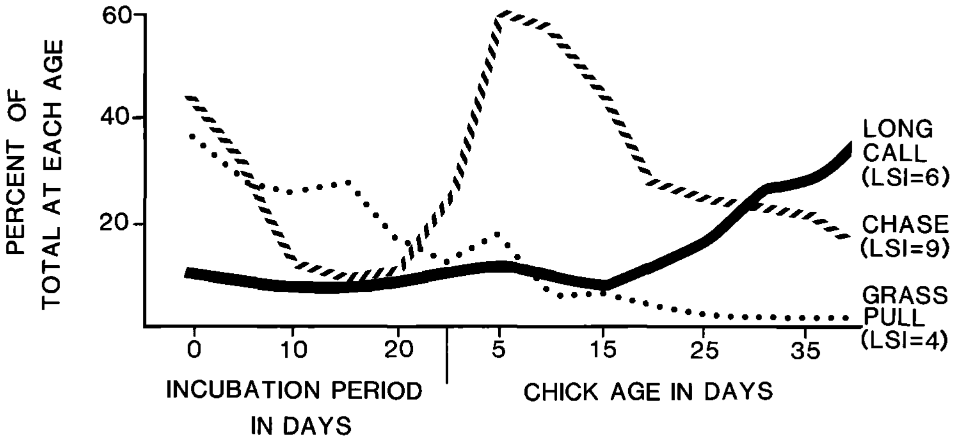

FIG. 9. Aggressive responses of territorial birds on Clam Island as a function of stage in the reproductive cycle (LSI = Least Significant Interval).

Gulls nesting in the grass, but within the colony, primarily displaced intruders, although they also fought. Gulls nesting in the bushes usually defended their territories by Walking Toward or displacing intruders. Differences in the types of aggression used largely reflect differences in territory size. At high densities, when territories were small (i.e., in bush habitats, Table 6), gulls responded to intruders by Walking Toward them.

Territorial birds responded differently depending upon the type and age of the intruder. To avoid biases in responses due to date of egg-laying, density, and habitat differences, I made observations in sections of the colony with equivalent densities and dates of initiation of egg-laying. The proportions of the various displays given to neighors and non-neighbors differed significantly in intermediate bush habitat ($\chi^2 = 36.2$, d.f. = 7, N = 684 displays, $P < 0.001$, Table 8). Gulls nesting in the bushes directed more Grass-pulling and fewer ground chases and fights at neighbors than at non-neighbors. In other words, a territorial clash between neighbors usually involved threat and displacements rather than overt attack. Gulls nesting in intermediate bushes responded to immature gulls (N = 98) by Walking Toward them, displacing them, or chasing them aerially. The frequencies at which displays were given between colonial birds nesting in intermediate bushes and those nesting in open grass differed significantly ($\chi^2 = 32.3$, d.f. = 7, N = 1047, $P < 0.001$, Table 8).

In 1977 I recorded aggressive displays of 15 pairs for 860 hr in intermediate bush habitat. Display behavior in defense of territories varied according to stage in the reproductive cycle. Low intensity responses such as Long Calls were used frequently when chicks were older (Fig. 9). Although Long Calls were used to call chicks, I counted only those directed at intruders. High intensity reactions to neighbors (Grass Pulling) were most common in the pre-laying and early incubation phase, and chases (ground or aerial) were most common from hatching until chicks were two weeks old.

Aggressive behavior of Herring Gulls in the New York colonies was similar to

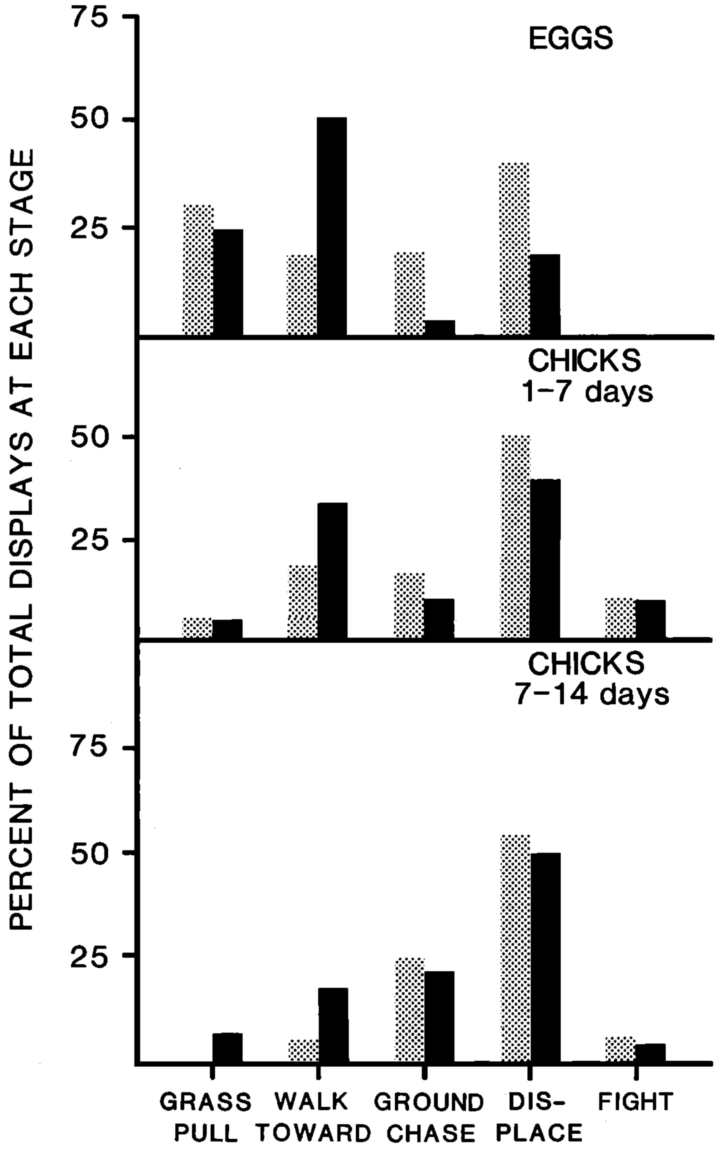

FIG. 10. Responses of territorial birds as a function of stage in the reproductive cycle for pairs observed at Captree (black bar, N = 310 encounters) and Meadow Island (shaded bar, N = 230 encounters).

that observed at Clam Island (compare Figs. 8 and 10). I observed 540 displays at 12 nests at Captree and 14 nests at Meadow Island. In both colonies low level aggressive behavior decreased seasonally compared to displacing and fighting (Fig. 10). Again, fighting was more common when parents had chicks less than 7 days old. During incubation, the gulls in the Captree colony performed fewer displacements and more Walkings Toward intruders, whereas those at Meadow Island

## TABLE 9

## RATES OF AGGRESSION AND DISTANCE AT WHICH INTRUDERS WERE CHASED AS A FUNCTION OF TIME OF DAY DURING THE PRE-INCUBATION PERIOD[1]

| Time of day | Rate of aggression[2] | Approach distance (m) |
|---|---|---|
| 5–6 | 2.5 ± 0.87 | 2.5 ± 0.81 |
| 6–7 | 9.5 ± 4.23 | 2.7 ± 0.54 |
| 7–8 | 5.6 ± 3.20 | 3.0 ± 0.91 |
| 8–9 | 3.0 ± 2.00 | 1.58 ± 0.36 |
| 9–10 | 1.57 ± 5.30 | 1.4 ± 0.19 |
| 10–11 | 0.86 ± 0.63 | 1.5 ± 0.13 |
| 11–12 | 0.43 ± 0.44 | 1.3 ± 0.20 |
| 12–13 | 0.43 ± 0.44 | 1.3 ± 0.20 |
| 13–14 | 0.50 ± 0.50 | 1.4 ± 0.20 |
| 14–15 | 0.99 ± 0.77 | 1.8 ± 0.20 |
| 15–16 | 2.14 ± 1.77 | 2.5 ± 1.01 |
| 16–17 | 1.71 ± 0.49 | 2.5 ± 1.01 |
| 17–18 | 5.71 ± 2.14 | 3.57 ± 1.14 |
| 18–19 | 8.86 ± 4.60 | 3.1 ± 0.27 |
| 19–20 | 3.4 ± 2.23 | 2.2 ± 0.19 |
| *F* | 11.70 | 10.27 |
| d.f. | 14, 181 | 14, 181 |
| LSI | 0.64 | 0.17 |

[1] Data taken 15–30 April 1977 on Clam Island; values given are means ± standard deviation; N = 195 hr of observation, 15 pairs, ANOVA on log transformed data, LSI = least significant interval.

[2] Interactions/pair/hour.

performed more displacements than Walkings Toward intruders (Fig. 10). I attributed this difference to habitat. The gulls at Captree nested on the open sand where they could easily walk toward an intruder and were quickly perceived. Meadow Island gulls nested in beach grass (*Ammophila*), which provided a visual as well as physical barrier to intrusion. In both New York colonies the gulls performed almost no aerial chases.

### LEVELS OF AGGRESSION

The rates of aggression of individuals and pairs varied temporally (daily), by stage in the reproductive cycle, with the type of intruder (neighbor or non-neighbor), within and between pairs, and with environmental variables (vegetative cover, location in the colony, tidal stage).

*Daily variation.*—Combined rates of aggression (interactions/pair/hour) varied throughout the day, particularly at times in the reproductive cycle when rates were high. In the pre-incubation period combined rates of aggression were highest at 05:00–10:00 and 15:00–20:00, and lowest around noon (Table 9).

*Seasonal and habitat variations.*—Data on rates of aggression by date are useful for comparative purposes because in some studies on larids the exact timing of the reproductive cycle is unknown. Combined rates of aggression on Clam Island varied by date and as a function of habitat (N = 15 pairs/habitat, 1977; Fig. 11). Although rates of aggression were high in all habitats in late April, they were high in late May only in birds nesting colonially. Further, the late May peak was significantly higher ($F = 12.2$; d.f. = 1, 10, 935; $P < 0.001$) for colonial birds nesting in intermediate bush habitat than for those nesting in grass (ANOVA

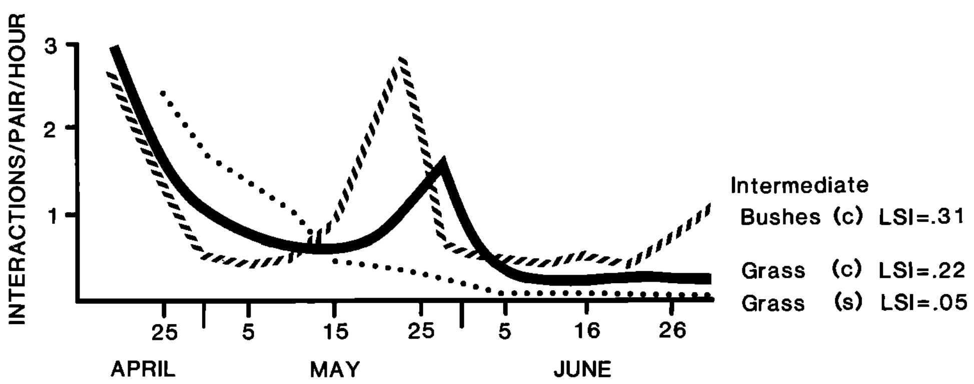

FIG. 11. Rates of aggression (interactions/pair/hour) of Herring Gulls as a function of date and habitat (Clam Island). c = colonial pairs, s = solitary pairs, LSI = least significant interval.

comparisons using LSI's, Fig. 11). The April peak in aggression corresponded to pre-incubation, and the May peak corresponded to the hatching period. The slightly later May peak in rates of aggression for pairs nesting in the grass reflects the fact that birds nesting in the grass had a later mean date of egg-laying ($\bar{X}$ =

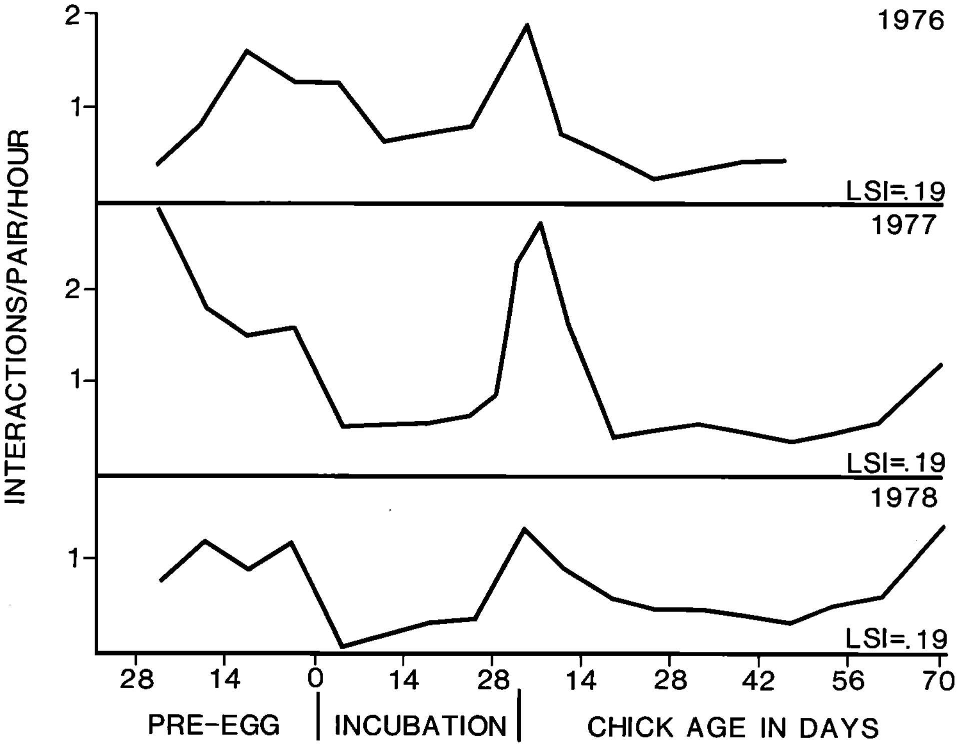

FIG. 12. Rates of aggression of Herring Gulls as a function of stage (in days) in the reproductive cycle (Clam Island, N = 14 pairs for 1976, 15 pairs for 1977, 14 pairs for 1978; LSI = Least Significant Interval).

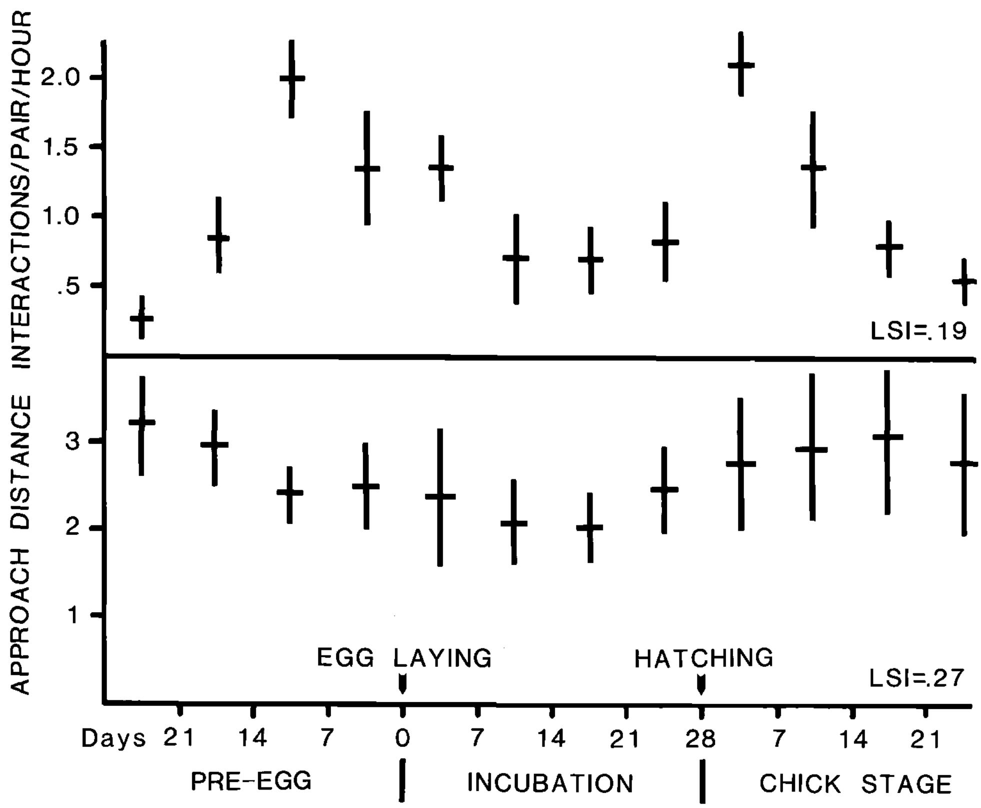

FIG. 13. Rates of aggression and approach distances (m), as a function of stage in the reproductive cycle, for Herring Gulls in intermediate bush habitat observed on Clam Island in 1976 (N = 14 pairs; LSI = Least Significant Interval, mean = horizontal line, ± one standard deviation = vertical line).

20 May, s.d. = 13 days) than those nesting in bushes ($\bar{X}$ = 14 May, s.d. = 10 days). Similarly, rates of aggression of Herring Gull pairs nesting on Appledore Island were highest in early June following hatching ($\bar{X}$ = 3.2 ± 0.6, N = 18 nests, see Burger 1983). Rates of aggression were similar in two study areas in the same habitat, although the peak was delayed by 3 to 4 days in one area.

*Stage in the reproductive cycle.*—Changes in rates of aggression for pairs could be related to seasonal shifts in hormone levels, to shifts in hormone levels caused by changes in stage of their reproductive cycle, or to shifts in intruder pressure occurring as a result of stage in the reproductive cycle. Although reproductive cycle and season (date) are obviously highly correlated, I examined the data separately because breeding of gull pairs is not perfectly synchronized and because the two independent variables may have different effects. Examining rate of aggression by date masks differences when the reproductive activities of birds are not synchronous.

Rates of aggression of pairs nesting in bushes on Clam Island differed significantly by stage of the reproductive cycle, ($F$ = 14.48, d.f. = 2, 9, 935, $P < 0.001$, least significant interval = 0.19). Rates of aggression were high in the pre-incubation phase, decreased during incubation, increased following hatching, and

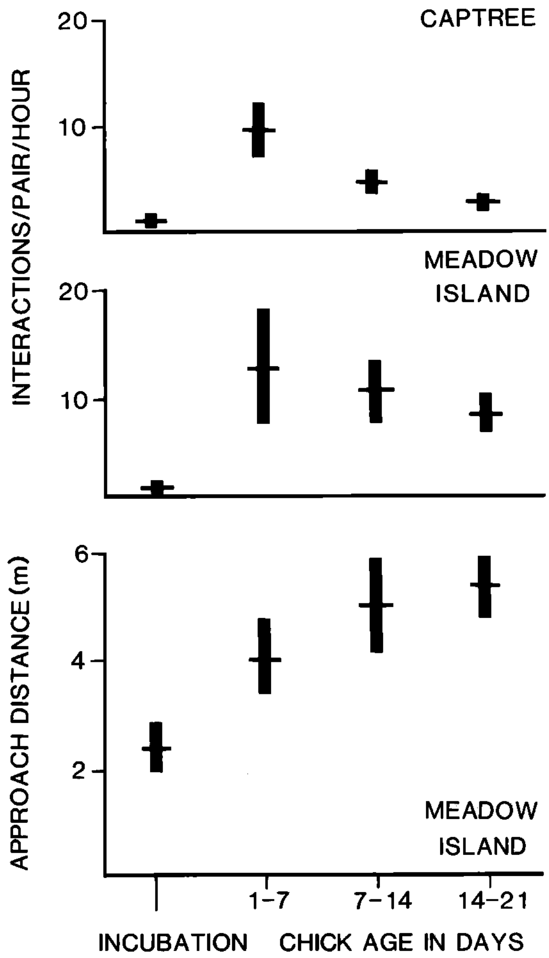

FIG. 14. Rates of aggression and approach distances (mean = horizontal line, ± one standard deviation = vertical line) as a function of stage in the reproductive cycle for Herring Gulls observed on open sand at Captree and Meadow Islands.

decreased when the chicks were older than 19 days (Figs. 12, 13). In 1976 on Clam Island (Fig. 12) aggression levels were low a month before egg-laying and increased in the period just before egg-laying. In 1977, levels were very high during the pre-incubation stage. The winter was mild in 1977, and gulls arrived on the island in late February, much earlier than they did in the other years (mid-March). Although I was not present in February, I suspect that aggression was lower a month and a half before egg-laying in 1977 when the birds first arrived.

Between 14 to 50 days post-hatching, aggressive encounters with neighbors usually involved Grass Pulling; after that, males also fought with neighbors (22% of 510 encounters). In 1977 and 1978 I observed until the chicks were 70 to 90 days old, and found an increase in aggression rates at 60 days of age (Fig. 12; Burger 1981a).

At Captree and Meadow Islands similar increases in rates of aggression of pairs

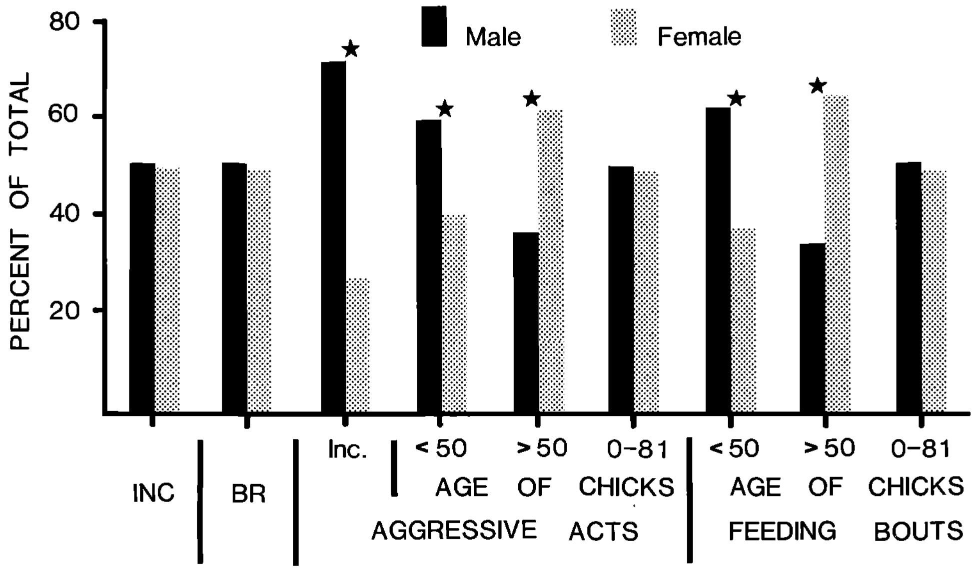

FIG. 15. Mean relative contribution of male and female Herring Gulls on Clam Island to care (defense, feeding) of the young. All categories add up to 100%. Inc = incubation, Br = brooding, Star = significant sex difference (Clam Island).

occurred at hatching; rates of aggression were higher at these localities than on Clam Island (Fig. 14). Mean rates of aggression at different reproductive stages differed significantly both at Captree ($\chi^2 = 15.2$, d.f. = 3, $P < 0.01$, N = 80 hr) and at Meadow Island ($\chi^2 = 34.2$, d.f. = 3, N = 80 hr, $P < 0.001$).

*Within and among pair variations.*—In the above sections I computed combined rates of aggression for each pair. These rates differed significantly among pairs (Table 10, $F = 24.05$, d.f. = 2, 112, $P < 0.001$, Clam Island 43 pairs, 1976–1978), ranging from 0.05 to 3.45 during incubation and from 0.03 to 2.17 during the chick phase. In general, females engaged in fewer total interactions than males during incubation ($\chi^2 = 5.0$, d.f. = 1, $P < 0.01$) and while chicks were less than 50 days old ($\chi^2 = 16.2$, d.f. = 1, $P < 0.001$, Fig. 15), although after chicks were 50 days old, females were aggressive in defense of chicks more frequently than were males ($\chi^2 = 17.3$, d.f. = 1, $P < 0.001$, all $\chi^2$ on raw data).

Males and females showed similar patterns of aggression during the reproductive cycle in 1978 (14 pairs, 960 hr; Fig. 16). Birds of both sexes that were present, but not incubating, were more aggressive than gulls that were incubating. Between 45 and 63 days females were aggressive only when the chicks were present, whereas males were also aggressive when their chicks were absent from the territory. These aggressive encounters of males usually involved only neighbors and occurred at territory boundaries. Unlike the encounters with neighbors that occur when birds are defending chicks, these territorial clashes were prolonged, often lasting 10 to 15 min (see Burger 1981a). Rates of aggression for pairs increased as the percent of time both members were present on the territory increased (Fig. 17, Kendall tau = +.57, $P < 0.001$, 24 pairs, 1977–1978, Clam Island).

Table 11 shows the correlations of frequency of aggression with date for males

## TABLE 10

AGGRESSIVE BEHAVIOR OF MALE AND FEMALE HERRING GULLS[1]

| | | 1976 | 1977 | 1978 | 1976–1978 |
|---|---|---|---|---|---|
| Passive defense | | | | | |
| Male incubates (%)[2] | range | 43–58 | 37–55 | 48–61 | |
| | mean[3] | 50 ± 6.0 | 47 ± 66 | 53 ± 4.0 | 52 ± 6.5 |
| Female incubates (%)[2] | range | 42–57 | 45–63 | 39–52 | |
| | mean | 50 ± 6.3 | 53 ± 6.8 | 47 ± 4.0 | 48 ± 6.9 |
| Male present (%)[4] | range | 10–47 | 8–52 | 10–42 | |
| | mean | 34 ± 21 | 36 ± 28 | 33 ± 16 | 34 ± 22 |
| Female present (%)[4] | range | 16–50 | 5–47 | 14–50 | |
| | mean | 31 ± 20 | 31 ± 25 | 32 ± 17 | 32 ± 21 |
| Active defense | | | | | |
| Approach distance (m) | | | | | |
| During incubation | range | 1.0–5.1 | 2.5–5.6 | 1.6–5.3 | |
| | mean | 2.6 ± 0.9 | 3.9 ± 0.9 | 3.2 ± 0.8 | 3.1 ± 1.1 |
| During chick phase | range | 1.0–3.6 | 0.2–4.6 | 0.3–2.6 | |
| | mean | 0.7 ± 0.5 | 1.1 ± 0.8 | 0.9 ± 0.9 | 0.9 ± 0.6 |
| Aggression frequency[5] | | | | | |
| Male | range | 0.22–1.96 | 0.23–1.84 | 0.12–2.31 | |
| | mean | 0.71 ± 0.48 | 0.74 ± 0.47 | 0.62 ± 0.64 | 0.68 ± 0.55 |
| Female | range | 0.09–1.10 | 0.01–0.50 | 0.08–1.22 | |
| | mean | 0.29 ± 0.20 | 0.30 ± 0.16 | 0.38 ± 0.33 | 0.34 ± 0.25 |
| Aggression rates for pairs[6] | | | | | |
| Incubation | range | 0.35–2.80 | 0.54–3.45 | 0.05–2.37 | |
| | mean | 0.87 ± 0.55 | 1.30 ± 0.81 | 0.42 ± 0.69 | 0.88 ± 0.73 |
| Chick phase | range | 0.09–1.82 | 0.22–2.17 | 0.03–0.78 | |
| | mean | 0.67 ± 0.47 | 0.47 ± 0.57 | 0.45 ± 0.25 | 0.71 ± 0.49 |

[1] All Clam Island; 1976, N = 14 pairs, 1977 = 15 pairs, 1978 = 14 pairs.
[2] Percent of total time observed.
[3] All means ± one standard deviation.
[4] Present when not incubating.
[5] Interactions/bird/hr.
[6] Interactions/pair/hr.

and females. In all the above analyses I examined rates of aggression by time of day, date, season, habitat, and stage in the reproductive cycle without examining the relative contribution of male or female, or type of intruder. Male aggression toward non-neighbors decreased seasonally, whereas it increased seasonally in females (Table 11). Further, male aggression increased seasonally against neighbors. Thus, although general patterns in rates of aggression are apparent (e.g., Fig. 12), the relative contributions of males and females, and their responses to types of intruder varied seasonally.

*Variation by type of intruder.*—Defending gulls could respond differently to three classes of intruders: neighbors, non-neighbor adults, and non-neighbor immatures. In the three week period of pre-egg-laying, Herring Gulls nesting under bushes on Clam Island were more aggressive toward neighbors than toward non-neighbors (three-way ANOVA, $F = 35.60$, d.f. = 3, 164, N = 1,285 encounters, $P < 0.001$), although their responses differed yearly ($F = 3.5$, d.f. = 1, 166, $P < 0.05$). Males were significantly more aggressive ($F = 12.80$, d.f. = 1, 166, $P < 0.001$) than females toward neighbors (Fig. 18). Females sometimes responded

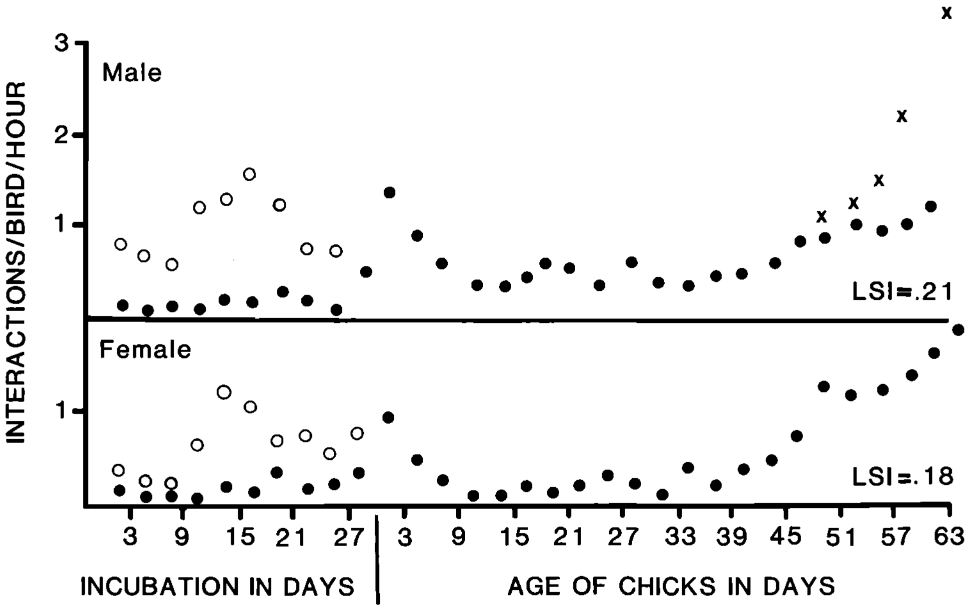

FIG. 16. Mean rates of aggression for male and female Herring Gulls on Clam Island as a function of stage in the reproductive cycle. (Solid dots during incubation = gulls incubating, open circles = gulls merely present on the territory, × = birds engaged in territorial clashes in the absence of young.)

to non-neighbors as frequently as males (1977), but at other times they did not (1976).

*Variation with tide stage.*—Because gulls are influenced by tidal variables (Delius 1970), I examined rates of aggression as a function of tide stage. This analysis was based on the 350 15-min samples gathered throughout the day, every 3 days from incubation to 65 days post-hatching in 1978 (N = 14 pairs). Although total rates of aggression (all aggression lumped for the 14 pairs) did not vary by tide

TABLE 11

CORRELATIONS BETWEEN AGGRESSIVE BEHAVIOR AND DATE FOR MALE AND FEMALE HERRING GULLS[1]

| | Male | Female |
|---|---|---|
| Date and approach distance | | |
| Against neighbor | +.385* | +.328 |
| Against non-neighbors | −.856* | −.686* |
| Against immatures | −.533* | −.624* |
| Gets off nest | −.157 | −.686* |
| Date and frequency of aggression | | |
| Against neighbor | +.412* | +.268 |
| Against non-neighbor | −.866* | +.462* |
| Against immatures | +.281 | +.886* |
| Gets off nest | −.133 | −.476 |

[1] Clam Island; * = $P < 0.05$, N = 43 pairs. Values given are correlation coefficients.

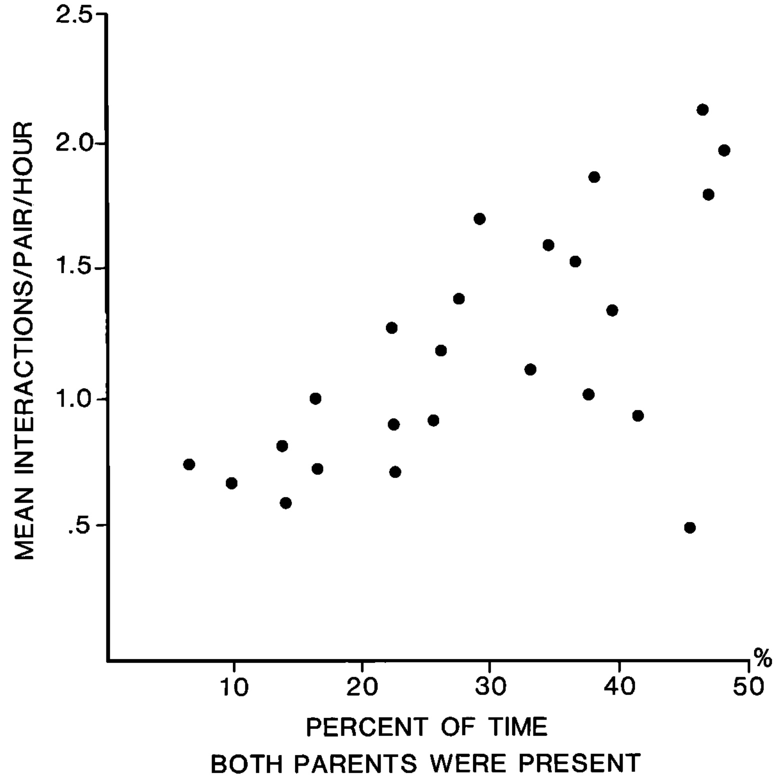

FIG. 17. Mean rates of aggression per pair of Herring Gulls on Clam Island (1977, 1978) for the 20 days following hatching as a function of the percent of time both parents were present on the territory.

stage, there was significantly more neighbor aggression and less non-neighbor aggression during high tide than during low tide (Table 12). These differences were not due solely to attempts to pirate food from parents feeding chicks, as feeding rates did not vary by stage in the tide cycle. I attribute the high rate of neighbor aggression at high tide to the greater number of non-incubating neighbors present on territories during high tide.

## PASSIVE DEFENSE

In the above sections I concentrated on aggressive displays and rates of aggression as the mechanism of territorial defense. However, simple presence on the territory no doubt discourages neighbors from intruding, and strangers circling overhead may not land. I analyzed the same 350 15-min sample periods to determine the percent of time males and females were present on territory. In general males were present when not incubating more often than females, and females were present more than males during the chick phase (Table 13).

## INTRUSION PRESSURE

Aggression could be a result of the tendency of territory holders to attack, or of the number of intruders (where all intruders are attacked). Even where all

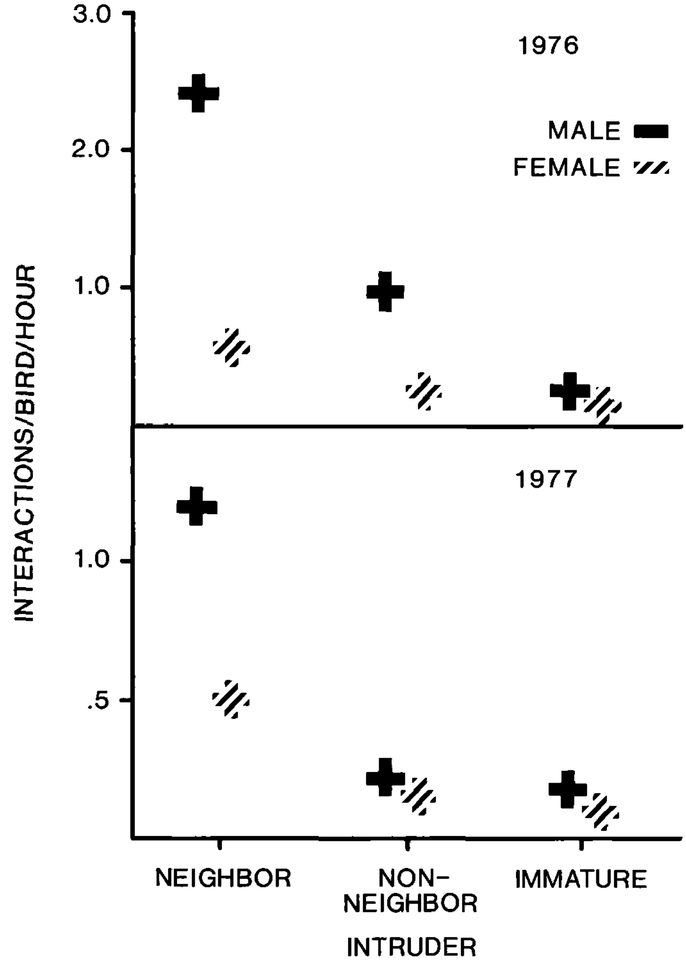

FIG. 18. Rates of aggression (mean = horizontal line, Least Significant Interval = vertical line) as a function of type of intruder for male and female Herring Gulls nesting in intermediate bush habitat on Clam Island.

intruders are attacked, rates of aggression may be partially a result of the aggressiveness of territory holders because a significant portion of the aggression is directed at neighbors. Presumably, some clashes with neighbors at territory boundaries could be avoided if the territory holder chose not to attack, although long term effects of such action are unknown.

On Clam Island most intruders landing within 3 m of a nest evoked either Long Calls or more overt actions from the territory owners. Gulls in pairs nesting solitarily failed to respond to less than 4 percent of the intruders (N = 159) throughout the season, those nesting colonially in grass failed to respond to 7 percent of the intruders (N = 282), and those nesting in intermediate bush habitat failed to respond to 6 percent of the intruders (N = 712).

Observations on Appledore Island, however, indicate that Herring Gull response to intruders varied with the stage in the reproductive cycle and with

### TABLE 12

### EFFECT OF TIDE ON FEEDING AND AGGRESSIVE BEHAVIOR OF HERRING GULLS[1]

| | High tide | Low tide | *t* | *P* |
|---|---|---|---|---|
| Feeding/hour[2] | 1.08 ± 0.01 | 0.96 ± 1.00 | 0.50 | NS |
| Neighbor aggression/hour | 0.78 ± 0.88 | 0.55 ± 0.74 | 2.21 | .02 |
| Non-neighbor aggression/hour | 0.67 ± 0.97 | 0.97 ± 1.50 | 2.14 | .03 |
| Total aggression/hour | 1.45 ± 0.92 | 1.52 ± 1.12 | 0.54 | NS |

[1] Low tide refers to the 3 hours before and after low tide, and high tide refers to the 3 hours before and after high tide. Values given are means ± one standard deviation; d.f. = 348. *t* values based on raw data; NS = not significant.

[2] Rates computed per pair for 14 pairs.

distance intruders landed from the nest (Table 14). Herring Gulls responded to fewer intruders while they were incubating than while they were defending chicks.

## FACTORS AFFECTING RATES OF AGGRESSION

I examined the effects of several independent variables (presence of males or females, stage in cycle, time of day, tide state, precipitation) on rates of aggression by taking data in 15-min sample periods throughout the reproductive cycle (N = 342, 1978, Clam Island). This represents only one of the data sets gathered in 1978. Male and female presence refers to their being present and not incubating (their mate incubated), and these are not correlated (Table 15).

During the incubation period, neighbor aggression and total aggression were significantly correlated with time of day and percent of time males and females were present, whereas non-neighbor aggression was not correlated with any of the variables (Table 15).

During the chick phase, one or both parents could be present on territory at any time. Neighbor aggression was positively correlated with the presence of males and females, time of day, and with the number of times chicks were fed; non-neighbor aggression was positively correlated with age of the chicks and the number of times chicks were fed; and total aggression was positively correlated with age of chicks, the percent of time males and females were present, and the number of times chicks were fed (Table 16).

### TABLE 13

### COMPARISON OF HERRING GULL BEHAVIOR DURING INCUBATION AND THE CHICK PHASE[1]

| | Incubation (0–24 days) | Chick stage (0–65 days) | *t* | *P* |
|---|---|---|---|---|
| Males incubating or present (%)[2] | 58 ± 15 | 37 ± 21 | 9.51 | .001 |
| Females incubating or present (%)[2] | 42 ± 16 | 46 ± 22 | 3.13 | .002 |
| Both present (%)[2] | 35 ± 23 | 21 ± 38 | 7.15 | .001 |
| Neighbor aggression[3] | 0.60 ± 0.48 | 0.68 ± 0.42 | 0.89 | NS[4] |
| Non-neighbor aggression[3] | 0.36 ± 0.41 | 0.98 ± 1.32 | 5.07 | .001 |
| Total aggression[3] | 0.96 ± 0.48 | 1.66 ± 0.82 | 3.99 | .0001 |

[1] Clam Island, 1978. Student's *t* calculated on raw data, N = 14 pairs, 350 samples; d.f. = 348.

[2] Percent of 350 samples, ± one standard deviation.

[3] Interactions/pair/hour; values given are mean ± one standard deviation.

[4] NS = not significant.

### TABLE 14

### PERCENT OF NON-NEIGHBOR INTRUDERS IGNORED BY HERRING GULLS AS A FUNCTION OF STAGE IN THE REPRODUCTIVE CYCLE[1]

| Distance from nest (m) | Pre-incubation | Incubation | Chick phase |
|---|---|---|---|
| 0–2 | 0 | 29 | 0 |
| 2–4 | 0 | 85 | 2 |
| 4–6 | 50 | 86 | 35 |
| 6–8 | 75 | 88 | 65 |
| 8–10 | 100 | 100 | 100 |
| Sample size | 50 | 300 | 150 |

[1] Appledore Island, 1980.

It is important to examine the types of aggression (neighbor and non-neighbor) separately because they could respond in opposite directions to the same variable; many studies on gulls examine *only* total aggression and do not distinguish the type of intruder. Total aggression was not correlated with time of day although neighbor aggression was. Further, both total aggression and non-neighbor aggression were correlated with age of the chicks. This resulted from the increased number of intruders attempting to cannibalize unguarded one to two week old chicks.

The percent of time that males and females were present on territory was negatively correlated with day during incubation when parents spent less time defending boundaries with neighbors, and during the chick stage when parents spent more time foraging to meet increased food requirements of chicks (Tables 15, 16). The number of times chicks were fed decreased with their age (although the amount of food presented during each feeding seemed to increase) and increased with the amount of precipitation. The latter correlation was not due to

### TABLE 15

### CORRELATIONS OF TIME OF DAY, PRECIPITATION, STAGE OF INCUBATION, SEX PRESENT, NEIGHBOR AGGRESSION AND NON-NEIGHBOR AGGRESSION DURING INCUBATION IN CLAM ISLAND HERRING GULLS[1]

| | Time of day | Stage of incubation | Male present | Female present | Neighbor aggression | Non-neighbor aggression | Aggression total |
|---|---|---|---|---|---|---|---|
| Time of day | — | −.08 | −.18 | −.06 | −.26** | .05 | −.24* |
| Tide stage | NS | .03 | .02 | −.01 | −.06 | .09 | .01 |
| Precipitation[2] | NS | .19 | −.03 | −.23 | .01 | .16 | .13 |
| Stage of incubation | | — | −.25** | −.26** | −.12 | −.01 | .05 |
| Male present[3] | | | — | −.13 | .25* | .00 | .20* |
| Female present[3] | | | | — | .20* | .09 | .20* |
| Neighbor aggression | | | | | — | .08 | .74*** |
| Non-neighbor aggression | | | | | | — | .69*** |
| Total aggression | | | | | | | — |

[1] Data were taken in 15 min samples (N = 92) on 14 pairs; * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$. Values given are correlation coefficients.

[2] Low value = sunny with no rain.

[3] Present but not incubating (mate was incubating).

## TABLE 16

CORRELATIONS OF TIME OF DAY, PRECIPITATION, AGE OF CHICKS, SEX PRESENT, NEIGHBOR AGGRESSION AND NON-NEIGHBOR AGGRESSION DURING THE CHICK PHASE FOR CLAM ISLAND HERRING GULLS[1]

| | Time of day | Precipitation | Age of chicks | Male present | Female present | Chick feeds | Neighbor aggression | Non-neighbor aggression | Total aggression |
|---|---|---|---|---|---|---|---|---|---|
| Time of day | — | −.12* | .10 | .09 | .04 | .07 | .19*** | −.06 | .11 |
| Precipitation[2] | | — | .13* | −.18** | −.33*** | .20*** | .02 | .06 | .06 |
| Age of chicks | | | — | −.75*** | −.47*** | −.21*** | .07 | .21*** | .12* |
| Male present[3] | | | | — | .50*** | .24*** | .13* | .06 | .13* |
| Female present[3] | | | | | — | .10 | .22*** | .08 | .19** |
| Chick feeds | | | | | | — | .28*** | .26*** | .35*** |
| Neighbor aggression | | | | | | | — | .14* | .64*** |
| Non-neighbor aggression | | | | | | | | — | .84*** |
| Total aggression | | | | | | | | | — |

[1] Data were taken in 15 min samples (N = 250) on 14 pairs; * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$. Values given are correlation coefficients.

[2] Low value = sunny with no rain.

[3] Present but not brooding (mate was brooding).

# TABLE 17

## FACTORS CONTRIBUTING TO AGGRESSION BY HERRING GULLS OBSERVED FROM THE BLIND ON CLAM ISLAND, 1978[1]

| | Entire model[2] | | | Variable | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | $r^2$ | $F$ | $P$ | Chick feeds | Female present | Male present | Both present | Stage in cycle | Time of day | Rain | Tide |
| Incubation[3] | | | | | | | | | | | |
| Neighbor aggression | 28 | 3.58 | .001 | | | | 9.3** | | 7.0** | | 7.1** |
| Non-neighbor aggression | 15 | 2.62 | .05 | | | | 36.2*** | | | | |
| Total aggression | 26 | 3.75 | .01 | | | | 6.8** | | 5.6* | | |
| Chick Stage[4] | | | | | | | | | | | |
| Neighbor aggression | 18 | 13.48 | .004 | | 11.8** | | 11.9*** | 4.2* | | | |
| Non-neighbor aggression | 39 | 18.60 | .001 | 23.6*** | | | | 24.3*** | | | |
| Total aggression | 29 | 33.8 | .0001 | 4.5** | | | 45.2*** | 5.4** | | | |
| Feeding behavior | 41 | 24.7 | .0001 | | | | 9.9*** | 56.8*** | 26.9*** | 13.8*** | |
| Entire reproductive cycle[5,6] | | | | | | | | | | | |
| Neighbor aggression | 39 | 5.54 | .001 | | 15.7*** | | 20.5*** | 9.5** | 4.0* | | 7.2** |
| Non-neighbor aggression | 28 | 11.1 | .0001 | 20.6*** | | | 29.7*** | 24.7*** | 8.9** | | |
| Total aggression | 36 | 11.8 | .0001 | 66.8*** | | 10.9*** | 25.2*** | 66.1*** | 3.9** | | |

---

[1] Based on 350 15-min samples from the start of incubation until the chicks were 65 days old. Given are $F$ values and levels of significance (* = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$, general linear models procedure).

[2] Given are $r^2$, levels of significance, and $F$ values for the models.

[3] For models during incubation stage, d.f. = 2, 98 (and 4, 96 for neighbor aggression).

[4] For models during chick stage, d.f. = 3, 247; 2, 248; 3, 247, and 4, 246, respectively.

[5] For models of the entire reproductive cycle variables also given the computer were percent male and female incubating. Also contributing were neighbor ($F = 21.2$, $P < 0.001$) and non-neighbor aggression ($F = 16.4$, $P < 0.001$).

[6] d.f. = 5, 345; 4, 346 and 5, 345, respectively.

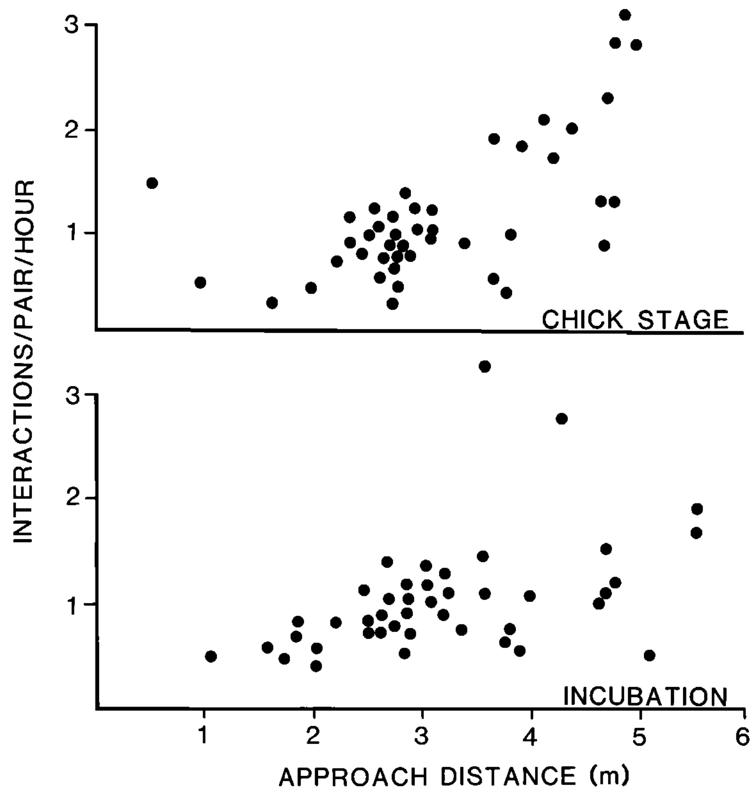

FIG. 19. Mean rates of aggression as a function of mean approach distances for the pairs of gulls observed from the Clam Island blind in intermediate bush habitat (N = 43 pairs).

increased presence of males and females during heavy rainstorms as the presence of both sexes was negatively correlated with rain (Table 16).

I used regression procedures to determine the amount of variability in rates of aggression explained by different independent variables (Table 17). The procedure produces models that include only variables that increase the $r^2$ significantly. Thus, variables that vary co-linearly are included only when their contribution exceeds that due to co-linearity (Draper and Smith 1981).

During incubation, 28 percent of the variance in the rates of neighbor aggression was explained by time of day, tide stage, and the percent of pairs having both members of the pair present; 15 percent of the variance in rates of non-neighbor aggression was explained by the percent of pairs having both members present, and 26 percent of the variance in rates of total aggression was explained by time of day and the percent of pairs having both members present. During the chick phase, only 18 percent of the variance in neighbor aggression was explained by the percent of females present, percent of time both members were present, and stage in the reproductive cycle; 39 percent of the variance in non-neighbor aggression was explained by the number of chick feedings, and stage in the reproductive cycle; and 29 percent of the variance in total aggression was explained by the number of times chicks were fed, the percent of pairs where both sexes were present, and stage in the reproductive cycle.

TABLE 18

MEAN APPROACH DISTANCE AS A FUNCTION OF HABITAT AND STAGE IN THE REPRODUCTIVE CYCLE FOR HERRING GULLS[1]

| | Dense bushes | Intermediate bushes | Open grass |
|---|---|---|---|
| No. pairs (hours of observation) | 14 (112) | 14 (114) | 12 (58) |
| Pre-incubation | 1.21 ± 0.21 | 2.21 ± 0.31 | 2.82 ± 0.43 |
| Incubation | 0.71 ± 0.10 | 2.43 ± 0.32 | 2.60 ± 0.38 |
| Hatching | 2.04 ± 0.21 | 3.84 ± 0.61 | 3.91 ± 0.54 |
| Chick Stage | 1.32 ± 0.11 | 2.21 ± 0.37 | 2.61 ± 0.18 |
| $F$[2] | 5.21 | 4.39 | 4.19 |
| d.f. | 1, 111 | 1, 113 | 1, 57 |
| $P$ | .05 | .05 | .05 |

[1] Clam Island, 1976; values given are means ± one standard deviation, in meters.

[2] One-way ANOVA with repeated measures.

Overall, 36 percent of the variability in total aggression was explained by the percent of pairs having males or both members present, the number of chick feedings, stage in the reproductive cycle, and time of day (Table 17). Over the entire reproductive cycle, the variance in neighbor aggression was explained by presence of both parents, stage in cycle, time of day, tide stage and the presence of the females, while the variance for non-neighbor aggression was explained by the number of times chicks were fed, as well as presence of both parents, stage in cycle, and time of day. This analysis clearly indicated that, of the variables measured, stage in the reproductive cycle, presence of both members of a pair, and the number of times chicks were fed were the most important variables contributing to the rates of aggression.

## APPROACH DISTANCE

Another component of aggression is the distance from the nest or scrape at which an intruder will elicit a response from a nesting gull (approach distance). The approach distance might be expected to vary with rates of aggression. Indeed, if birds act optimally with respect to energetics, they might invest a given amount of time and energy in defense at each stage in the cycle, thus changing the approach

TABLE 19

CORRELATION OF AGGRESSION FREQUENCY OF HERRING GULLS WITH APPROACH DISTANCE AS A FUNCTION OF TYPE OF INTRUDER[1]

| | Male | | Female | |
|---|---|---|---|---|
| | 1976 | 1977 | 1976 | 1977 |
| Number of pairs (interactions) | 14 (387) | 12 (360) | 14 (210) | 12 (193) |
| Type of intruder | | | | |
| Neighbor (adult) | .29* | .69*** | .21 | .43*** |
| Non-neighbor (adult) | .93*** | .93*** | .76** | .68*** |
| Immature | −.36* | −.89** | .93*** | —[2] |

[1] Clam Island 1976, 1977; values given are correlation coefficients and levels of significance (* = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$).

[2] Females almost never chased immatures in 1977.

FIG. 20. Approach distances of birds nesting in intermediate bush habitat on Clam Island as a function of type of intruder (mean = horizontal line, least significant interval = vertical line; N = 29 nests).

distance depending on the amount of intruder pressure. Although the approach distance bears a relationship to territory size, it also is a measure of the defender's sensitivity at a particular time. Approach distance is a measure of defensive aggression toward all intruders in all directions and is influenced by the presence of other birds (neighbors) available to chase intruders. Further, because undisturbed Herring Gulls normally stand very close to their nests (Fig. 4), at least until their chicks are 25 days old, approach distance is an indirect measure of how far they move toward intruders.

*Daily variation.*—The mean approach distances tolerated by gulls during the pre-incubation period varied as a function of time of day (Table 9; 15–30 April 1977, N = 195 hr observation, 15 pairs, $F = 10.27$, d.f. = 15, 181, $P < 0.001$). In general the approach distance was greatest at times of the day when gulls were also most aggressive. This correlation is not due merely to high levels of aggression, because the two were not correlated in the pre-egg-laying period (Fig. 13). How-

## TABLE 20

### CORRELATIONS OF PASSIVE AND ACTIVE DEFENSE WITH TERRITORY SIZE AND NEAREST NEIGHBOR DISTANCES FOR HERRING GULLS[1]

| | Internest distance | | Territory size | | |
|---|---|---|---|---|---|
| | Closest neighbor | Second neighbor | Primary | Secondary | Unique |
| Passive defense | | | | | |
| Time spent incubating, male | NS | NS | NS | −.67** | −.68** |
| Time spent incubating, female | NS | NS | NS | .67 | .68** |
| Time present but not incubating, male | NS | .41** | NS | .45** | −.60** |
| Time present but not incubating, female | NS | .55** | NS | .54* | NS |
| Active defense | | | | | |
| Approach distance, pre-incubation | .62** | .59** | .63** | .71*** | .64** |
| Approach distance, incubation | NS | NS | NS | NS | NS |
| Approach distance, chick phase | NS | NS | .39* | NS | NS |
| Rate of aggression, pre-incubation | .40** | .45** | .51** | NS | NS |
| Rate of aggression, incubation | −.40** | −.41** | −.40** | NS | NS |
| Rate of aggression, chick phase | NS | NS | NS | NS | NS |
| Rate of aggression, entire cycle | −.29 | −.28 | NS | NS | −.45** |
| Rate of aggression, male | −.55** | −.45** | −.47* | NS | −.56** |
| Rate of aggression, female | NS | NS | NS | NS | NS |

[1] Clam Island; values are correlation coefficients and levels of significance; * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$, NS = not significant; d.f. = 43.

ever, the mean approach distance and the mean rate of aggression were directly related during incubation and the chick stage for individual pairs (Fig. 19, means for 43 pairs in 1976, 1977, 1978).

*Stage in reproductive cycle.*—Overall, the mean approach distance was higher when Herring Gulls had newly-hatched chicks than during incubation (Table 18, Figs. 13, 14). With time, the approach distance increased for neighbors while it decreased for non-neighbors (Table 11). In part this reflects defense of larger territories against neighbors. In addition parents only chased non-neighbors that landed near their chicks; at this stage non-neighbor intruders are not always seeking space, but usually are cannibals. In the dense bushes approach distances were significantly lower during incubation than during the pre-incubation and chick phases (Fig. 13). Similarly at Meadow Island, the mean approach distance to intruders was less during incubation than when chicks were 1 to 7 days old ($t$ = 7.55, d.f. = 204, $P < 0.001$), and less when they were one week old than when they were two weeks old ($t$ = 5.40, d.f. = 258, $P < 0.001$, Fig. 14).

*Within and among pair variations.*—The mean approach distance of pairs during incubation varied from 1.9 to 5.6 m ($\bar{X} = 2.2 \pm 0.61$, N = 29 pairs), whereas during the chick phase, it varied from 1.0 to 5.2 m ($\bar{X} = 3.4 \pm 0.91$, N = 29 pairs). The approach distance of females was significantly lower than that of males for all types of intruders (Fig. 20; two-way ANOVA, $F$ = 12.80, d.f. = 2, 165, $P < 0.001$), and there were differences between years for each sex ($F$ = 4.1, d.f. = 2, 165, $P < 0.05$). In general, rates of aggression and approach distances were highly correlated for both sexes (Table 19). That is, birds that engaged in frequent encounters initiated attacks when intruders were farther from their nests than were intruders eliciting a response from birds engaging in fewer encounters.

*Variation by type of intruder.*—As shown above, the approach distance differed

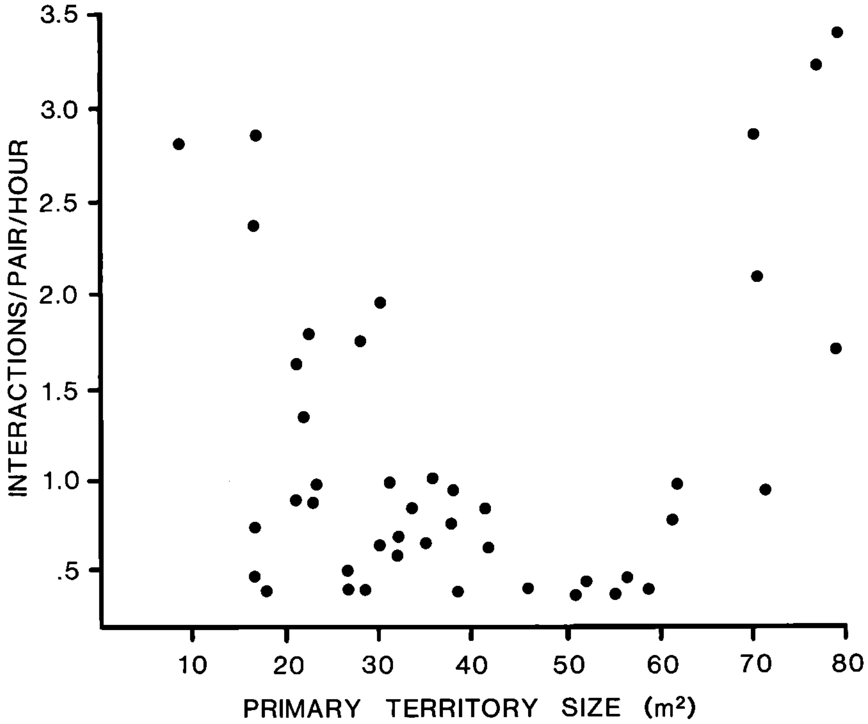

FIG. 21. Mean rates of aggression as a function of primary territory size for pairs observed from the blind on Clam Island, 1976–1978.

depending on the type of intruder (Fig. 20). The mean approach distance at which neighbors were chased by males was greater than that at which non-neighbors were chased, although this was not always the case for females. Incubating birds of both sexes left the nest only to chase intruders within 3 m of the nest.

## TERRITORY SIZE AND AGGRESSIVE BEHAVIOR

On Clam Island Herring Gulls defended territories passively, simply by their presence, and actively, by being aggressive toward intruders. The percent of time at least one member of the pair was present was significantly correlated with the size of secondary and unique (but not primary) territories for the 43 pairs I watched from my blind (Table 20). The percent of time males incubated was correlated negatively with the size of the secondary territory, largely because when males were not incubating they were free to chase intruders. The internest distance to the second nearest neighbor was positively correlated with the amount of time a non-incubating male or female was present (i.e., the more often either member of the pair was present, the farther away neighbors were likely to build nests).

The highest correlation between territory size and any active defense behavior occurred for the approach distance and rates of aggression during the pre-incubation phase (Table 20). For the 43 pairs observed around my blind, mean aggression per pair was highest for birds on small and large territories (Fig. 21). As predicted, gulls defending intermediate-sized territories had the lowest rates of aggression.

## DISCUSSION

### DISPLAY BEHAVIOR

I examined displays from the view of the owner of a territory. The types of aggressive displays used to defend space varied in intensity and as a function of habitat, nest density, type and age of intruder, and stage in the reproductive cycle. Gulls in dense nesting areas with clear visibility walked directly toward their opponents, while gulls in less dense areas usually flew at their opponents. Because it was difficult to walk toward an intruder in dense grass, it was quicker to fly at an intruder that was more than 3 or 4 m from the nest.

Gulls nesting in intermediate bush habitat did not respond in the same way to neighbors and strangers. For neighbors, gulls usually engaged in prolonged bouts of Grass Pulling, whereas non-neighbors were immediately chased (by Walking or Flying Toward them). This confirms Tinbergen's (1960) suggestion that gulls are more tolerant of neighbors. Further, Grass Pulling seems to establish the exact location of territory boundaries. Non-neighbors, on the contrary, were either in search of space to establish a territory or in search of eggs and chicks for food. In either case, it takes less energy immediately to chase away an intruder than to displace an established bird.

The use of particular behavior patterns and displays also varied by stage in the reproductive cycle. Chasing was most frequent in the pre-egg-laying period and when chicks were hatching, again reflecting the vulnerability of the territory boundaries to non-neighbor intruders and of chicks to cannibalism. Grass Pulling was most prevalent early in the season when boundaries were being established. Observations at three different colonies indicated that the increase in overt aggression at hatching and the week following was typical of Herring Gulls, and may reflect the high rates of cannibalism prevalent in Herring Gull colonies (see pp. 58–65; Parsons 1971; Davis and Dunn 1976). Small chicks are most vulnerable to cannibalism, the majority of deaths occurring when chicks are less than 10 days old (e.g., Paynter 1949; Hunt and Hunt 1976).

### SEASONAL VARIATIONS IN RATES OF AGGRESSION AND APPROACH DISTANCES

Several authors have reported that rates of aggression in colonial birds vary as a function of stage in the reproductive cycle. For example, rates of aggression increase at hatching in terns (Veen 1977) and penguins (Spurr 1974). In gulls, aggression rates are often highest early in the season, when territories are being established, and decrease thereafter, although they increase seasonally in Great Black-backed Gulls (Verbeek 1979) and are greatest after hatching in Western Gulls (Pierotti 1981). Although they did not quantify aggressive defense, Hunt and Hunt (1976) reported that Glaucous-winged Gulls with chicks were more aggressive than those with eggs.

Rates of aggression of Herring Gulls varied as a function of stage of the reproductive cycle; they were highest during the pre-egg-laying stage and at hatching. This pattern differs from that reported for most gulls for several reasons (but see Pierotti 1981). First, if I had examined aggression rates during only a few days of the pre-egg-laying and incubation periods, I might also have reported a seasonal decrease in aggression. Second, the very high rates of aggression in the chick phase only occurred for a short period following hatching. Third, the seasonal pattern of rates of aggression of small-sized gulls seems to differ from that of the larger species such as Glaucous-winged Gull (Hunt and Hunt 1976), Great Black-backed Gull (Verbeek 1979), and Herring Gull (this study). All gull species are highly aggressive in the pre-egg-laying stage, when they are defending territories against conspecifics, but only the large gulls are highly aggressive after hatching. I attribute this increase in aggression at hatching to cannibalism which is more prevalent in large than in small gulls. Hunt and Hunt (1976) reported that most chick killings are due to territorial clashes in Glaucous-winged Gulls. Further, in the large-sized gulls more neighbors and strangers become cannibals and search for chicks to eat (Parsons 1971). However, large chicks are difficult to kill and carry away. Thus, chicks are vulnerable to cannibalism only for the first 10 to 14 days post-hatching, the period corresponding to the most intense aggression in the Herring Gulls studied.

The pattern of approach distance varied in Herring Gulls according to stage in the reproductive cycle (Fig. 13). Herring Gulls had the highest approach distances in the pre-incubation phase, and again in the chick stage. The initial drop in approach distance during the pre-incubation phase reflects the settling of territory boundaries. When gulls first arrived, they defended large territories. Gradually newcomers established territories by insinuating themselves between existing pairs. Establishment of a new boundary reduced the overall approach distance and territory size. In becoming more aggressive when chicks hatched, parents often succeeded in driving away neighbors, killing neighboring chicks, and annexing whole territories (or dividing them with other neighbors). Some gulls that lose chicks become more aggressive (Davis and Dunn 1976; Pierotti 1981). In this study, rates of aggression dropped after the chicks were two weeks old, but the approach distance did not. The gulls continued to defend the large territories acquired earlier in the chick stage. Because chicks were larger, fewer conspecifics landed to attempt cannibalism. Thus, intruder pressure (and aggression levels) dropped (Fig. 12).

## SEXUAL DIFFERENCES IN RATES OF AGGRESSION AND APPROACH DISTANCES

Trivers (1972) asserted that in monogamous species in which both sexes contribute to the care of the young, females show greater investment in the young than males. Thus, the pattern of the seasonal allocation of time and energy by males and females is of theoretical interest. Each sex should try to increase its own survival by minimizing its contribution to the young while maximizing that of its mate. Further, because a male must defend its female in the pre-egg-laying phase, it should be more aggressive during this period (Emlen and Oring 1977). Indeed males seem to protect females, or to be more aggressive than females in the pre-egg-laying phase in many species (e.g., Western Gull, Pierotti 1981; Black Skimmer, Burger 1981b). In the present study aggression rates were very high in the pre-incubation phase.

Trivers' (1972) model predicts that females should be more aggressive than males during the chick phase because they have invested more in the egg than have males. By the time chicks hatch both parents have invested heavily in incubation and defense. Pierotti (1981) reported that Western Gull males perform more aggressive acts than females when they have chicks. He did not, however, follow the chicks past fledging. In this study males also were more aggressive when chicks were young. During this stage, female Herring Gulls were present on territory as much as males and so were passively engaged in defense. Morris and Black (1980) also found that male and female Herring Gulls nesting in a colony spent equal time on their nesting territories. Pierotti (1981) reported that male Western Gulls on Southeast Farallon Island spent more time on their territories than did females in one year (1973), but not in another (1974), whereas on Santa Barbara Island females were present more than males.

Southern (1981) recently examined sex-related differences in territorial aggression in Ring-billed Gulls (*Larus delawarensis*) and found that during the incubation period and pre-fledging period, males performed more aggressive behavior in defense of the territory and chicks than females. Similarly, Butler and Janes-Butler (1983) found that male Great Black-backed Gulls exhibited higher levels of agonistic acts than females. However, when I examined parental reproductive effort from incubation to a month and a half post-fledging, Herring Gulls of both sexes fed the chicks an equal number of times and had equal rates of aggression in defense of the chicks over the entire chick phase combined (0–81 days). Holly (1982) also reported that both sexes fed Herring Gull chicks during the post-fledging period, although he did not quantify the relative contribution of each sex. In monogamous species both sexes contribute to the reproductive effort, and the relative allocation of care at any time may vary from pair to pair depending on individual behavioral patterns (Burger 1981b). In monogamous species, selection should favor large investment by both parents in the care of the young (Burger 1980b, 1981a). A bird forced by its mate to perform well beyond half of the required duties may theoretically desert its mate and the present offspring in favor of protecting its future offspring (by staying alive). Indeed at the end of the breeding season in the absence of a mate, a Franklin's Gull will desert 20 day old young, leaving them to die (Burger 1974a).

In many gulls, including Herring Gulls, males are significantly larger than females in body size and bill dimensions (Bianki 1967; Harris and Jones 1969; Ingolfsson 1969; Shugart 1977; Ryder 1978; Fox et al. 1981; Pierotti 1981). Thus, one might expect males, not females, to defend against males, particularly if physical contact was required. Indeed, male Herring Gulls in this study were involved in 90 percent of the fights. But fighting is only a small part of territorial and brood defense although it does involve potential for injury. Further, the difference in rates of aggression between male and female Herring Gulls was greatest when the intruders were neighbors (Fig. 18). Females may be defending eggs or chicks because non-neighbor intruders are often cannibals, whereas many neighbor encounters are boundary disputes. In this study, males were involved in more than twice as many encounters with neighbors as females. Similarly, Vermeer (1963) found that male Glaucous-winged Gulls became involved in more border clashes than females although females often initiated the encounters.

Few studies have examined approach distances. In this study, Herring Gull males consistently responded to all types of intruders at greater distances from the nest than did females (Fig. 20). This may reflect a reluctance on the part of females to move very far from the eggs and chicks and the tendency of males to defend the territory (see General Discussion; Hunt and Hunt 1975, 1976; Davis and Dunn 1976; Pierotti 1981).

### EFFECTS OF TIDE, TIME, AND HABITAT ON RATES OF AGGRESSION AND APPROACH DISTANCES

Herring Gulls had higher rates of aggression and greater approach distances in the early morning and late afternoon, were involved in aggressive interactions with more neighbors and fewer non-neighbors at high tide, and had higher rates of aggression in the intermediate bush habitat. Tidal patterns are known to affect gull distributions and feeding patterns (Bianki 1967; Drent 1967; Delius 1970; Vernon 1970; Galusha and Amlaner 1978; Verbeek 1979; Burger 1980c). Herring Gulls nesting on Clam Island frequently foraged at low tide, leaving only one member of the pair on the territory. As the tide rose, more gulls returned to loaf about the nest sites. Thus, more non-incubating neighbors were present to engage in neighbor aggression (Table 12). During low tides, non-neighbor aggression was more frequent, largely because while most non-incubating mates were absent non-neighbor intruders attempted to land to establish territories or steal eggs. When such an intruder landed, the incubating bird often repelled the intruder itself using the Long Call, or summoned its mate from the nearby bay to chase the intruder.

The activity patterns of gulls are affected by time of day (Drent 1967; Spaans 1971; Burger 1976; Conover and Miller 1980). Conover and Miller (1980) reported that nesting Ring-billed Gulls engaged in more territorial behavior in the morning, whereas California Gulls (*Larus californicus*) showed a constant rate of territorial behavior all day. Burger (1976) found that Laughing Gulls had a clear diurnal pattern similar to that of the Herring Gulls in this study. The increased rates of aggression in the early morning and late afternoon were in part a result of (1) increased wandering about the territories by resident birds which increased neighbor aggression, and (2) increased intrusion by pairs seeking territories. Such territory-hunting birds loafed at the edge of the colony during the heat of the day. The increase in the number of intruders resulted in an increase in rates of aggression as there was an increase in border clashes.

Birds nesting in the intermediate bush habitat engaged in more aggression than those nesting in other habitats (Fig. 11). In part, this different reflected differences in intruder pressure, because the same relative proportion of intruders (about 7%) was ignored in all habitats (Fig. 8). However, nest density was greater in all the bush habitats compared to the grass habitat (Table 6). Areas with bushes were preferred as nesting habitat because they provided adults and chicks with cover for protection from sun and predators. Thus, pairs seeking territories often landed in the bush habitat. In addition, small territory size resulted in frequent interactions with neighbors.

## REPRODUCTIVE SUCCESS IN HERRING GULLS

In this section I examine reproductive success as a function of date of egg-laying, nest location, nest density, habitat, and parent quality. I also determine the effects of predation and weather-related events on reproductive success of Herring Gulls nesting on Clam Island.

### RESULTS

### REPRODUCTIVE SUCCESS

Reproductive success data were available for 1,080 nests from the Clam Island colony and for the 43 pairs of gulls I observed near my blind (1976–1978, Table

### TABLE 21

### REPRODUCTIVE SUCCESS OF HERRING GULLS[1]

| | 1976 | 1977 | 1978 |
|---|---|---|---|
| Birds followed by field assistance | | | |
| Number of nests | 256 | 382 | 442 |
| Clutch size | 2.85 ± 0.42 | 2.88 ± 0.38 | 2.78 ± 0.37 |
| Hatching rate/nest | 2.10 ± 0.61 | 2.30 ± 0.82 | 2.00 ± 0.37 |
| Nest hatching success (%) | 99 | 94 | 83 |
| Fledging rate/nest at | | | |
| 15 days of age | 1.60 ± 0.98 | 1.88 ± 0.96 | 1.73 ± 0.10 |
| 35 days of age[2] | 1.26 ± 0.77 | 1.58 ± 1.01 | 1.13 ± 1.02 |
| Number chicks alive at 35 days of age/nest having at least one chick hatch[2] | 1.27 ± 0.76 | 1.68 ± 1.01 | 1.37 ± 1.05 |
| Birds observed from the Blind | | | |
| Number of nests | 14 | 15 | 14 |
| Clutch size | 2.81 ± 0.52 | 2.84 ± 0.34 | 2.76 ± 0.41 |
| Hatching rate/nest | 2.27 ± 0.80 | 2.55 ± 1.29 | 2.70 ± 0.90 |
| Fledging rate/nest at 35 days of age | 1.38 ± 1.09 | 1.20 ± 1.00 | 2.10 ± 1.06 |

[1] Clam Island (1976–1978); values given are means ± one standard deviation.

[2] Computed on the basis of 35-day old chicks found within the colony as well as on the adjacent bay (see Appendix I).

21, Appendix I). The increase in the number of nests from 1976 to 1978 represents a population increase on Clam Island (Burger and Shisler 1979). The success of the general population was similar to that of the pairs observed around my blind (Table 21) except in 1977 when territorial clashes resulted in unusually high chick losses among the pairs near my blind. The study site used for my behavioral observations on aggression and territory size was chosen to minimize differences due to year, location, habitat, stage in reproductive cycle, clutch size, and parental quality. Therefore, this sample was unsuitable for certain analyses discussed below, for which I used only data from the large sample of nests which did not include the birds around my blind.

## INTERYEAR DIFFERENCES

Mean clutch size and hatching rate per nest did not differ significantly among years, although fledging success did (one-way ANOVA, N = 1,080 nests). In 1976 Herring Gulls fledged fewer three-chick broods and more one-chick broods; in 1977 pairs fledged more two and three-chick broods, and in 1978 pairs fledged fewer three-chick broods and had more complete failures than expected ($\chi^2$ expected values computed from the combined 1976–1978 data; Table 22).

## LOCATION AND HABITAT DIFFERENCES

Several authors have noted that birds nesting in the center of colonies are more successful than those nesting on the periphery (reviewed by Burger 1981d). To test this I examined data only from nests that were initiated during the peak of egg-laying to eliminate differences due to date of egg-laying (Davis and Dunn 1976). In this study there were no significant differences in clutch size, hatching rates, or fleding rates by nesting location (Table 23).

Hatching and fledging rates varied by habitat with gulls nesting in dense and intermediate bushes and in grass fledging significantly more chicks than those

## TABLE 22

### YEARLY DIFFERENCES IN FLEDGING SUCCESS OF HERRING GULL NESTS ON CLAM ISLAND[1]

| | 1976 | 1977 | 1978 | $\chi^2$ | $P$ |
|---|---|---|---|---|---|
| Fledged no chicks | — | fewer | more | 29.2 | .001 |
| Fledged one chick | more | — | — | 9.2 | .01 |
| Fledged two chicks | — | more | — | 14.4 | .001 |
| Fledged three chicks | fewer | more | fewer | 39.3 | .001 |

[1] Values obtained by using a contingency $\chi^2$ test (d.f. = 2). Fewer means significantly fewer than predicted, more means significantly more than predicted, and — means no difference from expected. Fledged = reached 35 days of age.

nesting in clumped and sparse bush habitats (Table 24, $F = 14.2$, d.f. = 5, 1,075, $P < 0.0001$). Chicks hatched in dense or intermediate bushes had innumerable hiding places whereas those hatching in sparse bushes did not.

Mosquito control personnel dug ditches on Clam Island in 1976 and 1977, depositing the spoil on the marsh. Because these spoil piles are higher than the surrounding marsh, I expected gulls to select them as nesting sites and to exhibit higher reproductive success on them due to reduced flooding. Gulls nesting on spoil deposited the same year (i.e., well above the marsh level) fledged significantly more chicks than those nesting on spoil from the previous year (i.e., almost level with the marsh, Table 25). Overall a greater percent of eggs laid on new spoil than of those laid on old spoil or in *Spartina* resulted in fledged chicks.

### TIMING OF EGG-LAYING AND REPRODUCTIVE SUCCESS

Egg-laying occurred from 18 April to 3 June, 1976, 22 April to 27 May, 1977, and 17 April to 6 June, 1978. However, I analyzed data only from 1977 and 1978 because the exact date of egg-laying was not determined for eggs laid 29 April to 1 May 1976 due to heavy rains. In 1977, 63 percent of nests were initiated in the middle egg-laying period (1–14 May) compared with 43 percent in 1978. The large sample size in 1978 represented nearly all of the nests on Clam Island (Table 26). Many of these nests were not included in later analyses because chicks were not located after 20 days of age. Mean clutch size did not differ significantly in 1977 as a function of date of initiation of egg-laying, although it did in 1978. In both years predation, hatching, and fledging rates varied significantly as a function

## TABLE 23

### REPRODUCTIVE SUCCESS OF HERRING GULLS NESTING IN THE CENTER OR AT THE EDGE OF THE COLONY[1]

| | Center | Edge[2] | $\chi^2$ | $P$[3] |
|---|---|---|---|---|
| Number of nests | 466 | 276 | | |
| Clutch size | 2.80 ± 0.52 | 2.73 ± 0.34 | 0.16 | NS |
| Hatching rate | 1.77 ± 1.07 | 1.98 ± 0.81 | 3.37 | NS |
| Fledging rate at 30 days of age | 1.00 ± 0.88 | 1.09 ± 0.92 | 3.06 | NS |

[1] Clam Island 1977, 1978; values given are means ± one standard deviation.

[2] Edge was defined as 10 m from the edge of the colony.

[3] NS = not significant. Data were tested with a 2 × 4 contingency table (d.f. = 3).

## TABLE 24

### EFFECT OF HABITAT ON REPRODUCTIVE SUCCESS OF HERRING GULLS[1]

| | Dense bushes | Intermediate bushes | Clumped bushes | Sparse bushes | Open grass |
|---|---|---|---|---|---|
| Number of nests | 221 | 412 | 264 | 125 | 67 |
| Mean date of egg-laying | 2 June | 31 May | 5 June | 6 June | 7 June |
| Nearest neighbor distance (m) | 3.4 ± 1.6 | 4.5 ± 2.7 | 2.7 ± 2.7 | 3.9 ± 2.5 | 5.9 ± 5.2 |
| Number of eggs eaten/nest | 0.10 ± 0.5 | 0.17 ± 0.4 | 0.25 ± 0.5 | 0.17 ± 0.3 | 0.19 ± 0.2 |
| Hatching rate/nest | 2.40 ± 0.8 | 2.55 ± 0.8 | 1.75 ± 1.5 | 2.00 ± 0.8 | 2.40 ± 0.7 |
| Fledging rate/nest | 1.64 ± 0.9 | 1.75 ± 0.5 | 1.00 ± 1.2 | 1.00 ± 1.4 | 1.30 ± 0.9 |

[1] Clam Island, 1976–78; values given are means ± one standard deviation.

of date of egg-laying, with predation rates on eggs signifiantly higher in the late nests. In the middle egg-laying period predation was lower than expected in 1977, but not in 1978 (Table 26).

In both years there were a number of addled eggs that appeared infertile. In 1977 addled eggs were significantly fewer in the early egg-laying period, and significantly more common in the late egg-laying period; in 1978 there were fewer than expected in the late egg-laying period (Table 26). I am unable to account for this difference except that egg-laying occurred during a rainy period in 1977, which resulted in fewer copulations per pair (at least on their territories; Burger, unpubl. data). Nest checks were conducted by a similar method in both years.

Overall, hatching rate was higher for the pairs that laid in the early egg-laying period in 1977, and for the pairs that laid in the middle egg-laying period in 1978. Fledging success was highest for pairs that laid in the early egg-laying period and significantly lower for those laying in the late egg-laying period in both years (Table 26).

### CLUTCH SIZE AND REPRODUCTIVE SUCCESS

Reproductive success should vary as a function of clutch size. In this section I examine the effect of clutch size and hatching rate on fledging rate. In 1976 the

## TABLE 25

### EFFECT OF ELEVATION DIFFERENCES ON REPRODUCTIVE SUCCESS OF HERRING GULLS[1]

| | *Spartina* | Old spoil | New spoil | *F* | *P* |
|---|---|---|---|---|---|
| Number of nests | 374 | 20 | 27 | | |
| Clutch size | 2.27 ± 0.53 | 2.90 ± 0.36 | 2.93 ± 0.26 | 1.66 | NS |
| Hatching rate | 2.01 ± 1.11* | 2.30 ± 0.61 | 2.44 ± 0.51 | 2.92 | .05 |
| Fledging rate: | | | | | |
| 10 days | 1.36 ± 1.13 | 1.40 ± 0.91 | 1.81 ± 0.89 | 2.45 | NS |
| 20 days | 1.15 ± 1.13 | 1.05 ± 0.95 | 1.62 ± 0.92* | 2.94 | .05 |
| 30 days | 1.00 ± 1.01 | 0.90 ± 0.89 | 1.59 ± 0.51* | 4.60 | .01 |
| Fledging percent of all eggs laid[2] | 35 ± 36 | 31 ± 42 | 52 ± 0.27* | 3.52 | .03 |

[1] Clam Island, 1977, 1978; old spoil is slightly higher than *Spartina* grass, and new spoil is 8 to 15 cm higher than the *Spartina*. Values given are means ± one standard deviation. ANOVA on log transformed raw data, d.f. = 2, 419. * = Value that differs significantly from value in the other two habitats.

[2] Fledging refers to 35-day old chicks.

## TABLE 26

EFFECT OF LAYING DATE ON REPRODUCTIVE SUCCESS OF HERRING GULLS[1]

| | 17–30 April | 1–14 May | After 15 May | $\chi^2$ | $P$ |
|---|---|---|---|---|---|
| 1977 | | | | | |
| Number of nests | 75 | 240 | 67 | 150.00 | .001 |
| Number eggs laid[2] | 220 (2.95) | 705 (2.94) | 175 (2.61) | 3.49 | NS |
| Number eggs preyed on[3] | 7 (0.10) (−) | 36 (0.15) (−) | 47 (0.70) (+) | 73.92 | .001 |
| Number eggs addled[3] | 13 (0.18) (−) | 81 (0.34) | 41 (0.62) (+) | 20.69 | .001 |
| Number hatched[3] | 200 (2.66) (+) | 562 (2.34) | 120 (1.80) (−) | 14.58 | .001 |
| Number fledged[3,4] | 178 (2.37) (+) | 350 (1.46) | 67 (1.00) (−) | 46.41 | .001 |
| 1978 | | | | | |
| Number of nests | 280 | 344 | 176 | 57.20 | .001 |
| Number eggs laid[2] | 824 (2.85) (+) | 991 (2.84) (+) | 444 (2.52) (−) | 208.71 | .001 |
| Number eggs preyed on[3] | 50 (0.17) (−) | 103 (0.29) | 97 (0.55) (+) | 54.29 | .001 |
| Number eggs addled[3] | 20 (0.06) | 30 (0.08) | 24 (0.13) (−) | 8.96 | .05 |
| Number hatched[3] | 523 (1.81) | 711 (2.04) (+) | 222 (1.26) (−) | 550.20 | .001 |
| Number fledged[3,4] | 353 (1.22) (+) | 408 (1.17) (+) | 72 (0.41) (−) | 233.68 | .001 |

[1] Clam Island; chi square value computed on an expected frequency derived from all data. + = more than expected, − = less than expected, where contribution of the variable was significant at the $P < 0.05$ level; NS = not significant.

[2] Number in parentheses = mean clutch size.

[3] Number in parentheses = number/nest.

[4] Fledged = alive at 30 days.

most common brood size at hatching was two, whereas it was three in 1977 and 1978 (Fig. 22, Appendix I). The most common number of young fledged differed among all three years; it was 0 in 1978, 1 in 1976, and 2 in 1977 (Fig. 22). In all three years chicks generally gained weight steadily, and there were no periods when large numbers of chicks lost weight. Similarly, after the first week, the mean number of times each chick was fed was constant throughout the period.

In all three years the number of chicks fledged was a function of clutch size (Table 27). In 1976 and 1978 parents with clutches of only one egg fledged almost no chicks. Overall, parents with clutches of three eggs fledged more than five times as many chicks as those with clutches of only one egg. Although the modal brood size was two in 1976, parents with two eggs were less successful than those with three eggs. The lower clutch sizes in 1976 may have been a result of prolonged cold and rainy weather prior to the egg-laying period.

In some gull species chicks from larger broods have higher survival rates (Brown 1967a; Coulter 1977; Hahn 1981). Indeed, Brown (1967a) found that Herring Gull chicks from broods of three had a higher probability of survival than chicks from other-sized broods. The implication is that parents that are able to hatch more chicks are also able to care for them better, or that the presence of two or three chicks begging results in more food being brought per chick than in one chick broods. However, I found that all chicks had an equal chance of surviving to 35 days of age regardless of brood size (Table 28; $\chi^2 < 1.2$ for all years). From 47 to 84 percent of the chicks survived to 35 days of age, with the highest survival rates occurring in 1977 in broods of one chick (Table 28).

The above analysis does not take into account initial clutch size of parents or loss of eggs to predators. Therefore, I examined hatching rates in gulls that laid three eggs, testing the null hypothesis that survival of chicks is independent of the number hatched in the nest (Table 29). This partially controls for age, in that

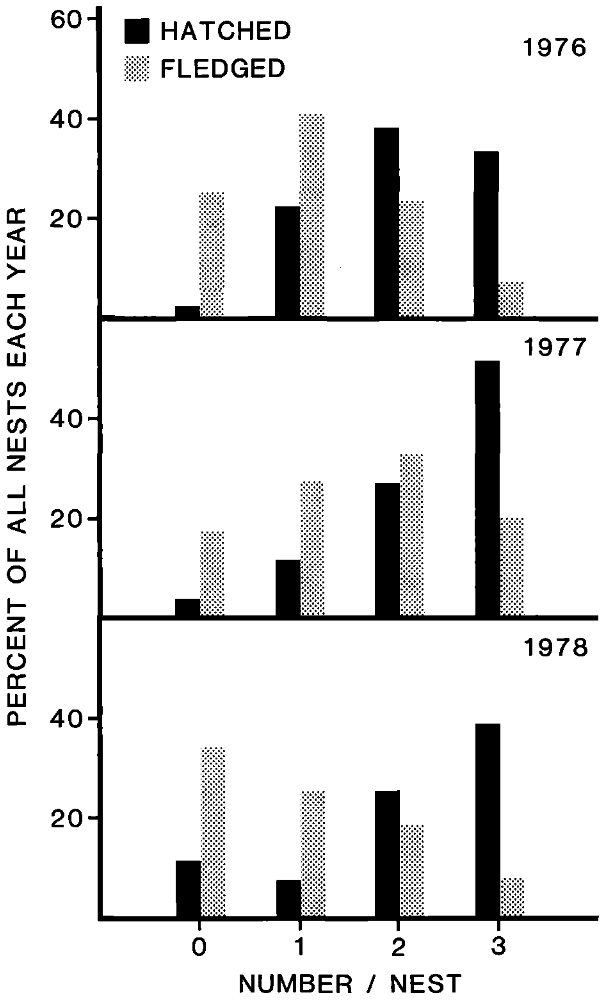

FIG. 22. Percent of nests hatching and fledging zero to three chicks in different years on Clam Island.

older birds have higher mean clutch sizes (Ryder 1980), and eliminates parents that lost an egg during the egg-laying period. There were no significant differences in survival of chicks as a function of brood size even among 3 egg clutches (Table 29). Survival of chicks ranged from 51 to 81 percent, slightly higher than that of chicks from clutches of all sizes (Table 28).

Pairs with three eggs may be higher quality parents than those with only one or two. Male gulls feed the females during courtship (Niebuhr 1981; this study). Being able to obtain sufficient food for production of three eggs may be a good predictor of ability to find sufficient food for three chicks (e.g., Nisbet 1973). I tested the hypothesis that parents hatching two eggs do not differ in the number of chicks they fledge, regardless of the number of eggs laid. Females of pairs used in this test laid two or three eggs, but parents that had three-egg clutches failed

TABLE 27

NUMBER OF CHICKS FLEDGED AS A FUNCTION OF CLUTCH SIZE[1]

| Year | | Clutch size | | | | |
|---|---|---|---|---|---|---|
| | | One | Two | Three | $\chi^2$ | *P* |
| 1976 | X̄ ± s.d. | 0.14 ± 0.38 | 0.63 ± 0.77 | 1.20 ± 0.86 | 2.1 | NS |
| | N | 7 | 24 | 225 | | |
| 1977 | X̄ ± s.d. | 0.60 ± 0.55 | 0.92 ± 0.77 | 1.64 ± 1.07 | 14.9 | .001 |
| | N | 5 | 39 | 338 | | |
| 1978 | X̄ ± s.d. | 0 | 0.61 ± 0.77 | 1.15 ± 1.03 | 7.7 | .01 |
| | N | 18 | 62 | 362 | | |
| 1976–1978 | X̄ ± s.d. | 0.25 ± 0.61 | 0.72 ± 0.77 | 1.33 ± 0.98 | 25.5 | .001 |
| | N | 30 | 125 | 925 | | |

[1] Chi-square test compares whether gulls with 2 or 3 egg clutches reared 0 or 1 chick compared to 2 or 3 chicks to 35 days of age (d.f. = 1). Values given are means ± one standard deviation. Based on 1080 nests. N = number of nests.

to hatch one egg. In 1976 and 1977, but not 1978, parents with three-egg clutches fledged significantly more young than parents with two-egg clutches even though both hatched only two eggs (Table 30). I cannot account for the differences between years although the number of cannibals in the central areas of the colony increased in 1978.

## PREDATION AND REPRODUCTIVE SUCCESS

Predation was the major cause of egg and chick mortality on Clam Island (Table 31). Each year predators took 5 to 15 percent of the eggs and 7 to 11 percent of the chicks, and another 11 to 20 percent were assumed to have been taken by predators (missing when very young, when siblings were still present). Overall, 22 to 30 percent of the eggs that were laid were preyed upon in the egg or chick stage.

Over the three years on Clam and Carvel Islands, I saw 68 eggs being eaten, one (1%) by a Blue Jay (*Cyanocitta cristata*), four (6%) by Common Grackles

TABLE 28

FLEDGING RATE OF HERRING GULLS AS A FUNCTION OF NUMBER OF EGGS HATCHED[1]

| | | Number hatched | | |
|---|---|---|---|---|
| | | One | Two | Three |
| 1976 | X̄ ± s.d. | 0.50 ± 0.30 | 1.10 ± 0.62 | 1.52 ± 0.62 |
| | % | 50 | 55 | 51 |
| | N | 62 | 101 | 92 |
| 1977 | X̄ ± s.d. | 0.84 ± 0.52 | 1.28 ± 0.58 | 2.02 ± 0.61 |
| | % | 84 | 65 | 67 |
| | N | 44 | 107 | 208 |
| 1978 | X̄ ± s.d. | 0.48 ± 0.40 | 0.94 ± 0.54 | 1.59 ± 0.61 |
| | % | 48 | 47 | 53 |
| | N | 50 | 133 | 191 |

[1] Clam Island; values given are mean numbers of young fledged/egg hatched and percents of hatched eggs producing fledglings 35 days old. N = number of clutches.

## TABLE 29
### FLEDGING RATE OF HERRING GULLS LAYING THREE EGGS AS A FUNCTION OF NUMBER OF EGGS HATCHED[1]

| | | Eggs hatched | | |
|---|---|---|---|---|
| | | One | Two | Three |
| 1976 | X̄ ± s.d. | 0.55 ± 0.50 | 1.06 ± 0.72 | 1.52 ± 0.93 |
| | % | 55 | 53 | 51 |
| | N | 49 | 84 | 92 |
| 1977 | X̄ ± s.d. | 0.81 ± 0.50 | 1.38 ± 0.70 | 2.02 ± 0.93 |
| | % | 81 | 69 | 67 |
| | N | 32 | 79 | 208 |
| 1978 | X̄ ± s.d. | 0.56 ± 0.56 | 0.91 ± 0.83 | 1.59 ± 1.02 |
| | % | 56 | 45 | 53 |
| | N | 36 | 100 | 191 |
| 1976–1978 | X̄ ± s.d. | 0.62 ± 0.52 | 1.10 ± 0.75 | 1.76 ± 0.96 |
| | % | 62 | 55 | 55 |
| | N | 117 | 263 | 491 |

[1] Clam Island. Values given are mean numbers of young fledged/egg hatched, and percents of hatched eggs producing fledgings. Contingency table $\chi^2$ tests showed no significant differences in survival of chicks from broods of different sizes within years ($\chi^2$ values < 2.2).

(*Quiscalus quiscula*), 14 (21%) by Fish Crows (*Corvus ossifragus*), and the rest (72%) by gulls. I observed 42 instances of chick predation, all by gulls.

To examine the effect of habitat (and cover) on predation rates and reproductive success, I compared hatching and fledging rates as a function of habitat (Table 24). Predation rates were generally lowest in dense cover. To establish that gulls were largely responsible for these depredations and that habitat affects predation rates, I constructed 12 nests with clutches of three eggs in each of six habitats that varied by percent bush cover and nest density (Table 32). I observed these nests from a blind for 6 hrs and checked them every hour thereafter. All eggs were eaten by other gulls, and the mean time it took for all eggs to be eaten was directly related to percent bush cover (Table 32). Once a nest was discovered, all

## TABLE 30
### NUMBERS OF YOUNG FLEDGED FROM THREE-EGG AND TWO-EGG CLUTCHES WHEN TWO EGGS HATCHED[1]

| Year | | Two-egg parents | Three-egg parents | $\chi^2$ | P |
|---|---|---|---|---|---|
| 1976 | X̄ ± s.d. | 0.71 ± 0.84 | 1.06 ± 0.72 | 6.82 | .01 |
| | N | 17 | 84 | | |
| 1977 | X̄ ± s.d. | 1.00 ± 0.86 | 1.38 ± 0.70 | 7.26 | .01 |
| | N | 28 | 79 | | |
| 1978 | X̄ ± s.d. | 1.03 ± 0.72 | 0.91 ± 0.83 | 1.90 | NS |
| | N | 33 | 100 | | |
| 1976–1978 | X̄ ± s.d. | 0.95 ± 0.82 | 1.10 ± 0.78 | 3.00 | NS |
| | N | 78 | 263 | | |

[1] Clam Island; contingency table $\chi^2$ test compares whether they fledged 0, 1 or 2 young (d.f. = 2); values given are means ± one standard deviation.

TABLE 31

FATE OF EGGS AND CHICKS OF HERRING GULLS ON CLAM ISLAND[1]

| | 1976 | 1977 | 1978 |
|---|---|---|---|
| Total number of nests | 256 | 382 | 442 |
| Eggs | | | |
| Number laid | 730 | 1099 | 1295 |
| Addled | 48 (7)[2] | 135 (12) | 74 (6) |
| Preyed on[3] | 53 (7) | 53 (5) | 188 (15) |
| Unknown | 89 (12) | 29 (3) | 147 (11) |
| Hatched | 540 (74) | 882 (80) | 886 (68) |
| Chicks | | | |
| Total hatched | 540 | 882 | 886 |
| Starved[4] | 41 (8) | 77 (9) | 89 (10) |
| Unknown-no marks, not underweight | 28 (5) | 14 (2) | 44 (5) |
| Killed by conspecifics[5] | 38 (7) | 90 (10) | 100 (11) |
| Assumed killed[5] | 109 (20) | 96 (11) | 153 (17) |
| Total fledged | 324 (60) | 605 (68) | 500 (57) |
| Total losses and fledged | | | |
| Addled | 48 (7) | 135 (12) | 74 (6) |
| Eaten or killed by conspecifics | 200 (27) | 239 (22) | 371 (30) |
| Starved | 41 (6) | 77 (7) | 89 (7) |
| Unknown | 117 (16) | 43 (4) | 191 (16) |
| Fledged | 324 (44) | 605 (55) | 500 (41) |

[1] Only data from nests for which the fates of all eggs and chicks were known until 35 days of age are included.

[2] Percents of all eggs laid are given in parentheses for each major category.

[3] Eggs with peck holes.

[4] Significantly underweight compared to other chicks their age.

[5] Dead with peck marks on body.

eggs were eaten immediately. Eggs in the dense bushes sometimes went undiscovered for more than 18 hrs, whereas all eggs placed in nests in the grass outside the gull colony disappeared within 3 hr.

To determine if predation varied as a function of time of day and sex of predator I set up 12 nests (with three eggs each) near blinds in each of three intermediate bush habitats (arranged so no nest was within 4 m of another gull nest) at 05:30, 12:00, and 17:30 hr. Predation times differed significantly as a function of time of day ($F = 38.06$, d.f. = 2, 36, $P < 0.01$). Nests exposed at 05:30 were preyed upon after an average of 10.08 min (s.d. = 5.5). Those exposed at 17:30 were preyed upon in an average of 20 min (s.d. = 16.0), and those exposed at noon disappeared in an average of 158 min (s.d. = 78.0). In this experiment, 76 percent of the 324 eggs were eaten by gulls nesting within 10 m of the experimental nests, and 63 percent of them were eaten by males. When I set up 12 nests around my blind, 11 of 12 females and all 12 males ate eggs. Females were more timid than males and often ate eggs only after the males began eating them.

## DISCUSSION

### REPRODUCTIVE SUCCESS OF THE CLAM ISLAND COLONY

The mean clutch size (2.80 ± 0.42) of Herring Gulls nesting on Clam Island was similar to that reported from other Herring Gull colonies in North America (Paynter 1949; Burger and Shisler 1978b, 1979) and Europe (Harris 1964). In

## TABLE 32

EFFECTS OF HABITAT AND NEST DENSITY ON PREDATION OF HERRING GULL EGGS IN ARTIFICIAL NESTS[1]

| Habitat | Percent bush cover[2] | Nest density (no./10 $m^3$) | Time (hr) for all eggs to be eaten[3,4] |
|---|---|---|---|
| Dense bushes (center) | 80 | 2.1 ± 1.3 | 10.7 ± 2.2 |
| Dense bushes (edge) | 60 | 5.4 ± 2.5 | 8.8 ± 4.5 |
| Intermediate bushes | 40 | 3.8 ± 1.3 | 6.7 ± 2.4 |
| Clumped bushes | 6 | 8.0 ± 2.7 | 5.5 ± 3.7 |
| Grass in colony | 0 | 1.6 ± 1.5 | 3.5 ± 1.1 |
| Grass outside colony[5] | 0 | 0 | 1.3 ± 0.5 |

[1] Clam Island.

[2] Above ground cover.

[3] Values given are means ± one standard deviation.

[4] $F = 18.17$, d.f. = 5, 66 (12 nests per habitat, $P < 0.001$, LSI = 0.46).

[5] Includes only nests located 200 m or more from any other gull nests.

general, clutch sizes range from 2.43 (Davis 1975) to 2.91 (Paludan 1951). Clutch size differences may well reflect sampling procedures rather than true variation (Harris 1964; Keith 1966; Kadlec and Drury 1968). Similarly, the percentage of eggs that hatched (72–80% on Clam Island) is within the range reported in the literature (51%, Davis 1975, to 82%, Erwin 1971).

It is difficult to compare fledging success among studies because investigators often compute this measure differently or do not state their methods. Success rates reported for the 1,080 nests sampled on Clam Island ($\bar{X} = 1.45 \pm 0.96$ chicks fledged/nest, range = 1.27–1.68; Table 21) were higher than for most studies. This difference may be real, or it may reflect the reduced human disturbance in this study compared to others. Although human disturbance decreases reproductive success in gulls (Hunt 1972; Gillett et al. 1975; Robert and Ralph 1975; Burger 1981c), the specific effects of disturbance and the nature of the relationship between amount and frequency of human disturbance and reproductive success have generally not been determined. One measure of disturbance is the number of gulls that are in the air over a person walking through a colony to check nests compared to the number of gulls that remain on the ground where they can protect eggs and chicks. On Clam Island usually not more than 15 to 25 gulls flew above the assistants when they checked nests; most gulls remained on the ground until approached within 5 m. In contrast, on Long Island I have observed 300 to 400 gulls fly over picnickers walking through a colony. Clam Island is entirely salt marsh. The muck and marsh grass deter picnickers; no one was observed to visit the island. Because of the frequency of nest checks (every other day), the nesting gulls may have habituated to the assistants, becoming more tolerant of disturbance and, therefore, more protective of their nests, eggs, and chicks (Burger and Gochfeld 1983). Similarly, Common Terns habituate to the presence of gulls nesting nearby and no longer mob them (Lemmetyinen 1971). Such habituation is essential, particularly for incubating gulls whose eggs may be cannibalized in their absence (Parsons 1971; Hunt and Hunt 1976). Frequent nest checks also insured that chicks were located at least once during every four to six days and allowed field workers to learn the hiding places of chicks.

On the other hand, reproductive success actually may be higher on Clam Island than in other North American colonies. The population nesting on Clam Island increased from the early 1960's until 1979 (Burger 1979a) but has remained stable since then (Burger, unpubl. data). Increasing population levels could result from increased reproductive success, decreased mortality, or both. The abundance of garbage dumps in New Jersey certainly provides young and adults with a constant and dependable food supply during the winter. However, the gulls nesting on Clam Island fed little or no garbage to their chicks but instead brought back natural foods such as clams, crabs, mussels, and fish. Parents beseiged by begging chicks frequently flew off only to return in 3 to 4 minutes with a crab or fish. Another indication of an abundant food supply was the time parents spent on territory (Table 10). During the incubation phase, males were present an average of 86 percent of the time, and females were present an average of 80 percent of the time. Further, when one member of the pair gave a Long Call to an intruder, the mate often returned immediately (from a nearby club) to chase that intruder. Gulls having difficulty finding sufficient food would not spend time loafing in clubs. Thus, food does not appear to be generally limiting. However, short periods of heavy rains resulted in temporary difficulties in finding food. When these periods corresponded to egg-laying, more two-egg clutches were laid than normal. When heavy rain occurred when chicks were less than one week old, some died from starvation, exposure, or both. In 1977 and 1978, more than 75 percent of the chicks that starved did so during cold, rainy weather in late May. When chicks starved, the problems seemed to be behavioral (1–2 day old chicks were unable to compete with 3–5 day old siblings), rather than due to a low food supply. Chicks that starved usually came from three-chick broods.

Herring Gull populations are still sufficiently low in New Jersey so that gulls can nest in preferred habitats, high on salt marsh islands above the flood tides. Indeed only 23 of 1,350 Herring Gull nests were washed away by high tides from 1976 through 1978 on Clam Island. Herring Gulls have usurped the high nesting areas in *Spartina patens* and under bushes, forcing other salt marsh species such as Common Terns and Laughing Gulls to nest in lower sections of the marsh that are vulnerable to high tides (Burger 1980c). In 1978 terns and Laughing Gulls fledged almost no young because their nests and young were washed away or drowned by high tides (Burger 1980c). The Herring Gulls' choice of remote salt marsh islands for nesting also protects them from mammalian predators (see below).

## PREDATION AND OTHER CAUSES OF REPRODUCTIVE LOSS

The advantages and disadvantages of coloniality can be related directly to predation (including cannibalism) and resource use (Burger, in press). Nesting in groups reduces predation and enhances anti-predator behavior such as early warning and mobbing of predators. Nesting with conspecifics theoretically increases the potential for information transfer concerning patchily distributed food (Krebs 1974, 1978). Nesting in colonies also confers disadvantages. Large colonies of birds are obvious to predators, and birds must compete for space, mates, nest material, and food.

In most colonial birds the primary causes of egg and chick mortality are intraspecific or interspecific predation (Patterson 1965; Parson 1971; Hunt and Hunt 1975; Montevecchi 1977, 1979; Burger 1979a, 1981d). Other causes such as starvation, diseases, and chilling are less frequent (but see Austin 1933, Veen 1977). In the large gulls, such as Herring, Great Black-backed, and Glaucous-winged, predation by conspecifics is the most common cause of egg and chick mortality, although interspecific predation by Great Black-backed Gulls is also important (Harris 1964; Camberlein and Flote 1979; Verbeek 1979). For the small-sized gulls and terns such as Laughing Gulls, Black-headed Gulls, Common Tern, and Sandwich Tern, the primary predators are often the larger gulls nesting nearby (Fuchs 1977; Montevecchi 1977; Burger and Lesser 1978; Burger 1979a; Nehls 1979; Viksne and Janaus 1980). It is the relative sizes of the species involved that determines the predatory relationships among them.

Many colonial species warn conspecifics against avian predators. When such a predator enters a colony, incubating birds usually mob it, following it until it leaves the colony. In gulls the mass attacks of mobbing birds are usually effective at deterring avian predators (Tinbergen 1963, 1967; Kruuk 1964; Hayward et al. 1975). In Kittiwakes (*Rissa tridactyla*) the success of the predator is inversely related to the number of Kittiwakes mobbing (Andersson 1976). Some colonial birds, however, do not mob predators (Taylor and Wodzicki 1958; Kepler 1967), or their mobbing is unsuccessful (Windsor and Emlen 1975). Most of the above studies involved mobbing of heterospecific predators. Large gulls also mob conspecific predators, but usually only after an egg or chick has been taken. The problem lies in the identification of a potential cannibal. Presumably, it is difficult to detect when a gull flying over the colony will suddenly swoop and steal an unguarded chick, whereas it is always possible to assume that a heterospecific flying overhead is a potential predator. The only defense against cannibalism is alertness and guarding by parents. In species such as Herring Gulls, in which cannibalism is frequent, parental investment in alertness and guarding should be greater than in gulls in which cannibalism is rare. On Clam Island siblings usually remained close together and near parents.

Because cannibalism is so prevalent, one may question why more gulls do not simply nest solitarily. First, eggs placed in unattended experimental nests away from the colony (Table 32) were located and eaten by gulls more quickly than were eggs in the colony. Presumably, neighbors served as a partial deterrent to gulls that did not know the birds individually. Second, birds nesting solitarily do not benefit from early warning and group mobbing of predators. Third, a solitary gull may not be able to select a spot free from tidal floods and predators, whereas colonies generally are located in nesting areas that have been free from heavy predation and tidal floods in the past. In many areas some proportion of Herring Gulls do nest solitarily.

All gulls are subject to mammalian predation, and losses in mainland colonies to which mammals have easy access can be substantial. Repeated depredations by fox on a mainland Herring Gull colony near Clam Island resulted in its desertion. Most gulls are unable to defend themselves successfully against mammalian predators, particularly nocturnal ones such as fox (*Vulpes vulpes*; Kruuk 1964; Patton and Southern 1978; Southern and Southern 1979), raccoon (*Procyon lotor*; Emlen et al. 1966), or even the smaller mink (*Mustela vison*; Burger 1974a; Conover and Miller 1979).

Starvation is more difficult to isolate as a cause of chick mortality because such determinations require repeated weighings of chicks and data on normal weights for each age class. Nonetheless, starvation has been reported for some species

(Veen 1977). In addition underweight chicks may be more vulnerable to predation, obscuring the effects of starvation (Lack 1968; Kadlec et al. 1969). Chicks do starve if they are smaller than brood mates (Coulter 1977; Hahn 1981) or become separated from their parents. Foraging ability varies among parents, and some may be unable or unwilling to bring back sufficient food.

Deaths due to environmental stresses such as cold, wind, and rain also are hard to document (Austin 1933; Harris and Plumb 1965; Hunt and Hunt 1976). Floods often result in very high losses because eggs and chicks are washed out of nests or die from prolonged exposure to cold water (Bongiorno 1970; Montevecchi 1978; Burger 1979b; Burger and Shisler 1980). Flood damage is particularly prevalent in species nesting in unstable habitats such as sand bars (Black-billed Gulls, Beer 1966), salt marshes (Laughing Gulls, Montevecchi 1978), or freshwater marshes (Franklin's Gulls, Brown-hooded Gulls, Burger 1974a, 1974b; Black Terns, *Chlidonias niger,* Weller and Spatcher 1965).

## TIMING OF BREEDING, PREDATION PRESSURE, AND REPRODUCTIVE SUCCESS

Differences in reproductive success as a function of the timing of egg-laying have been reported for several colonial birds (Harris 1969; Fisher 1971; Milne 1974; Nettleship 1972; Emlen and Demong 1975; Robertson and Wooller 1981). Generally, early nesting birds are most successful, although mid-nesting Brown Pelicans (*Pelecanus occidentalis,* Schreiber 1979) and Glaucous-winged Gulls (Hunt and Hunt 1976) were more successful than early or late nesters. For most gulls and terns, such as Black-headed Gull (Viksne and Janaus 1980), Lesser Black-backed Gulls (Brown 1967a), Herring Gulls (Brown 1967a; Davis 1975; Spaans and Spaans 1975), and Sandwich Terns (Veen 1977), however, early-nesting birds are more successful than late-nesting birds. Parsons (1975) found that Herring Gulls nesting at the peak of egg-laying had the highest reproductive success. In this study, Herring Gull nests initiated early in the season were the most successful.

Hunt and Hunt (1976) suggested that if non-conspecific predators are the primary cause of chick mortality, then chicks hatched early in the season should be most successful; if cannibalism is most important, then chicks hatched in mid-season will have the highest survival. Certainly the studies cited above support their model. Most authors have reported high predation or cannibalism rates late in the season (Kruuk 1964; Brown 1967a; Davis and Dunn 1976; Veen 1977), but a few (Weidmann 1956; Nisbet 1975) recorded high predation rates early in the season, and Parsons (1975) found that predation was high both at the beginning and at the end of the season in Herring Gulls. Lower predation rates on mid-season nesters compared to early and late nesters have been shown for other species as well (Ashmole 1963; Patterson 1965; Yom-tov 1975).

One way in which birds in a colony may avoid predation is by nesting synchronously (reviewed in Burger 1979c; Gochfeld 1979, 1980). Social facilitation presumably occurs as a function of the number of birds nesting in a colony, and synchrony of breeding activities results (Darling 1938). Nesting during the peak of egg-laying lowers the risk of predation because predators are unable to take more than a certain number of young at any one time. For example, predators took a greater proportion of the available young Common Terns early in the season compared to later when more and larger chicks were available (Nisbet 1975).

In the present study predation (largely cannibalism) increased seasonally. Theoretical considerations of "predator swamping" predict that relative predation losses should be lowest during the peak of egg-laying. Predator "swamping" can occur only if the number and food requirements of the predators remain constant throughout the season, as may happen with owl predators (Nisbet 1975). If the same number of predators requires the same food each day, then a chick has less chance of being eaten when it is part of a large, rather than a small cohort. These conditions are violated, however, in the case of egg and chick cannibalism. The number of potential cannibals increases seasonally (predator recruitment), and their food requirements increase. Early in the season, adult gulls are feeding only themselves. When the first chicks hatch, few gulls are seeking food for their broods. As the season progresses, more parents have chicks to feed, and the chicks are larger and require more food. Davis and Dunn (1976) reported that after chick loss, Lesser Black-backed Gulls tended to become cannibals. However, my predation experiments clearly showed that all gulls ate available eggs, particularly those on nearby territories.

### Location Effects, Density, and Reproductive Success

In some species birds nesting in the center of a colony have higher breeding success than those nesting at the edge (e.g., Darling 1938; Fisher 1952; Nelson 1966; Coulson 1968; Harris 1978). Other species, however, show no differences (Cullen 1960; Kruuk 1964; Patterson 1965; Buckley and Buckley 1972; Dexheimer and Southern 1975; Ryder and Ryder 1981). In the Herring Gulls I studied there were no differences. The apparent contradictions can be understood after examining predator types, age factors (Ryder 1980), nest density, and habitat variables.

Predator type influences where depredations occur. Mammalian predators naturally enter from the edge (Kruuk 1964; Tinbergen et al. 1967) making edge nests particularly vulnerable. Avian predators, however, may fly to the center of a colony where eggs and chicks are dense (Burger and Lesser 1978), and where increased aggression due to territorial defense may render chicks less well-guarded.

Nest density affects the number of aggressive interactions that occur (this study), rates of intrusion by conspecifics (Ewald et al. 1980), and reproductive success. In some species reproductive success is low at high densities (Glaucous-winged Gull, Hunt and Hunt 1976; Great Black-backed Gull, Butler and Trivelpiece 1981), whereas for other species reproductive success is highest at the average nest density (Herring Gulls, Parsons 1976; Sandwich Terns, Veen 1977) or in high density areas (Lesser Black-backed Gull, Davis and Dunn 1976). I found no clear relationship between nest density and fledging success. However, nest density increased in areas of increasing bush cover. Reproductive success is higher for birds nesting in cover in several species, presumably because vegetation acts as a visual barrier and protects young from inclement weather (Brown 1967a; Burger 1977b; Buckley and Buckley 1980).

### Clutch Size, Brood Size, and Reproductive Success

Several authors have asserted that hatching rates depend on initial clutch size (Paynter 1949; Harris 1964; this study). Parents maximize their reproductive output by investing more in a large clutch. Harris (1964) suggested that parents having two-egg clutches are more accident prone than those having three-egg

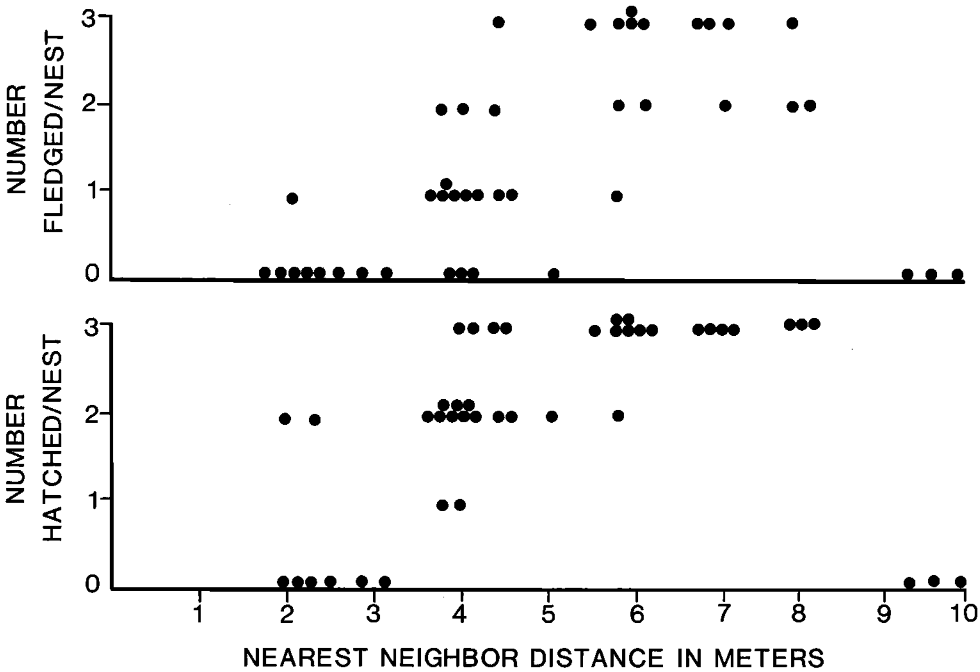

FIG. 23. Numbers of eggs hatched and chicks fledged as a function of internest distances (m) for gulls observed from the Clam Island blind in intermediate bush habitat (N = 43 pairs).

clutches, and Beer (1961) noted that Black-headed Gulls having only two eggs do not incubate as tightly as those having three eggs.

A gull egg has a greater chance of hatching if it is part of a two- or three-egg clutch than if it occurs alone (Paynter 1949; Brown 1967a; Parsons 1975; this study). Paynter (1949) and I (this study) have found that once hatched, Herring Gull chicks have equal probabilities of survival regardless of brood size. In contrast, Brown (1967a) found that Herring Gull chicks from three-chick broods had a higher probability of survival than those from smaller broods although no differences were found in Lesser Black-backed Gulls. This discrepancy reflects differences in food availability; when food is readily available, parents may be able to feed three chicks easily (Paynter 1949). Social facilitation within three-chick broods may stimulate parents to bring more than three times as much food as one chick alone can stimulate them to bring; this requires field testing. Holly (1982) reported that Herring Gulls with broods larger than one fed chicks longer (an average of 90 days) than did those with solitary chicks (an average of 73 days). Nisbet and Drury (1972) found that chicks fledged from three-chick broods had higher post-fledging success than those fledging from one- or two-chick broods.

One aspect of parental quality, ability to lay three eggs, clearly affects chick survival. In two of three years, chicks of parents with three eggs (but hatching only two) had a higher probability of survival than those of parents with two eggs even though the three-egg parent failed to hatch one egg (Table 30). This difference in fledging success may reflect parental feeding ability. A female able to obtain food reserves sufficient to lay three eggs may be able to forage efficiently enough to invest more heavily in the two remaining chicks.

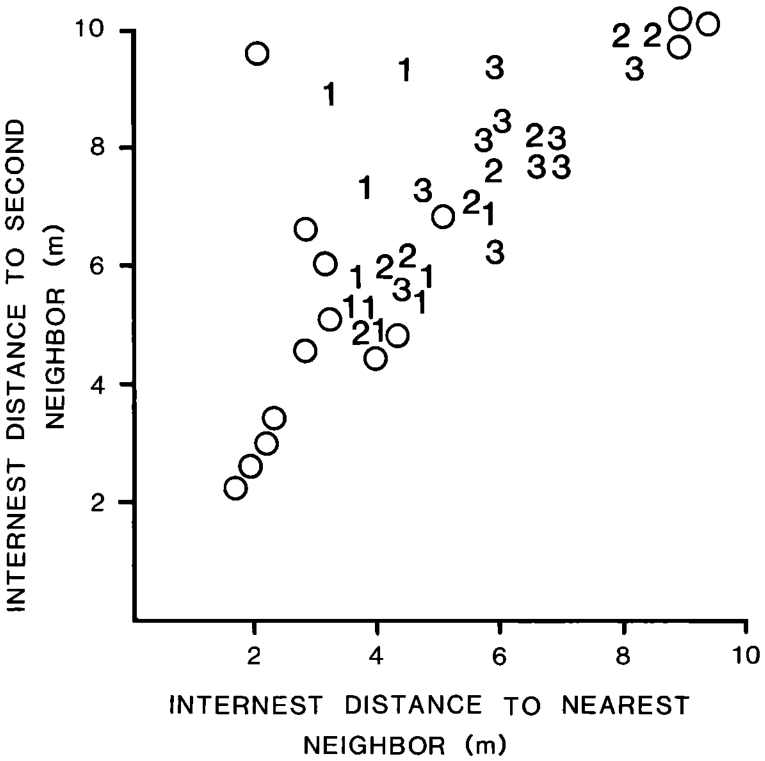

FIG. 24. Relationship of number of chicks fledged per nest to the internest distances to the nearest and second nearest neighbors for Clam Island Herring Gulls in intermediate bush habitat. Numbers (0–3) indicate the number of young fledged.

## AGGRESSION, TERRITORY SIZE, AND REPRODUCTIVE SUCCESS

In this section I examine the effects of aggression and territory size on reproductive success based on data from 43 pairs observed on Clam Island. I predicted that Herring Gulls having intermediate-sized territories and engaging in low levels of aggression would have the highest reproductive success.

### RESULTS

### TERRITORY SIZE AND REPRODUCTIVE SUCCESS

The numbers of young hatched and fledged were significantly correlated with the internest distance to the nearest neighbor, one indicator of territory size (Table 33, Fig. 23). In general, pairs with intermediate internest distances hatched and fledged more young than pairs with internest distances greater than 9 m or less than 3.4 m. Fledging success was also related to the internest distance to the second closest neighbor; most parents fledging three young had closest and second closest neighbors about the same distances from their nests (Fig. 24). This result is not due to differences in habitat or date of initiation, as the pairs observed were in the same habitat and initiated egg laying within four days of one another.

The numbers of young hatched and fledged were related directly to primary

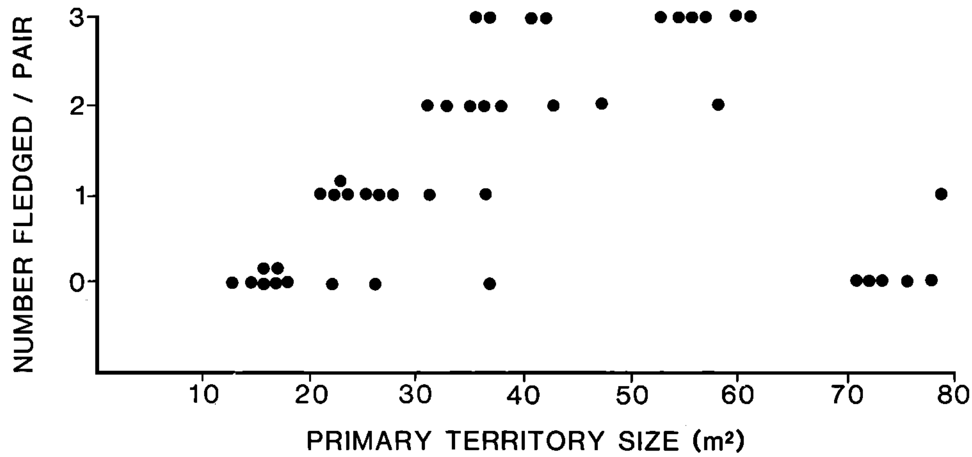

FIG. 25. Number of Herring Gull young fledged per pair as a function of primary territory size for 43 pairs observed from the Clam Island blind in intermediate bush habitat.

## TABLE 33

## REPRODUCTIVE SUCCESS OF HERRING GULLS AS A FUNCTION OF INTERNEST DISTANCE, PRIMARY TERRITORY SIZE, AND RATES OF AGGRESSION[1]

| | N | Number of eggs hatched | Number of chicks fledged[2] |
|---|---|---|---|
| Internest distance to nearest neighbor (m) | | | |
| 0–3.3 | 8 | 4 (17) | 1 (4) |
| 3.4–6.6 | 25 | 59 (79) | 37 (49) |
| 6.7–9.0 | 7 | 21 (100) | 18 (86) |
| >9.0 | 3 | 0 (0) | 0 (0) |
| $\chi^2$ | | 21.02 | 21.22 |
| d.f. | | 3 | 3 |
| *P* | | .001 | .001 |
| Primary territory size (m$^2$) | | | |
| 0–20 | 7 | 2 (10) | 0 (0) |
| 21–45 | 22 | 59 (89) | 33 (50) |
| 46–70 | 8 | 23 (96) | 22 (92) |
| >70 | 6 | 0 | 1 (6) |
| $\chi^2$ | | 34.03 | 30.08 |
| d.f. | | 3 | 3 |
| *P* | | .001 | .001 |
| Rate of aggression (interactions/pair/hr) | | | |
| 0–1.0 | 29 | 67 (77) | 48 (55) |
| 1.1–2.0 | 8 | 14 (58) | 7 (29) |
| 2.1–3.0 | 4 | 3 (25) | 1 (8) |
| >3 | 2 | 0 (0) | 0 (0) |
| $\chi^2$ | | 9.13 | 9.73 |
| d.f. | | 3 | 3 |
| *P* | | .05 | .02 |

---

[1] Clam Island, 1976–78. Data within each category compared with a Chi-square Goodness of Fit test. Given in parentheses are percent of eggs that hatched or produced fledglings for that data class.

[2] From total number of eggs laid.

## TABLE 34

PARAMETERS AFFECTING NUMBERS OF YOUNG FLEDGED BY HERRING GULLS[1]

| | Number fledged | | |
|---|---|---|---|
| | 3 vs. 2 | 3 vs. 1 | 3 vs. 0 |
| Internest distance to nearest neighbor | NS[2] | 5.6*** | 6.9*** |
| Internest distance to second neighbor | NS | 2.7** | 3.2** |
| Primary territory area | NS | 6.1*** | 3.1** |
| Parental behavior | | | |
| Male incubates | NS | 2.5* | NS |
| Female incubates | NS | 2.5* | NS |
| Male present[2] | NS | NS | NS |
| Female present[2] | NS | NS | NS |
| Aggressive behavior | | | |
| Approach distance chased during incubation | NS | NS | |
| Approach distance chased during chick phase | NS | NS | 3.3**<br>3.6** |
| Rate of aggression | | | |
| During incubation | 2.2* | 2.1* | 2.8** |
| During chick phase | 2.6* | 2.3* | 3.1** |
| Aggression frequency | | | |
| By male | NS | NS | 2.8* |
| By female | NS | NS | NS |
| Number of nests | 18 | 20 | 25 |

[1] Clam Island; values given are *t* values comparing characteristics of nests fledging different numbers of young and significance levels; * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$; NS = not significant.

[2] Present but not incubating.

territory size (Table 33, Fig. 25). The relationship is curvilinear with pairs having intermediate-sized territories (21–70 m$^2$) hatching and fledging more young than those with smaller and larger territories. Within the intermediate-sized territory group, pairs with territories of 21 to 45 m$^2$ had high hatching success, but only 50 percent of their eggs produced fledglings. In contrast, more than 90 percent of the eggs of pairs with territories of 46 to 70 m$^2$ resulted in fledglings (Table 33). Only one pair with a territory larger than 65 m$^2$ reared a chick (Fig. 25).

I determined the factors affecting the number of young fledged by identifying significant differences among several independent variables using an ANOVA, and by determining which variables varied significantly among success categories (fledging 0, 1, 2, or 3 young) using *t*-tests (Table 34). Differences in internest distances and primary territory size did not affect whether parents fledged two or three chicks, but they did affect whether parents fledged three compared to one or no chicks.

### AGGRESSIVE BEHAVIOR AND REPRODUCTIVE SUCCESS

The approach distance of pairs (averaged over the season) was negatively correlated with the number of eggs they hatched ($r = -.46$, d.f. $= 41$, $P < 0.01$), but not with the number of young they fledged. Parents that fledged three young allowed intruders to get closer to their nests before they were chased (i.e., were more tolerant) than parents that fledged no young.

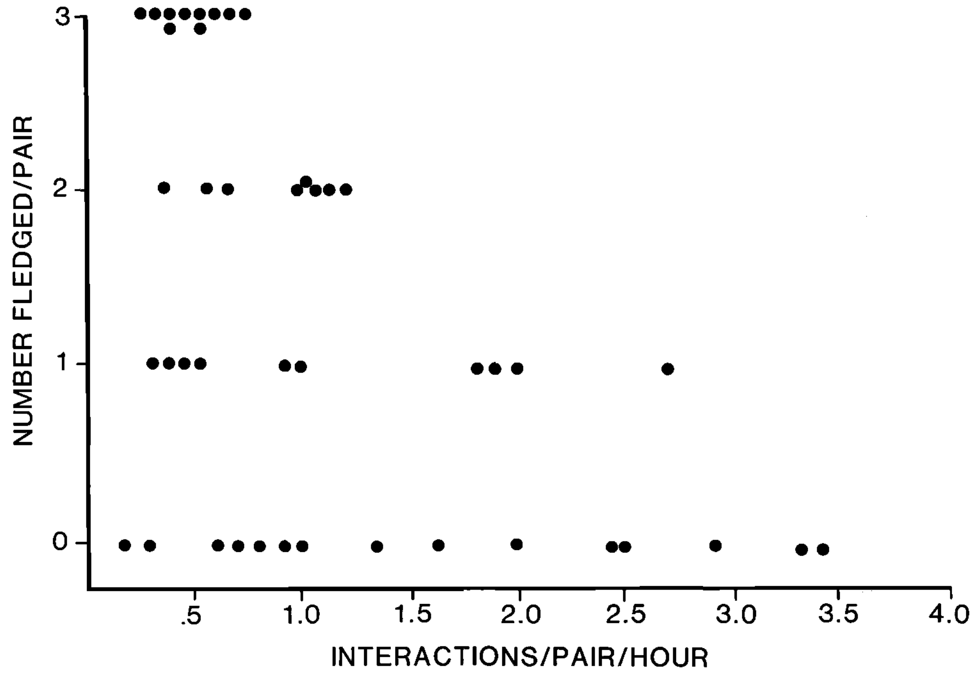

FIG. 26. Number of Herring Gull young fledged per pair as a function of rates of aggression for 43 pairs observed from the Clam Island blind in intermediate bush habitat.

Hatching and fledging success were related to aggression; pairs with the lowest rates of aggression were the most successful (Table 33, Fig. 26). The relationship between mean rates of aggression and the number of young fledged was not linear, however. Although pairs with very high rates of aggression (>1.5 interactions/hr) reared few or no young, nearly half of the pairs with low rates of aggression (<1.5 interactions/hr) fledged one or no young (Fig. 26). Thus, although all pairs with high rates of aggression fledged few young, not all pairs with low rates of aggression fledged three young.

Rates of aggression by the pair significantly influenced the number of young fledged. However, rates of aggression for males or females alone did not generally influence fledging success (except for male aggression, comparing pairs with 3 versus 0 young fledged, Table 34).

Rates of aggression during incubation and the chick phase were generally correlated within pairs ($r = .53$, $N = 43$, $P < 0.01$). Nonetheless, of the pairs that were more aggressive in the chick phase 71 percent fledged two or three chicks, whereas only 41 percent of the pairs that were more aggressive during incubation had comparable success.

Overall, pairs with low levels of aggression and intermediate-sized territories fledged more young than pairs that were more aggressive and had very large or very small territories (Fig. 27; Table 35), confirming my original prediction. Within a certain range of territory sizes (30–60 m$^2$), the level of aggression in which pairs engaged did not usually affect whether they fledged chicks or not (Fig. 27).

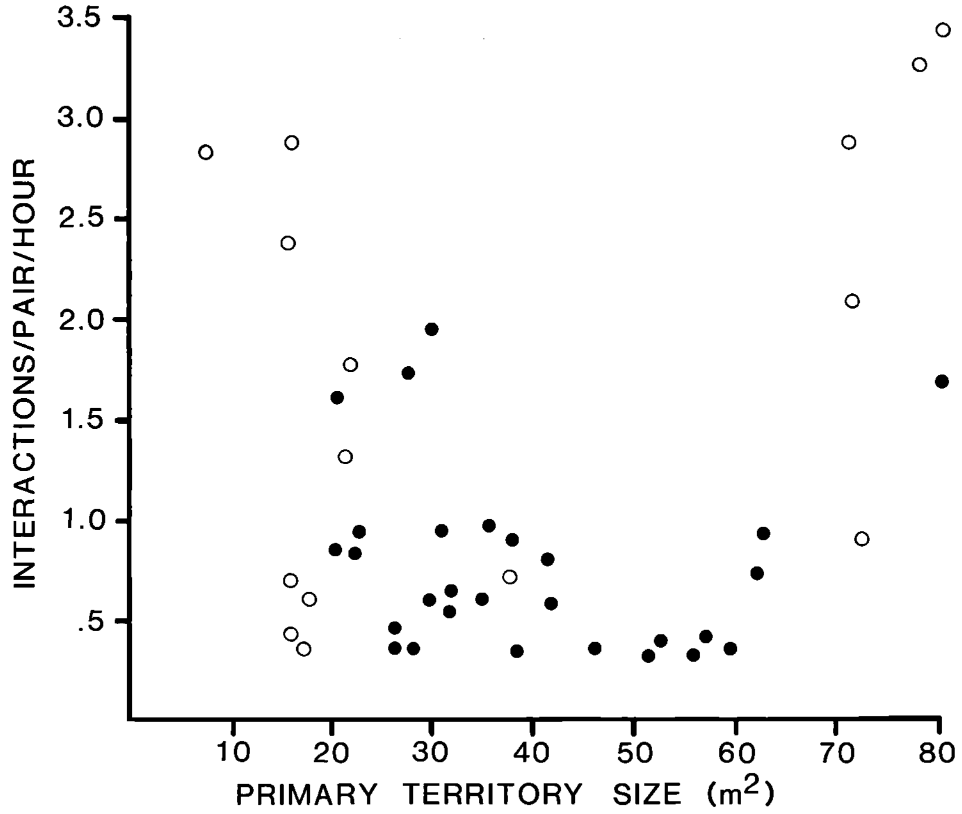

FIG. 27. Relationship of reproductive success (open circle = none fledged, solid circle = some fledged) to primary territory size and rate of aggression for 43 Herring Gull pairs observed in intermediate bush habitat on Clam Island.

## MODELS OF FACTORS AFFECTING REPRODUCTIVE SUCCESS

I used MaxR stepwise regression procedures to determine which of the factors I examined contributed significantly to explaining the variation in hatching and fledging success on Clam Island. Although some of the variables may be related, the analysis enters a second variable to the model only when its contribution not due to colinearity is significant (Draper and Smith 1981).

Percent of time males and females were present on the territory, mean approach distance during incubation, mean rate of aggression during incubation, and frequency of aggression of females contributed significantly to the variation in hatching success (Table 36). Variation in fledging success was explained by approach distance during the chick phase, habitat type, internest distance to the second nearest neighbor, primary territory size, time both parents were present together, aggression frequency by males, and rates of aggression by pairs. Thus, hatching success was influenced by both passive and active defense, whereas fledging success was influenced by territory size as well as by passive and active defense.

For the 1977 and 1978 data I used stepwise regression techniques to determine if territory size affected reproductive success for the nests followed by the field

TABLE 35

CHARACTERISTICS OF PAIRS OF HERRING GULLS FLEDGING DIFFERENT NUMBERS OF YOUNG[1]

| | Number of young fledged | | | |
|---|---|---|---|---|
| | 3 | 2 | 1 | 0 |
| Internest distance to nearest neighbor (m) | 6.3 ± 1.9 | 5.9 ± 1.7 | 4.2 ± 0.6 | 3.0 ± 1.1 |
| Internest distance to second neighbor (m) | 7.6 ± 1.4 | 7.2 ± 1.9 | 5.4 ± 2.1 | 4.7 ± 2.5 |
| Primary territory size ($m^2$) | 48.1 ± 10.4 | 39.6 ± 9.9 | 25.8 ± 5.2 | 27.1 ± 18.1 |
| Rate of aggression (incubation) | 0.43 ± 0.33 | 0.77 ± 0.31 | 1.06 ± 0.92 | 1.28 ± 0.90 |
| Rate of aggression (chick phase) | 0.46 ± 0.25 | 0.82 ± 0.73 | 0.71 ± 0.73 | 0.97 ± 0.41 |
| Aggression frequency by male | 0.41 ± 0.23 | 0.60 ± 0.13 | 0.66 ± 0.71 | 1.24 ± 0.74 |
| Number hatched | 3.0 ± 0 | 2.91 ± 0.35 | 2.0 ± 0 | 0.89 ± 0.92 |
| Number of nests | 10 | 8 | 10 | 15 |

[1] Birds observed from a blind on Clam Island; values given are means ± one standard deviation.

assistants (N = 1,080, Table 37). The Clam Island colony was not particularly dense and internest distances to the closest and second closest neighbors were not highly correlated ($r = .38$). In neither year did internest distance or density affect clutch size. The variance in the number of eggs hatched was partially explained by density in both years, but internest distance was important only for 1977. More than 15 percent of the variation in the number of eggs eaten by predators was due to differences in nest density and internest distance. Habitat and nest location (center-edge) were not significant variables in explaining the number of eggs eaten by other gulls. A high percent of the variation in the number of chicks eaten was explained by nesting density and nearest neighbor distance (35% in 1977, 38% in 1978, Table 37). Of the variation in the number of chicks alive at 30 days of age, 20 percent (1977) and 39 percent (1978) were explained by density and internest distance to the closest neighbor. These data indicate that territory size (as indicated by nest density and internest distances) affects hatching and fledging success. In addition, the presence of close neighbors increases the probability of predation on both eggs and chicks.

## DISCUSSION

Despite the attention devoted to the study of territoriality over the last several years, few quantitative data exist on the pattern, mechanism, and adaptive significance of territoriality in one species. For example, Hunt and his colleagues investigated territory size, aggression, intruder pressure, and reproductive success, but their work concerned different gull species in different colonies, and they did not attempt to separate variations in reproductive success resulting from density, location, or date of egg-laying (Hunt and Hunt 1975, 1976; Ewald et al. 1980). Nonetheless, they showed that territory size sometimes influences reproductive success, that chicks on small territories are more frequently killed by conspecifics than heterospecifics, and that owners of large territories spend more time in territorial defense than those on small territories. They also clarified the importance of intrusion rates.

The usual assumptions about the relationships between aggressive behavior and

## TABLE 36

## FACTORS AFFECTING HATCHING AND FLEDGING SUCCESS OF CLAM ISLAND HERRING GULLS[1]

| | $r^2$ | $F$ | $P$ |
|---|---|---|---|
| Hatching success (no. eggs hatched/nest) | | | |
| Overall model (d.f. = 5, 38) | 99.3 | 45.9 | .02 |
| Factors | | | |
| Percent of time female present but not incubating | | 31.4 | .03 |
| Percent of time male present but not incubating | | 19.2 | .04 |
| Mean approach distance during incubation | | 21.6 | .04 |
| Rate of aggression during incubation | | 15.0 | .05 |
| Aggression frequency of female | | 15.8 | .05 |
| Fledging success (no. young fledged/nest) | | | |
| Overall model (d.f. = 7, 36) | 98.2 | 89.9 | .03 |
| Factors | | | |
| Approach distance during chick phase | | 92.1 | .01 |
| Habitat type | | 91.2 | .01 |
| Internest distance to second nearest neighbor | | 82.2 | .01 |
| Primary territory size | | 52.6 | .01 |
| Percent of time both parents were present together on territory | | 46.2 | .01 |
| Aggression frequency by male | | 30.0 | .03 |
| Mean rate of aggression of pairs during entire reproductive cycle | | 24.4 | .04 |

[1] Values are given for the regression models (MaxR procedures) and the factors that contributed significantly to the variation in either hatching or fledging success.

territory size (more aggressive animals get larger territories), and territory size and reproductive success (larger territories improve reproductive success) were not supported by my observations on Herring Gulls. On Clam Island, rates of aggression were lowest on intermediate-sized territories, success was highest on intermediate-sized territories, and success was highest for pairs with the lowest rates of aggression (Fig. 28), confirming my original predictions. Similarly Veen (1977) showed that Sandwich Terns nesting at intermediate distances from neighbors had the highest hatching success. In his study gull predation rather than cannibalism was the primary cause of mortality.

For Herring Gulls nesting in the center of the Clam Island colony, reproductive success was maximized by defense of an intermediate-sized territory. Since Herring Gulls respond aggressively to most intruders in their territories, low intrusion pressure results in low rates of aggression. Small territories have high rates of intrusion by neighbors, and low rates of intrusion by strangers. Neighbors rarely intrude in large territories but strangers commonly do. Because the distance from the nest to the territory boundary increases linearly, the area to be defended increases as the square of the distance, and the number of intruders who are strangers increases markedly. Thus, intermediate-sized territories would have the lowest rates of intrusion and aggression. Intrusion rates and the resultant rate of aggression exhibited by the territory owner can also be reduced by nesting far from loafing areas (Ewald et al. 1980) and at sites covered with vegetation where territory-seekers have difficulty landing (Burger 1977b). Thus, gulls should attempt to establish themselves in dense areas of the colony where territorial boundaries

TABLE 37

FACTORS AFFECTING REPRODUCTIVE SUCCESS OF CLAM ISLAND HERRING GULLS[1]

|  | Clutch size | No. addled eggs | No. eggs hatched | No. eggs eaten | No. chicks eaten | No. chicks alive at 20 days | No. chicks alive at 30 days |
|---|---|---|---|---|---|---|---|
|  |  |  | 1977 (N = 382 nests) |  |  |  |  |
| Overall model $F$ | 6.63** | 3.41* | 5.70** | 11.5** | 14.2*** | 4.51* | 14.61* |
| $r^2$ | .23 | .09 | .14 | .30 | .35 | .18 | .39 |
| Date | *** | *** | *** |  |  |  |  |
| Nest location |  |  |  |  |  |  |  |
| Habitat | ** |  |  |  |  |  |  |
| Distance to: |  |  |  |  |  |  |  |
| Nearest neighbor |  |  | * | * | * | * | * |
| Second neighbor |  |  | * |  | * |  |  |
| Neighbors within 5 m |  |  | * | * | * | * | * |
| Neighbors within 10 m |  |  | * | * | * | * |  |
|  |  |  | 1978 (N = 442 nests) |  |  |  |  |
| Overall model $F$ | 7.08*** | 2.40 | 9.66*** | 12.20*** | 13.10*** | 15.32*** | 14.73*** |
| $r^2$ | .14 | .06 | .15 | .16 | .38 | .26 | .20 |
| Date | * | * | *** |  | * | * | *** |
| Nest location |  |  |  |  |  |  |  |
| Habitat | ** |  |  |  |  |  |  |
| Distance to: |  |  |  |  |  |  |  |
| Nearest neighbor |  |  |  |  | * | * |  |
| Second neighbor |  |  |  |  | * | * | * |
| Neighbors within 5 m |  |  | ** |  | * | * | ** |
| Neighbors within 10 m |  |  | * | * | * | * | ** |

[1] MaxR values given are the $F$ Values and levels of significance (* = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$) for the model as well as levels of significance for each variable affecting the parameters influencing reproductive success. A significant variable accounts for some of the variation in the dependent variable.

have already been established. Patterson (1965) found this to be the case in Black-headed Gulls.

On Clam Island, the most aggressive pairs fledged the fewest young (Fig. 28). However, individuals showing low levels of aggression had variable productivity. When aggression levels were low because there were few intrusions, reproductive success was generally high. When aggression levels were low despite high intrusion pressure, then reproductive success was generally low because eggs or young were killed or eaten by conspecifics. Davis and Dunn (1976) reported that most egg and chick losses of Lesser Black-backed Gulls were due to neighbors, whereas Hunt and Hunt (1976) reported that only about half of the chick losses in Glaucous-winged Gulls were due to neighbors. The importance of neighbors as predators no doubt varies with species, density, territory size, cover (Brown 1967a), and chick behavior (Hunt and McLoon 1975).

## GENERAL DISCUSSION

### AGGRESSION, INTRUSION PRESSURE, AND TERRITORY SIZE

Although on theoretical grounds biologists have assumed that rates of aggression are related directly to territory size, few quantitative data support this. On Clam

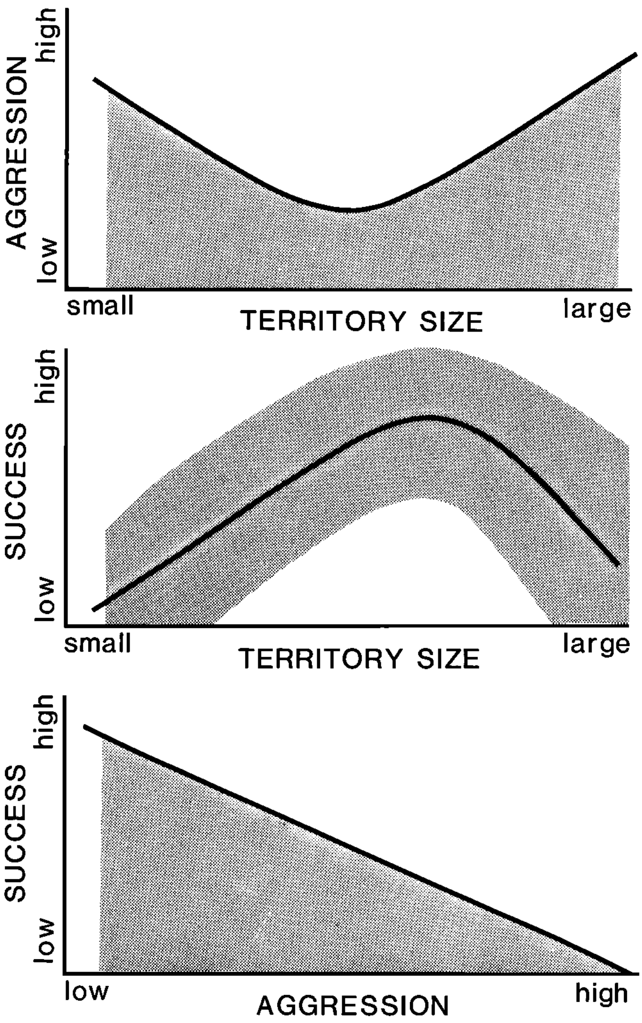

FIG. 28. Schematic representation of relationships among territory size, rate of aggression, and reproductive success for Clam Island Herring Gulls. The actual values for pairs fell within the stippled areas.

Island Herring Gulls with intermediate-sized territories engaged in less aggression than pairs nesting on smaller or larger territories. Hutson (1977) similarly reported that the birds occupying prime sites did not always show "the greatest tendency" to defend.

Itzkowitz (1979) stressed the importance of examining intrusion pressure as an indication of the cost of territoriality. He assumed that not all territories were equally desirable, and that intrusion rates should be higher on prime territories. Patterson (1965) found that the presence of males on territory reduced the likelihood of intrusion in Black-headed Gulls. When either territory owner was present, intruder pressure was approximately equal at all distances from the nest; if both owners were absent, intrusion pressure peaked at 1 to 2 m from the nest or

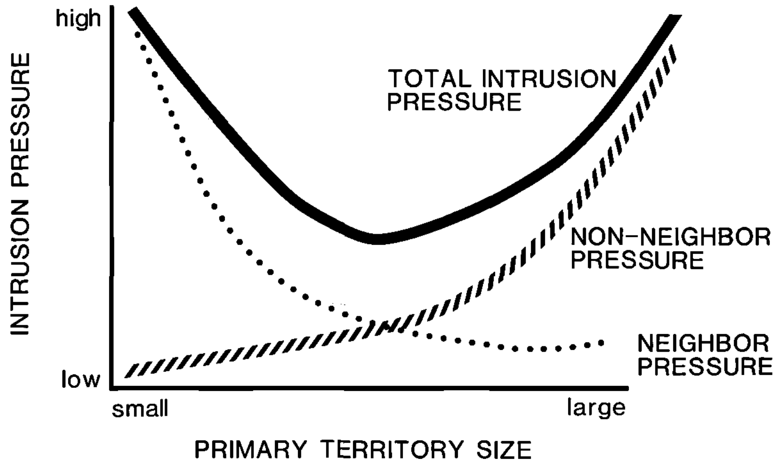

FIG. 29. Schematic representation of intrusion pressure as a function of primary territory size in Herring Gulls.

scrape (Patterson 1965). Ewald et al. (1980) examined intrusion pressure in Western Gulls and found that variations in intrusion rate per unit area best explained variations in territory size, with small territories having the highest intrusion rates; they did not distinguish between aggression directed at neighbors and non-neighbors. Moreover, in their study area, Western Gulls nested at relatively low densities, mean territory size was more than 10 times larger than that of the Herring Gulls I observed, and some territories differed in size by a factor of 10. Such large territories present a problem since time required to reach an intruder increases with the size of the territory.

Presumably, the size of a territory is the outcome of two processes, (1) the expansionist tendencies of the resident birds, and (2) the pressure exerted on the residents by conspecifics seeking territories. Expansionist tendencies of residents should reflect the value of the resources being defended (Brown 1964) for courtship and copulation, egg protection, and chick rearing. The uses of the territory, thus, change seasonally, and the required space may also change seasonally. Herring Gulls did defend larger territories during the pre-incubation and chick stage, and smaller territories during incubation when only the nest and eggs must be protected. Since territory holders have neighbors, they cannot simply shrink the defended space to only the size of the nest, or they would not be able to enlarge the space sufficiently in the chick stage to accommodate chick movements.

Space within a gull colony is not static, because non-neighbor intruders in search of space attempt to establish themselves among existing pairs. Thus, pressure from intruders continues through some part of the breeding season. Presumably, territory seeking pairs will first try to establish territories in preferred habitat and/or in areas with low competition. Thus, theoretically, territory size should be smaller in preferred habitats.

Intrusion pressure is due both to non-neighbors seeking territories, and to neighbors. Neighbors interact mostly at territory boundaries. Non-neighbors can land anywhere within the territory although they tend to land equidistant from adjacent residents. On small territories neighbors interact frequently, whereas on large territories non-neighbor interactions are more numerous (Fig. 29). As the territory increases in area, the number of non-neighbor intruders increases exponentially, and it becomes more time consuming for territory holders to move to the margins to defend the territory. Thus, the resultant total pressure from conspecifics will be highest on small and large territories.

It may at first appear that rates of aggression are a function of intrusion pressure alone, since the gulls in all habitats responded to more than 90 percent of the intruders. However, more than half of the aggressive behavior of territorial birds was directed at neighbors rather than at non-neighbors (Fig. 18). It often is difficult to determine when a neighbor is intruding, because it frequently wanders at the edge of a mutual territory boundary. Thus, intrusion pressure, itself, is hard to determine, particularly at territory boundaries. Non-neighbor intruders, however, simply land within a gulls' territory and can easily be recognized as intruders by both the defending bird and the investigator.

The data from Appledore Island (Table 14) indicate that levels of aggression are not simply a response to intrusion pressure since territory holders do not respond to all intruders at a given distance. In addition, the rapid increase in levels of aggression at hatching (Fig. 12) suggests that other factors ("motivation" or hormonal state) influence the response to intruders. Parents become more aggressive and seem to respond more quickly to intruders than they did prior to hatching. Potential cannibals flying over the colony in search of small chicks often do not land because they cannot see very young chicks still being brooded in the nest (particularly when one egg remains to hatch). Yet even while incubating an egg and brooding a chick, a parent begins to respond more quickly to non-neighbors, and a pair attempts to enlarge its territory into those of its neighbors.

Similarly, high vegetation, such as bushes, decreases intrusion pressure (there are fewer places to land) and decreases the response of territorial birds since their field of vision is reduced (Burger 1977b). Thus, it appears that intrusion pressure is only one of many variables that affect rates of aggression, other variables being types of intruder, habitat, and territory size. Gulls can minimize intrusion pressure by having intermediate-sized territories in high vegetation and by defending areas that contain space for only one nest site (e.g., a clump of bushes surrounded by vegetation). Further, gulls can choose not to respond to neighbors standing on their mutual territory boundary.

## TERRITORIAL AGGRESSION LATE IN THE SEASON

Aggression levels increased markedly when the chicks were over 60 days of age. At this stage chicks had been flying for two weeks and spent considerable time away from the nest site (Paynter 1949; Harris 1964; Burger 1981a). Although the parents continued to defend chicks when they wandered to the edges of the territory or landed in a neighboring territory, much of this post-fledging aggression occurred when chicks were not even present (Burger 1981a). Indeed, in some pairs the parents continued to defend their territories even though their chicks had not returned for over a week. All pairs that successfully fledged chicks exhibited this aggression, and all interactions were between neighbors. This increase in aggression when chicks were 60 to 90 days old has not been reported for other gulls (Burger

1981a), probably because investigators generally leave the colonies before this stage in the cycle. This behavior also occurs in Northern Gannets (*Sula bassana*), which remain on nesting ledges two to three months after the chicks have departed (Nelson 1970; Burger, unpubl. data).

I consider the increase in aggressive behavior just before Herring Gulls leave the colony to be a reaffirmation of territorial boundaries and a statement that the territory will be occupied in the following year by the current defending pair. Philopatry to nest sites is characteristic of Herring Gulls (Tinbergen 1956), as well as other species of gulls (Vermeer 1963; Patterson 1965; Brown 1967a; Onno 1967; Bongiorno 1970). The advantages of remaining on the same territory include a known place to locate mates the following year, familiarity with landmarks and neighbors, and the use of a territory where the pair may have successfully fledged young previously. The territories examined were all centrally located far from the colony edge where mammalian predators might enter. Further, I selected preferred nesting habitats for study. Since I did not watch pairs in less preferred habitats when their chicks were 60–90 days of age, I do not know if these pairs likewise showed increased territorial aggression. Animals should make tactical adjustments in their aggressive behavior with respect to habitat quality (Itzkowitz 1979), which suggests that peripheral pairs may attempt to shift to territory sites in more optimal habitats, and, thus, should be unlikely to invest time and energy in territorial defense late in the season.

## SPITE AND HERRING GULLS

Brown (1964) stated that the most important aspect of territoriality was the economic defendability of resources, and that aggressiveness would be maintained if it excluded other birds from breeding. Verner (1977) expanded this concept and stated that birds may defend a superterritory, which includes more of a given resource than is required for reproduction. Verner's model has generated many responses, primarily from authors arguing that such spiteful behavior would not evolve because the advantages of being a bully accrue to other conspecifics that hold normal-sized territories (Pleasants and Pleasants 1979; Rothstein 1979; Tullock 1979). Nonetheless, Harris (1979a, b) reported that Tree Swallows (*Iridoprocne bicolor*) do defend superterritories. Robertson and Gibbs (1982) recently reexamined superterritoriality in Tree Swallows and concluded that their territorial behavior had not evolved because of a relative increase in fitness gained by preventing conspecifics from breeding.

The superterritory hypothesis implies that birds may show spiteful behavior. In gulls it is difficult to examine spite because conditions in gull colonies seem to vary from year to year, suggesting that what seems to be a superterritory one year may not be one in another year. In the present study the size of Herring Gull territories varied from 10 to 80 $m^2$. However, most pairs on large territories did not fledge any young (Fig. 25). Thus, defense of large territories not only prevented others from breeding, but resulted in no success for the territory holder. Primary territory size ranged from 20 to 60 $m^2$ for birds that fledged young. One could argue that pairs defending 50–60 $m^2$ were defending superterritories and were preventing others from breeding. However, the data indicate that the pairs holding the largest territories within this range (40–60 $m^2$) fledged more young (two or three chicks per pair) than pairs with smaller primary territories (Table 33). Thus, within the range of successful territory sizes, birds with larger territories fledged more young and lost fewer young to cannibals than those with smaller territories, suggesting a direct relationship between territory size and reproductive success.

In addition, within the range of very successful territory sizes (50–60 $m^2$) variations in territory size were usually related to physical features of the environment. Territories in dense bushes were usually smaller than those in sparse bushes. The most successful territories (where three chicks fledged) contained many bushes that provided suitable hiding places for chicks and provided shelter from sun and inclement weather (Austin 1933; Brown 1967a). This suggests that territory quality must be considered as well as just territory size. In summary, territory size was an important determinant of fledging success, though not hatching success (Table 36). I saw no evidence that pairs defended superterritories. Instead, annexing space generally led to increased fledging success. Pairs that defended very large territories ($>60$ $m^2$), on the contrary, usually lost their eggs to cannibals while defending a territory border (Burger 1981e).

Herring Gulls do exhibit one behavior that could be considered spiteful. Pairs that have lost their clutches (or chicks) frequently become cannibals and prey on the eggs and chicks of their neighbors (Brown 1967a; Parsons 1975, 1976; Pierotti 1979). This tendency also has been noted for Lesser Black-backed Gulls (Brown 1967a; Davis and Dunn 1976). Attributing this behavior to spite, however, is inadvisable. When Herring Gulls are not incubating or brooding, they frequently wander about neighboring territories. If they encounter eggs, they eat them. In this study, all pairs tested engaged in cannibalism on eggs in unattended experimental nests. Thus, increased cannibalism by pairs that have lost their eggs seems to be due to increased activity of both sexes on neighboring territories, increasing the likelihood that they will encounter uncovered, unprotected eggs. This behavior can be extremely disruptive to a colony, because any cannibalism releases other pairs from incubation duties, thereby promoting more cannibalism. Some sections of a colony can have total loss of eggs or chicks to cannibalism.

For some gulls cannibalism is simply a form of foraging behavior that they use to feed themselves and their chicks (Parsons 1971). On Clam Island some males courtship fed females on Herring Gull eggs, and both parents sometimes fed cannibalized chicks or eggs to their own offspring. This behavior directly contributes to the production of eggs and survival of chicks, although it has the effect of lowering the contribution of conspecifics to the gene pool as well.

## Functions of Aggressive Behavior in Herring Gulls

I observed the aggressive behavior of Herring Gulls from the pre-incubation period until the chicks were 90 days old (well beyond fledging). On Clam Island there were few heterospecific predators, and few disturbances from man, dogs, cats, or rats. In all cases aggression occurred on the territory and was directed at conspecifics. The motivation for the aggression appeared to vary by sex and to be context-dependent. That is, males and females often were involved in different relative amounts of aggression depending on the stage in the reproductive cycle and the type of threat. In general, males were involved in more aggression in the pre-egg-laying period and at the end of the reproductive cycle, whereas females were more aggressive during the late incubation and chick stages. These differences suggest that males are mate-guarding and defending space in addition to defending

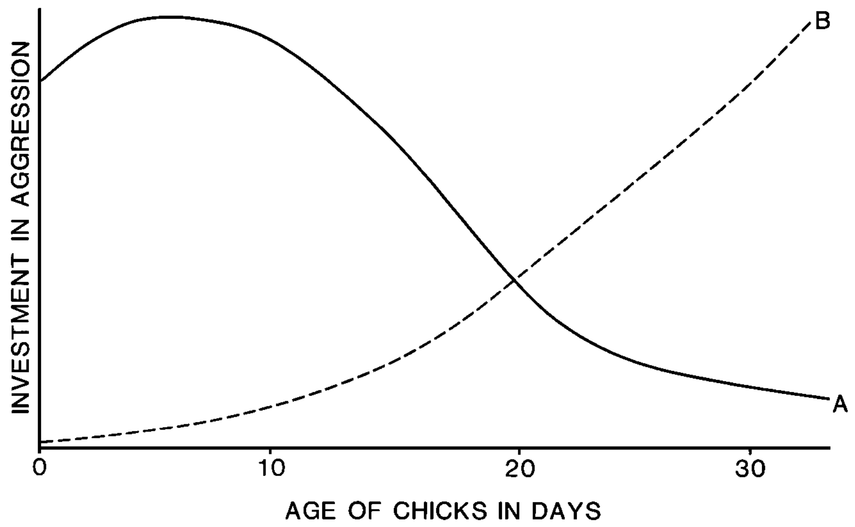

FIG. 30. Models of parental investment in aggressive behavior in defense of chicks as a function of chick age. A = the pattern of aggression in defense of chicks shown by Herring Gulls on Clam Island. B = Andersson et al.'s (1980) model of increasing investment for birds as chicks near fledging. See text for explanation.

eggs and chicks; females are defending primarily eggs and chicks. Nonetheless, the aggressive behavior of both parents directly affects the survival of their eggs and chicks. Over the entire cycle, males and females engage in aggression with equal frequency.

In Herring Gulls, the pressures to defend chicks should be equal for both sexes because each sex has already invested three to four months in the reproductive effort. The relative contribution of the eggs and sperm (see Trivers 1972) is minute compared to the investment in parental care required for the pair to have hatched eggs. Thus, at the time chicks hatch, each sex has contributed equally to the reproductive effort and can expect to continue investing equally.

Andersson et al. (1980) predicted that the optimal level of aggressive defense should increase with offspring age until fledging (Fig. 30) since the relative differences between parent and offspring with respect to future survival (and, thus, future offspring) decrease with increasing offspring age. I suggest that the level of defense in which parents engage should be responsive to the direct threat on the chick's existence, as well as to considerations of the relative survival prospects of parents and young. Herring Gull chicks are most vulnerable at 1 to 10 days of age (from cannibalism), and parental investment in defense during this period contributes to the chick's survival. Defense of older chicks usually is not as essential to their survival. That is, if a 7 day old chick being attacked by a neighbor is not defended, it will surely perish, whereas a 37 day old chick attacked by a neighboring gull usually can defend itself adequately (Fig. 30). In Herring Gulls, adult defense against conspecifics does not usually result in death, although very occasionally battles do result in bleeding or broken wings. In Herring Gulls, a high level of defense is essential just following hatching to protect the chick through a particularly vulnerable period. Thereafter, parental efforts can be channeled to foraging behavior and territory maintenance, although continued protection is required. Territory defense is not only essential to provide an area for chicks to remain unmolested by neighbors but may be essential to insure that the pair has a territory the following year.

## CONCLUSIONS AND SUMMARY

Territoriality in birds is conspicuous and contributes to differences in reproductive success. Since Brown's (1964) classic discussion of the importance of the economic defendability of territories, theoretical discussion of the mechanisms and adaptive significance of territoriality has been considerable. Such discussion usually includes the assumptions that territory size is related directly to reproductive success, that the amount of aggression necessary to defend territories increases linearly with territory size, and that rates of aggression are related directly to territory size.

I examined the relationships among territory size, aggressive behavior, and reproductive success in Herring Gulls nesting in five colonies in New Jersey, New York, and Maine. Herring Gulls exhibited three types of territories, (1) Primary territories, defended against and possessing mutual boundaries with neighbors, (2) Secondary territories, larger areas defended against non-neighbor intruders and often extending into neighbors' primary territories, and (3) Unique territories defended against all intruders and smaller than the primary territories. Primary territories, the type most often described by biologists, were easy to delimit by mapping the boundary clashes between neighbors. The secondary territory was recognized as the area outside the primary territory boundaries that was defended only against non-neighbors. The unique territory was easily recognized as it was the area where all intruders were always chased. All three types of territories changed in size with stage of the reproductive cycle, and all were smallest during incubation. Territory size also varied with habitat, date of egg-laying, and among pairs. Chicks that were undisturbed remained within their parents' territories until fledging.

Aggressive behavior used to defend territories, eggs, and chicks included Long Calls, Grass Pulling, Walking or Flying Toward intruders (including displacing them), chasing intruders aerially, and fighting. The behaviors used varied by habitat. Gulls nesting in bushes used Grass Pulling and Walking Toward intruders, whereas gulls nesting in grass displaced and chased intruders. These differences were related to nest density and habitat. The types of aggression used were similar among colonies.

Rates of aggression varied temporally (daily), by stage in the reproductive cycle, with the type of intruder (neighbor, non-neighbor), with environmental variables (vegetation cover, location in the colony, tide stage), and among pairs. Aggression was high in the period immediately before egg-laying, decreased during incubation, increased dramatically at hatching, decreased when chicks were about two weeks old, and increased just prior to the departure of parents and chicks from the colony. High rates of aggression just prior to egg-laying may reflect mate guarding by males, high rates of aggression at hatching reflect protection of small chicks by both sexes, and high rates prior to departure from the colony may reflect the reaffirmation of territory boundaries for the following year by males.

Rates of aggression among pairs varied from 0.13 to 3.50 interactions/pair/hr, with higher rates occurring in the chick phase than during incubation. In general, females were less aggressive toward all neighbors than were males, although both were equally aggressive toward non-neighbors. Similarly, males responded to neighbors at greater distances from the nest than did females. Overall, males had higher frequencies of aggression during incubation than females, but the sexes were equally aggressive during the chick phase. Males and females contributed about equally to incubation, brooding, and feeding.

Intrusion pressure varied in different habitats and at different nest densities. Intrusion pressure was highest in the central portion of the colony, in intermediate bush habitat, and in dense nesting areas. On Clam Island gulls in all habitats ignored about 8 percent of all intruders, and on Appledore Island the percent of intruders ignored depended on the distance they landed from the nest and the stage in the reproductive cycle. Intrusion pressure was difficult to measure since territory holders may ignore intruders at varying distances from their nests and may ignore neighbors standing on their mutual territory borders.

Rates of aggression were influenced by amount of time males were present, amount of time both members of the pair were present, number of chick feedings, stage in the reproductive cycle, and time of day.

On Clam Island the gulls holding intermediate-sized territories (30–60 $m^2$) were least aggressive, and gulls with smaller and larger territories were more aggressive. Thus, territory size and aggression rates were *not* linearly related. Gulls defending small territories were very aggressive because they had frequent boundary clashes with their neighbors, whereas gulls with large territories had frequent encounters with non-neighbor intruders attempting to establish territories and usurp space. Aggression, therefore, was minimized by defending an intermediate-sized territory that minimized both neighbor and non-neighbor interactions.

Overall, the Herring Gulls on Clam Island had a mean clutch size of 2.80 ± 0.42, hatched 2.21 ± 0.68 eggs, and reared an average of 1.45 ± 0.95 chicks to 30 days of age. Reproductive success varied among pairs and as a function of habitat, date of egg-laying, parental quality, and clutch size. There were no differences in hatching rates and fledging rates of center and edge-nesting birds. Gulls nesting in cover fledged more young than those nesting in the open, primarily because eggs were less visible and chicks had more hiding places. Overall, pairs that laid earlier had higher hatching and fledging success than mid- or late-nesting gulls. Parents with larger clutch sizes and higher hatching rates fledged more chicks. Once chicks hatched, they had an equal probability of fledging regardless of brood size. Overall, reproductive success on Clam Island was higher than that generally reported in the literature for other colonies. I attributed this difference to an abundance of available food and suitable habitat.

Of the eggs laid in the 1,080 nests examined on Clam Island, 6 to 12 percent were addled, 22 to 30 percent were eaten (as eggs or chicks), 6 to 7 percent starved as chicks, 4 to 16 percent died of unknown causes (most probably were eaten), and 41 to 55 percent fledged. Predators included conspecifics (72%), Fish Crows, Blue Jays, and Great Black-backed Gulls. Both sexes were cannibals, and eggs or chicks left unattended were quickly eaten or killed. The time required to discover unattended eggs in experimental nests increased as a function of cover.

Territory size and rates of aggression affected reproductive success, but the relationships were not linear. Reproductive success was highest in pairs with intermediate-sized territories and lowest in those with very large and small territories. The relationship between rates of aggression and reproductive success was negative, with very aggressive pairs rearing few or no young. However, pairs that had low rates of aggression fledged from zero to three young, suggesting that maintaining low rates of aggression alone is not sufficient to insure high reproductive success.

The data do not support the superterritory model of Verner (1977), nor do they indicate that Herring Gulls behave spitefully with respect to the acquisition or defense of territories.

## ACKNOWLEDGMENTS

I would expecially like to thank Michael Gochfeld for valuable discussion, logistical support, statistical aid, comments on the manuscript, and for advice and criticism throughout this study. The manuscript was improved considerably by comments from M. S. Foster, J. P. Myers, and one anonymous reviewer. Richard Trout of the statistics department of Rutgers University helped design and run the statistical analyses, and I am grateful for his advice. Over the years I have had many valuable discussions about territoriality, sex roles, and reproductive success of colonial birds with many people, and I thank them now: C. G. Beer, F. G. Buckley, P. A. Buckley, M. Conover, K. Corbin, R. M. Erwin, M. Fitch, M. Gochfeld, G. L. Hunt Jr., J. Krebs, C. Leck, F. Lesser, D. McCrimmon, D. W. Mock, W. Montevecchi, B. G. Murray Jr., D. N. Nettleship, J. Ogden, H. Recher, P. J. Regal, J. Ryder, C. Safina, J. Shisler, G. Shugart, W. R. Siegfried, L. K. Southern, W. E. Southern, N. Tinbergen, and H. B. Tordoff. I particularly thank my field assistants who spent long hours collecting data and being hit by diving gulls: D. Chanda, H. Colyer, J. Fischl, E. Johnson, and R. Moran. I thank J. Bayliss for designing the computer program for territory size, J. Sherwood for typing the manuscript, and D. J. Gochfeld for help with the literature cited.

My research with gulls over the years has been supported by the Research Council, the Biomedical Sciences Support Grant, and the Center for Coastal and Environmental Studies of Rutgers University. Logistical support was provided by F. Lesser, J. Shisler, and the New Jersey State Mosquito Commission (New Jersey colonies); M. Gochfeld (New York colonies); and J. Heiser, A. Borror, and the Shoals Marine Laboratory (Maine colony). Manuscript preparation was aided by funds from the Charles and Johanna Busch Fund. I thank these people and organizations for their kind support.

## LITERATURE CITED

Amlaner, C. J., and J. F. Stout. 1978. Aggressive communications by *Larus glaucescens* Part VI: interactions of territory residents with a remotely controlled, locomotory model. Behaviour 66: 223–249.

Andersson, M. 1976. Predation and kleptoparasitism by Skuas in a Shetland seabird colony. Ibis 118:208–217.

Andersson, M. C., G. Wiklund, and H. Rundgren. 1980. Parental defense of offspring; a model and an example. Anim. Behav. 28:536–542.

Armstrong, E. A. 1947. Bird display and behaviour. Lindsay Drummond, London.

Ashmole, N. P. 1963. The regulation of numbers of tropical oceanic birds. Ibis 103b:458–473.

Ashmole, N. P. 1971. Sea bird ecology and the marine environment. Pp. 223–386, *In* D. S. Farner and J. R. King (eds.), Avian biology, Vol. 1. Academic Press, New York.

Austin, O. L., Jr. 1933. The status of Cape Cod terns in 1933. Bird-Banding 4:190–198.

Baerends, G. P., and R. H. Drent. 1970. The Herring Gull and its egg. Behaviour Suppl. 17:1–283.

Beer, C. G. 1961. Incubation and nest-building behaviour of Black-headed Gulls. II. Incubation behaviour in the laying period. Behaviour 19:283–304.

Beer, C. G. 1966. Adaptations to nesting habitat in the reproductive behaviour of the Black-billed Gull, *Larus bulleri.* Ibis 103:394–410.

Beer, C. G. 1976. Some complexities in the communication behavior of gulls. Ann. N.Y. Acad. Sci. 280:413–432.

Beer, C. G. 1980. The communication behavior of gulls and other seabirds. Pp. 169–205, *In* J. Burger, B. L. Olla, and H. E. Winn (eds.), Behavior of marine animals, Vol. 4: Marine birds. Plenum Press, New York.

Bent, A. C. 1921. Life histories of North American gulls and terns. U.S. Nat. Mus. Bull. No. 113.

Bianki, V. V. 1967. Gulls, shorebirds and alcids of Kandalaksha Bay. Proc. Kandalaksha State Res. 6:86–165. Israel Program for Scientific Translations, Jerusalem.

Bongiorno, S. F. 1970. Nest-site selection by adult Laughing Gulls (*Larus atricilla*). Anim. Behav. 18:434–444.

Brown, J. L. 1964. The evolution of diversity in avian territorial systems. Wilson Bull. 76:160–169.

Brown, J. L., and G. H. Orians. 1970. Spacing patterns in mobile animals. Ann. Rev. Ecol. Syst. 1:239–262.

Brown, R. G. B. 1967a. Breeding success and population growth in a colony of Herring and Lesser Black-backed Gulls, *Larus argentatus* and *Larus fuscus.* Ibis 109:502–515.

Brown, R. G. B. 1967b. Courtship behaviour in the Lesser Black-backed Gull, *Larus fuscus.* Behaviour 29:122–153.

Buckley, F. G., and P. A. Buckley. 1972. The breeding biology of Royal Terns *Sterna* (Thalasseus) *maxima maxima.* Ibis 114:344–359.

Buckley, F. G., and P. A. Buckley. 1980. Habitat selection in marine birds. Pp. 69–111, *In* J. Burger, B. L. Olla, and H. E. Winn (eds.), Behavior of marine animals, Vol. 4: Marine birds. Plenum Press, New York.

Burger, J. 1974a. Breeding adaptations of Franklin's Gull (*Larus pipixcan*) to a marsh habitat. Anim. Behav. 22:521–567.

Burger, J. 1974b. Breeding biology and ecology of the Brown-hooded Gull in Argentina. Auk 9:601–613.

Burger, J. 1976. Daily and seasonal activity patterns in breeding Laughing Gulls, *Larus atricilla.* Auk 93:308–323.

Burger, J. 1977a. Nesting behavior of Herring Gulls: invasion into *Spartina* salt marsh areas of New Jersey. Condor 79:162–169.

Burger, J. 1977b. The role of visibility in the nesting behavior of 5 species of *Larus* Gulls. J. Comp. Physiol. Psych. 9:1347–1358.

Burger, J. 1979a. Competition and predation: Herring Gulls versus Laughing Gulls. Condor 81:269–277.

Burger, J. 1979b. Nest building in *Larus* gulls. J. Comp. Physiol. Psych. 11:189–199.

Burger, J. 1979c. Colony size: a test for breeding synchrony in Herring Gulls (*Larus argentatus*). Auk 96:694–703.

Burger, J. 1980a. Territory size differences in relation to reproductive stage and type of intruder in Herring Gulls. Auk 97:733–741.

Burger, J. 1980b. The transition from dependence to independence and post-fledging parental care in marine birds. Pp. 367–447, *In* J. Burger, B. L. Olla, and H. E. Winn (eds.), Behavior of Marine animals, Vol. 4: Marine birds. Plenum, New York.

Burger, J. 1980c. Nesting adaptations of Herring Gull (*Larus argentatus*) to salt marshes and storm tides. Biol. Behav. 5:147–162.

Burger, J. 1981a. On becoming independent in Herring Gulls: parent-young conflict. Am. Nat. 117:444–456.

Burger, J. 1981b. Sexual differences in parental activities of breeding Black Skimmers. Am. Nat. 117:975–984.

BURGER, J. 1981c. Effects of human disturbance on colonial species, particularly gulls. Colonial Waterbirds 4:28–36.

BURGER, J. 1981d. A model for the evolution of mixed species colonies of Ciconiiformes. Q. Rev. Biol. 56:143–167.

BURGER, J. 1981e. Superterritories: a comment. Am. Nat. 118:578–580.

BURGER, J. 1983. Competition between two species of nesting gulls: on the importance of timing. Behav. Neurosci. 97:492–501.

BURGER, J. in press. Advantages and disadvantages of mixed-species colonies of seabirds. Proc. XVIII Intl. Ornithol. Congr. (Moscow, 1982).

BURGER, J., AND C. G. BEER. 1975. Territoriality in the Laughing Gull (*L. atricilla*). Behaviour 55: 301–320.

BURGER, J., AND M. GOCHFELD. 1981a. Unequal sex ratios and their consequences in Herring Gulls (*Larus argentatus*). Behav. Ecol. Sociobiol. 8:125–128.

BURGER, J., AND M. GOCHFELD. 1981b. Colony and habitat selection of six Kelp Gull *Larus dominicanus* colonies in South Africa. Ibis 123:298–310.

BURGER, J., AND M. GOCHFELD. 1981c. Nest site selection in Kelp Gulls in Southern Africa. Condor 83:243–251.

BURGER, J., AND M. GOCHFELD. 1983. Behavioural responses to human intruders of Herring (*Larus argentatus*) and Great Black-backed (*L. marinus*) Gulls with varying exposure to human disturbance. Behav. Processes 8:327–344.

BURGER, J., AND F. LESSER. 1978. Selection of colony sites and nest sites by Common Terns *Sterna hirundo* in Ocean County, New Jersey. Ibis 120:433–449.

BURGER, J., AND F. LESSER. 1979. Breeding behavior and success in salt marsh Common Tern colonies. Bird-Banding 50:322–337.

BURGER, J., AND J. SHISLER. 1978a. Nest site and competitive interactions of Herring and Laughing Gulls in New Jersey. Auk 95:252–266.

BURGER, J., AND J. SHISLER. 1978b. The effect of ditching on nest site selection in Herring Gulls. Am. Midl. Nat. 100:54–63.

BURGER, J., AND J. SHISLER. 1979. Immediate effects of ditching a marsh on breeding Herring Gulls *Larus argentatus*. Biol. Conserv. 15:85–104.

BURGER, J., AND J. SHISLER. 1980. Colony and nest site selection in Laughing Gulls in response to tidal flooding. Condor 83:251–258.

BUTLER, R. G., AND W. TRIVELPIECE. 1981. Nest spacing, reproductive success and behavior of the Great Black-backed Gull (*Larus marinus*). Auk 98:99–107.

BUTLER, R. G., AND S. JANES-BUTLER. 1983. Sexual differences in the behavior of adult Great Black-backed Gulls (*Larus marinus*) during the pre- and post-hatch periods. Auk 100:63–75.

CAMBERLEIN, G., AND D. FLOTE. 1979. Le Goeland argente en Bretagne/Etude demographique et gestion de population. Penn. Bed. (Brest) 98:89–115.

CONOVER, M. R., AND D. E. MILLER. 1979. Reaction of Ring-billed Gulls to predators and human disturbance at their breeding colonies. Proc. Colonial Waterbird Group 2:41–47.

CONOVER, M. R., AND D. E. MILLER. 1980. Daily activity patterns of breeding Ring-billed and California Gulls. J. Field Ornithol. 51:329–339.

CONOVER, M. R., D. R. MILLER, AND G. L. HUNT, JR. 1979. Female-female pairs and other unusual reproductive associations in Ring-billed and California Gulls. Auk 96:6–9.

COULSON, J. C. 1963. Egg size and shape in the Kittiwake *Rissa tridactyla* and their use in estimating age composition of populations. Proc. Zool. Soc. Lond. 140:211–217.

COULSON, J. C. 1966. The influence of pair-bond and age on the breeding biology of the Kittiwake Gull, *Rissa tridactyla*. J. Anim. Ecol. 35:269–279.

COULSON, J. C. 1968. Differences in the quality of birds nesting in the centre and on the edges of a colony. Nature (London) 217:478–479.

COULTER, M. C. 1977. Growth, mortality and the third-chick disadvantage in the Western Gull, *Larus occidentalis*. Unpubl. Ph.D. dissert. University of Pennsylvania, Philadelphia.

CROOK, F. H. 1964. The evolution of social organization and visual communication in the weaver birds (Ploceinae). Behaviour Suppl. 10:1–178.

CULLEN, J. M. 1960. Some adaptations in the nesting behavior of terns. Proc. XII Int. Ornithol. Congr., pp. 153–157.

Darling, F. F. 1938. Bird flocks and the breeding cycle. Cambridge Univ. Press, London.

Davies, N. B. 1978. Ecological questions about territorial behaviour. Pp. 317–350, *In* J. R. Krebs and N. B. Davies (eds.), Behavioral ecology: an evolutionary approach. Blackwell, Oxford, England.

Davies, N. B. 1980. The economics of territorial behaviour in birds. Ardea 68:63–74.

Davis, J. W. F. 1975. Age, egg-size and breeding success in the Herring Gull, *Larus argentatus*. Ibis 117:460–473.

Davis, J. W. F., and E. K. Dunn. 1976. Intraspecific predation and colonial breeding in Lesser Black-backed Gulls *Larus fuscus*. Ibis 118:65–77.

Delius, J. D. 1970. The effect of daytime, tides and other factors on some activities of Lesser Black-backed Gulls, *Larus fuscus*. Rev. Comp. Animal 4:3–11.

Deusing, M. 1939. The Herring Gulls on Hat Island, Wisconsin. Wilson Bull. 51:170–175.

Dexheimer, M., and W. E. Southern. 1975. Breeding success relative to nest location and density in Ring-billed Gull colonies. Wilson Bull. 85:288–290.

Dhondt, A. A., and J. Huble. 1968. Age and territory of the Great Tit (*Parus major major* L.). Appl. Ornithol. 3:20–24.

Dow, D. D. 1979. Agonistic and spacing behaviour of the Noisy Miner *Manorina melanocephala*, a communally breeding honeyeater. Ibis 121:423–436.

Draper, N., and H. Smith. 1981. Applied regression analysis. John Wiley and Sons, New York.

Drent, R. H. 1967. Functional aspects of incubation in the Herring Gull (*Larus argentatus* Pont.). Behaviour Suppl. 17:1–125.

Drury, W. H., and J. A. Kadlec. 1974. The current status of the Herring Gull populations in the Northeastern United States. Bird-Banding 45:297–306.

Dutcher, W., and W. L. Baily. 1903. A contribution to the life history of the Herring Gull in the United States. Auk 20:417–431.

Dwight, J. D. 1925. The Gulls (Laridae) of the world: their plumages, moults, variations, relationships and distribution. Bull. Am. Mus. Nat. Hist. 52:63–401.

Emlen, J. T. 1957. Defended area?—a critique of the territory concept and of conventional thinking. Ibis 99:352.

Emlen, J. T., Jr., D. E. Miller, R. M. Evans, and D. H. Thompson. 1966. Predator induced parental neglect in a Ring-billed Gull colony. Auk 83:677–679.

Emlen, S. T., and N. J. Demong. 1975. Adaptive significance of synchronized breeding in a colonial bird: a new hypothesis. Science 188:1029–1031.

Emlen, S. T., and L. W. Oring. 1977. Ecology, sexual selection, and the evolution of mating systems. Science 192:1353–1354.

Erwin, M. 1971. The breeding success of two sympatric gulls, the Herring Gull and Great Black-backed Gull. Wilson Bull. 83:152–158.

Evans, R. M. 1970. Imprinting and mobility in young Ring-billed Gulls, *Larus delawarensis*. Anim. Behav. Monogr. 3:193–248.

Evans, R. M. 1982. Colony desertion and reproductive synchrony of Black-billed Gulls *Larus bulleri*. Ibis 124:491–501.

Ewald, P. W., G. L. Hunt, Jr., and M. Warner. 1980. Territory size in Western Gulls: importance of intrusion pressure, defense investments, and vegetation structure. Ecology 61:80–87.

Falls, J. B. 1969. Functions of territorial song in the White-throated Sparrow. Pp. 207–232, *In* R. A. Hinde (ed.), Bird vocalizations: their relations to current problems in biology and psychology, essays presented to W. H. Thorpe. Cambridge Univ. Press, Cambridge, England.

Fetterolf, P. M. 1979. Nocturnal behaviour of Ring-billed Gulls during the early incubation period. Can. J. Zool. 57:1190–1195.

Fisher, H. I. 1971. The Laysan Albatross: its incubation, hatching, and associated behaviors. Living Bird 10:19–78.

Fisher, J. 1952. The Fulmar. Collin's New Naturalist, London.

Fitch, M. A. 1979. Monogamy, polygyny and female-female pairs in Herring Gulls. Proc. Colonial Waterbird Group 3:44–48.

Fordham, R. A. 1964a. Breeding biology of the southern Black-backed Gull. I: pre-egg and egg stage. Notornis 11:3–34.

Fordham, R. A. 1964b. Breeding biology of the Southern Black-backed Gull. II: incubation and chick stage. Notornis 11:110–126.

FOX, G. A., C. R. COOPER, AND J. P. RYDER. 1981. Predicting the sex of Herring Gulls by using external measurements. J. Field Ornithol. 52:1–9.

FUCHS, E. 1977. Predation and anti-predator behaviour in a mixed colony of terns *Sterna* sp. and Black-headed Gulls *Larus ridibundus* with special reference to the Sandwich Tern *Sterna sandvicensis*. Ornis Scand. 8:17–32.

GALUSHA, J. G., JR., AND C. J. AMLANER, JR. 1978. The effects of diurnal and tidal periodicities in the numbers and activities of Herring Gulls *Larus argentatus* in a colony. Ibis 120:322–328.

GALUSHA, J. G., AND J. F. STOUT. 1977. Aggressive communications by *Larus glaucescens,* Part IV: experiments on visual communication. Behaviour 62:222–235.

GILLETT, W. H., J. L. HAYWARD, JR., AND J. F. STOUT. 1975. Effect of human activity on egg and chick mortality in a Glaucous-winged Gull colony. Condor 77:492–495.

GOCHFELD, M. 1979. Breeding synchrony in Black Skimmers: colony versus sub-colonies. Proc. Colonial Waterbird Group 2:171–177.

GOCHFELD, M. 1980. Mechanisms and adaptive value of reproductive synchrony in colonial seabirds. Pp. 207–270, *In* J. Burger, B. L. Olla, and H. E. Winn (eds.), Behavior of marine animals, Vol. 4: Marine birds. Plenum Press, New York.

GOCHFELD, M. 1981. Differences in behavioral responses of young Common Terns and Black Skimmers to intrusion and handling. Colonial Waterbirds 4:47–53.

HAHN, D. C. 1981. Asynchronous hatching in the Laughing Gull: cutting losses and reducing rivalry. Anim. Behav. 29:421–427.

HAND, J. L., G. L. HUNT, JR., AND M. WARNER. 1981. Thermal stress and predation: influences on the structure of a gull colony and possibly on breeding distributions. Condor 83:193–203.

HARRIS, M. P. 1964. Aspects of the breeding biology of the gulls *Larus argentatus, L. fuscus* and *L. marinus.* Ibis 106:432–456.

HARRIS, M. P. 1969. The biology of Storm Petrels in the Galapagos Islands. Proc. Calif. Acad. Sci. 37(Series 4):95–165.

HARRIS, M. P. 1970. Rates and causes of increases of some British gull populations. Bird Study 17: 325–335.

HARRIS, M. P. 1978. Supplementary feeding of young Puffins, *Fratercula arctica.* J. Anim. Ecol. 47: 15–23.

HARRIS, M. P., AND P. H. JONES. 1969. Sexual differences in measurements of Herring and Lesser Black-backed Gulls. Br. Birds 62:129–133.

HARRIS, M. P., AND W. J. PLUMB. 1965. Experiments on the ability of Herring Gulls *Larus argentatus* and Lesser Black-backed Gulls *L. fuscus* to raise larger than normal broods. Ibis 107:256–257.

HARRIS, R. N. 1979a. Aggression, superterritories, and reproductive success in Tree Swallows. Can. J. Zool. 57:2072–2078.

HARRIS, R. N. 1979b. Influence of weather on aggression in Tree Swallows. Can. Field-Nat. 93:437–438.

HAYWARD, J. L., JR., C. J. AMLANER, JR., W. H. GILLETT, AND J. F. STOUT. 1975. Predation on nesting gulls by a River Otter in Washington State. Murrelet 56:9–10.

HAYWARD, J. L., JR., W. H. GILLETT, AND J. F. STOUT. 1977. Aggressive communications by *Larus glaucescens,* Part V: orientation and sequences of behavior. Behaviour 62:236–277.

HINDE, R. A. 1956. The biological significance of the territories of birds. Ibis 98:340–369.

HOLLY, A. J. F. 1982. Post-fledging interaction on the territory between parents and young Herring Gulls *Larus argentatus.* Ibis 124:198–203.

HOWARD, E. 1920. Territory in bird life. Murray Press, London.

HUNT, G. L., JR. 1972. Influence of food distribution and human disturbance on the reproductive success of Herring Gulls. Ecology 53:1051–1060.

HUNT, G. L., JR. 1980. Mate selection and mating systems in birds. Pp. 113–151, *In* J. Burger, B. L. Olla, and H. E. Winn (eds.), Behavior of marine animals, Vol. 4: Marine birds. Plenum Press, New York.

HUNT, G. L., JR., AND M. W. HUNT. 1973. Habitat partitioning by foraging gulls in Marine and northwestern Europe. Auk 90:827–839.

HUNT, G. L., JR., AND M. W. HUNT. 1975. Reproductive ecology of the Western Gull: the importance of nest spacing. Auk 92:270–279.

HUNT, G. L., JR., AND M. W. HUNT. 1976. Gull chick survival: the significance of growth rates, timing of breeding and territory size. Ecology 57:62–75.

HUNT, G. L., JR., AND M. W. HUNT. 1977. Female-female pairing in Western Gulls *Larus occidentalis* in southern California. Science 196:1466–1467.

HUNT, G. L., JR., AND S. C. MCLOON. 1975. Activity patterns of gull chicks in relation to feeding by parents: their potential significance for density-dependent mortality. Auk 92:523–527.

HUTCHINSON, G. E., AND R. MACARTHUR. 1959. Appendix: On the theoretical significance of aggressive neglect in interspecific competition. Am. Nat. 93:133–134.

HUTSON, G. D. 1977. Agonistic display and spacing in the Black-headed Gull, *Larus ridibundus.* Anim. Behav. 25:763–773.

HUXLEY, J. S. 1934. A natural experiment on the territorial instinct. Br. Birds 27:270–277.

INGOLFSSON, A. 1969. Sexual dimorphism of large gulls (*Larus* sp.). Auk 86:732–737.

ITZKOWITZ, M. 1979. Territorial tactics and habitat quality. Am. Nat. 114:585–590.

JEHL, J. R., JR., AND B. A. SMITH. 1970. Birds of the Churchill region. Manitoba Spec. Publ. No. 1, Manitoba Mus. Man Nat.

KADLEC, J. A., AND W. H. DRURY, JR. 1968. Structure of the New England Herring Gull population. Ecology 49:644–676.

KADLEC, J. A., AND W. H. DRURY, JR., AND D. K. ONION. 1969. Growth and mortality of Herring Gull chicks. Bird-Banding 40:222–233.

KEITH, J. A. 1966. Reproduction in a population of Herring Gulls (*Larus argentatus*) contaminated by DDT. J. Appl. Ecol. 3:57–70.

KEPLER, C. B. 1967. Polynesian rat predation on nesting Laysan Albatrosses and other Pacific seabirds. Auk 84:426–30.

KING, J. A. 1973. The ecology of aggressive behavior. Ann. Rev. Ecol. Syst. 4:117–138.

KLUYVER, H. N., AND N. TINBERGEN. 1953. Territory and the regulation of density in Titmice. Arch. Neerl. Zool. 10:265–289.

KREBS, J. R. 1973. Behavioral aspects of predation. Pp. 73–112, *In* P. P. G. Baterson and P. Klopfer (eds.), Perspectives in ethology. Plenum Press, New York.

KREBS, J. R. 1974. Colonial nesting and social feeding as strategies for exploiting food in the Great Blue Heron (*Ardea herodias*). Behaviour 51:99–134.

KREBS, J. R. 1978. Colonial nesting in birds, with special references to the Ciconiiformes. Pp. 299–314, *In* A. Sprunt, J. Ogden, and S. Wickler (eds.), Wading Birds. Nat. Audubon Soc. Res. Rep. No. 7.

KREBS, J. R. 1982. Territorial defense in the Great Tit (*Parus major*): do residents always win? Behav. Ecol. Sociobiol. 11:185–194.

KRUUK, H. 1964. Predators and anti-predator behavior of the Black-headed Gull (*Larus ridibundus* L.). Behaviour Suppl. 11:1–129.

LACK, D. 1954. The natural regulation of animal numbers. Clarendon Press, Oxford, England.

LACK, D. 1968. Ecological adaptations for breeding in birds. Methuen, London.

LEMMETYINEN, R. 1971. Nest defense behaviour of Common and Arctic Terns and its effects on the success achieved by predators. Ornis Fenn. 48:13–24.

MACLEAN, S. F., JR., AND T. R. SEASTEDT. 1979. Avian territoriality: sufficient resources or interference competition. Am. Nat. 114:308–313.

MACROBERTS, M. H., AND B. R. MACROBERTS. 1972a. The relationship between laying date and incubation period in Herring and Lesser Black-backed Gulls. Ibis 114:93–97.

MACROBERTS, B. R., AND M. H. MACROBERTS. 1972b. Social stimulation of reproduction in Herring and Lesser Black-backed Gulls. Ibis 114:495–506.

MANUWAL, D. A. 1978. Effect of man on marine birds: a review. Pp. 140–160, *In* C. Kirkpatrick (ed.), Wildlife and people. Purdue Univ. Press, West Lafayette, Indiana.

MAYR, E. 1935. Bernard Altum and the territory theory. Proc. Linn. Soc. New York 45:1–15.

MILNE, H. 1974. Breeding numbers and reproductive rate of Eiders at the Sands of Forvie National Nature Reserve, Scotland. Ibis 116:135–152.

MONTEVECCHI, W. A. 1977. Predation in a salt marsh Laughing Gull colony. Auk 94:583–585.

MONTEVECCHI, W. A. 1978. Nest site selection and its survival value among Laughing Gulls. Behav. Ecol. Sociobiol. 4:143–161.

MONTEVECCHI, W. A. 1979. Predator-prey interactions between Ravens and Kittiwakes. Z. Tierpsychol. 49:136–141.

MORRIS, R. D., AND J. E. BLACK. 1980. Radio telemetry and Herring Gull foraging patterns. J. Field Ornithol. 51:110–118.

MOYNIHAN, M. 1955. Some aspects of reproductive behavior in the Black-headed Gull (*Larus ridibundus ridibundus* L.) and related species. Behaviour Suppl. 4:1–197.

MOYNIHAN, M. 1956. Notes on the behavior of some North American Gulls. I. aerial hostile behavior. Behaviour 10:126–178.

MOYNIHAN, M. 1958a. Notes on the behavior of some North American Gulls. II: non-aerial hostile behavior of adults. Behaviour 12:95–182.

MOYNIHAN, M. 1958b. Notes on the behavior of some North American Gulls. III: pairing behavior. Behaviour 13:112–130.

MOYNIHAN, M. 1959a. A revision of the family Laridae (Aves). Am. Mus. Novit. 1928:1–42.

MOYNIHAN, M. 1959b. Notes on the behavior of some North American Gulls. IV: the ontogeny of hostile behavior and display patterns. Behaviour 14:214–239.

MOYNIHAN, M. 1962. Hostile and sexual behavior patterns of South American and Pacific Laridae. Behaviour Suppl. 8:1–365.

MYERS, J. P., P. G. CONNORS, AND F. A. PITELKA. 1981. Optimal territory size and the Sanderling: compromises in a variable environment. Pp. 135–158, *In* A. C. Kamil and T. D. Sargent (eds.), Foraging behavior: ecological, ethological and psychological approaches. Garland STPM Press, New York.

NEHLS, H. W. 1979. Notwendigkeit und Ergebnisse der Bestandsregulierung bei Mowen (*Larus*). Beit. Vogelk. 25:41–49.

NELSON, J. B. 1966. The breeding biology of the Gannet *Sula bassana* on the Bass Rock, Scotland. Ibis 108:584–626.

NELSON, J. B. 1970. The relationship between behavior and ecology in the Sulidae with references to other sea birds. Oceanogr. Mar. Biol. Ann. Rev. 8:501–574.

NETTLESHIP, D. N. 1972. Breeding success of the Common Puffin *Fratercula arctica* L. on different habitats of Great Island, Newfoundland. Ecol. Monogr. 42:239–268.

NICE, M. M. 1933. Nesting success during three seasons in a Song Sparrow population. Bird-Banding 4:119–131.

NICE, M. M. 1941. The role of territory in bird life. Am. Midl. Nat. 26:441–487.

NIE, N. H., C. H.HULL, J. G. JENKINS, K. STEINBRENNER, AND D. H. BRENT. 1975. Statistical package for the social sciences. McGraw-Hill, New York.

NIEBUHR, V. 1981. An investigation of courtship feeding in Herring Gulls *Larus argentatus*. Ibis 213:218–223.

NISBET, I. C. T. 1973. Courtship-feeding, egg-size and breeding success in Common Terns. Nature (Lond.) 241:141–142.

NISBET, I. C. T. 1975. Selective effects of predation in a tern colony. Condor 77:221–226.

NISBET, I. C. T. 1978. Direct human influences: hunting and the use by birds of man's waste deposits. Ibis 120:134.

NISBET, I. C. T., AND W. H. DRURY. 1972. Post-fledging survial in Herring Gulls in relation to brood-size and date of hatching. Bird-Banding 43:161–172.

NOBLE, G. K. 1939. The role of dominance in the social life of birds. Auk 56:263–273.

ONNO, S. 1967. Nesting colony of the Common Gull. Ornitol. Kogumik, Tartu 4:114–148.

PALUDAN, K. 1951. Contributions to the breeding biology of *Larus argentatus* and *Larus fuscus*. Vidensk. Medd. Dan. Naturhist. Foren. 114:1–128.

PARKER, G. A., AND N. KNOWLTON. 1980. The evolution of territory size—some ESS Models. J. Theor. Biol. 84:445–476.

PARSONS, J. 1971. Cannibalism in Herring Gulls. Br. Birds 64:528–537.

PARSONS, J. 1975. Seasonal variation in the breeding success of the Herring Gull: an experimental approach to pre-fledging success. J. Anim. Ecol. 44:553–573.

PARSONS, J. 1976. Nesting density and breeding success in the Herring Gull, *Larus argentatus*. Ibis 118:537–546.

PATTERSON, I. J. 1965. Timing and spacing of broods in the Black-headed Gull *Larus ridibundus*. Ibis 107:433–459.

PATTERSON, I. J. 1980. Territorial behaviour and the limitation of population density. Ardea 68: 53–62.

PATTON, S. R., AND W. E. SOUTHERN. 1978. The effect of nocturnal Red Fox predation on the nesting success of colonial gulls. Proc. Colonial Waterbird Group 1:91–101.

PAYNTER, R. A., JR. 1949. Clutch-size, and the egg and chick mortality of Kent Island Herring Gulls. Ecology 30:140–166.

PIEROTTI, R. 1979. Spite and altruism in gulls. Am. Nat. 114:290–300.

PIEROTTI, R. 1981. Male and female parental roles in the Western Gull under different environmental conditions. Auk 98:532–549.

PITELKA, F. A. 1959. Numbers, breeding schedule, and territoriality in Pectoral Sandpipers of northern Alaska. Condor 61:233–264.

PLEASANTS, J. M., AND B. Y. PLEASANTS. 1979. The super-territory hypothesis: a critique, or why there are so few bullies. Am. Nat. 114:609–614.

POWER, C. 1964. Breeding success of the Common Tern on the north shore of the Gulf of St. Lawrence in 1961 and 1962. Arctic 17:51–53.

PULLIAM, R. H. 1973. On the advantages of flocking. J. Theor. Biol. 38:419–422.

PYKE, G. H. 1979. The economics of territory size and time budget in the Golden-winged Sunbird. Am. Nat. 114:131–145.

RALPH, C. J., AND C. A. PEARSON. 1971. Correlation of age, size of territory, plumage and breeding success in White-crowned Sparrows. Condor 73:77–80.

RICKLEFS, R. E. 1977. On the evolution of reproductive strategies in birds: reproductive effort. Am. Nat. 111:453–478.

RIPLEY, S. D. 1961. Aggressive neglect as a factor in interspecific competition in birds. Auk 78:366–371.

ROBERT, H. C., AND C. J. RALPH. 1975. Effects of human disturbance on the breeding success of gulls. Condor 77:495–499.

ROBERTSON, H. G., AND R. D. WOOLLER. 1981. Seasonal decrease in the clutch size of Hartlaub's Gulls *Larus hartlaubii* at Strandfontein in 1978. Cormorant 9:23–26.

ROBERTSON, R. J., AND H. L. GIBBS. 1982. Superterritoriality in Tree Swallows: a reexamination. Condor 84:313–316.

ROTHSTEIN, S. E. 1979. Gene frequencies and selection for inhibitory traits, with special emphasis on the adaptiveness of territoriality. Am. Nat. 113:317–331.

RYDER, J. P. 1978. Sexing Ring-billed Gulls externally. Bird-Banding 49:218–222.

RYDER, J. P. 1980. The influence of age on the breeding biology of colonial nesting birds. Pp. 153–168, *In* J. Burger, B. L. Olla, and H. E. Winn (eds.), Behavior of marine animals, Vol. 4: Marine birds. Plenum Press, New York.

RYDER, J. P., AND P. L. SOMPPI. 1979. Female-female pairing in Ring-billed Gulls. Auk 96:1–5.

RYDER, P. L., AND J. P. RYDER. 1981. Reproductive performance of Ring-billed Gulls in relation to nest location. Condor 83:57–60.

S.A.S. 1979. SAS users guide. SAS Institute, Cary, North Carolina.

S.A.S. 1982. SAS users guide: statistics. SAS Institute, Cary, North Carolina.

SCHOENER, T. W. 1968. Sizes of feeding territories among birds. Ecology 49:123–141.

SCHREIBER, R. W. 1979. Reproductive performance of the Eastern Brown Pelican, *Pelecanus occidentalis.* Nat. Hist. Mus. Los Ang. Co. Contrib. Sci. 317:1–43.

SHUGART, G. W. 1977. A method for externally sexing gulls. Bird-Banding 48:118–121.

SHUGART, G. W. 1980. Frequency and distribution of polygyny in Great Lakes Herring Gulls in 1978. Condor 82:426–429.

SHUGART, G. W., M. FITCH, AND V. SHUGART. 1981. Minimizing investigator disturbance in observational studies of colonial birds: access to blinds through tunnels. Wilson Bull. 93:565–569.

SHUGART, G. W., AND W. E. SOUTHERN. 1977. Close nesting, a result of polygyny in Herring Gulls. Bird-Banding 48:276–277.

SOUTHERN, L. K. 1981. Sex-related differences in territorial aggression in Ring-billed Gulls. Auk 98: 179–181.

SOUTHERN, L. K., AND W. E. SOUTHERN. 1979. Absence of nocturnal predator defense mechanisms in breeding gulls. Proc. Colonial Waterbird Group. 2:157–162.

SPAANS, A. L. 1971. On the feeding ecology of the Herring Gull *Larus argentatus* Pont. in the northern part of the Netherlands. Ardea 59:73–188.

SPAANS, M. J., AND A. L. SPAANS. 1975. Enkele Gegevens over de Broedbiologie van de Zilvermeeuw *Larus argentatus* op Terschelling. Limosa 48:1–39.

SPURR, E. B. 1974. Individual differences in aggressiveness of Adelie Penguins. Anim. Behav. 22: 611–616.

STEFANSKI, R. A. 1967. Utilization of breeding territory in the Black-capped Chickadee. Condor 69: 259–267.

STENGER, J., AND J. B. FALLS. 1959. The utilized territory of the Ovenbird. Wilson Bull. 71:125–140.

STOUT, J. F., AND M. E. BRASS. 1969. Aggressive communications by *Larus glaucescens,* Part II: visual communications. Behaviour 34:42–54.

STOUT, J. F., C. R. WILCOX, AND L. E. CREITZ. 1969. Aggressive communications by *Larus glaucescens,* Part 1: sound communication. Behaviour 34:29–41.

TAYLOR, R. H., AND K. WODZICKI. 1958. Black-backed Gull—a Gannet predator. Notornis 8:22–23.

TINBERGEN, N. 1952. On the significance of territory in the Herring Gull. Ibis 94:158–159.

TINBERGEN, N. 1956. On the functions of territory in gulls. Ibis 98:401–411.

TINBERGEN, N. 1957. The functions of territory. Bird Study 4:14–27.

TINBERGEN, N. 1959. Comparative studies of the behavior of gulls Laridae: a progress report. Behaviour 15:1–70.

TINBERGEN, N. 1960. The Herring Gull's world. Collin's, London.

TINBERGEN, N. 1963. On adaptive radiation in gulls Tribe *Larini.* Zool. Bonner. Beitr. 39:209–223.

TINBERGEN, N. 1967. Adaptive features of the Black-headed Gull, *Larus ridibundus* L. Proc. XIV Int. Ornithol. Congr. 14:43–59.

TINBERGEN, N., M. IMPEKOVEN, AND D. FRANK. 1967. An experiment on spacing-out as a defense against predators. Behaviour 28:307–321.

TRIVERS, R. L. 1972. Parental investment and sexual selection. Pp. 136–207, *In* B. Campbell (ed.), Sexual selection and the descent of man. Aldine, Chicago, Illinois.

TULLOCK, G. 1979. On the adaptive significance of territoriality: comment. Am. Nat. 113:772–775.

VAN RHIJN, J. G. 1981. Units of behaviour in the Black-headed Gull *Larus ridibundus* L. Anim. Behav. 29:586–597.

VEEN, J. 1977. Functional and causal aspects of nest distribution in colonies of the Sandwich Tern *Sterna s. sandvicensis* Lath. Behaviour Suppl. 20:1–193.

VERBEEK, N. A. M. 1979. Some aspects of the breeding biology and behavior of the Great Black-backed Gull. Wilson Bull. 91:575–582.

VERMEER, K. 1963. The breeding ecology of the Glaucous-winged Gull *Larus glaucescens* on Mandarte Island, B.C. Occ. Pap. Br. Col. Prov. Mus. 13:1–104.

VERNER, J. 1977. On the adaptive significance of territoriality. Am. Nat. 111:769–775.

VERNON, J. D. R. 1970. Food of the Common Gull on grassland in autumn and winter. Bird Study 17:36–38.

VIKSNE, J., AND M. JANAUS. 1980. Breeding success of the Black-headed Gull *Larus ridibundus* in relation to the nesting time. Ornis Fenn. 57:1–10.

WARD, H. L. 1906. Why do Herring Gulls kill their young. Science 24:593.

WEEDEN, J. S. 1965. Territorial behavior of the Tree Sparrow. Condor 67:193–209.

WEIDMANN, U. 1956. Observations and experiments on egg-laying in the Black-headed Gull (*Larus ridibundus* L.). J. Anim. Behav. 4:150–161.

WELLER, M. W., AND C. S. SPATCHER. 1965. Role of habitat in the distribution and abundance of marsh birds. Iowa Agric. Home Econ. Exp. Stn. Spec. Rep. 43.

WILLIAMS, G. C. 1966. Natural selection, the costs of reproduction, and a refinement of Lack's principle. Am. Nat. 100:687–692.

WILSON, E. O. 1971. Competitive and aggressive behaviour. Pp. 181–217, *In* J. F. Eisenberg and W. Dillon (eds.), Man and beast. Smithsonian Institution Press, Washington, D.C.

WINDSOR, D., AND S. T. EMLEN. 1975. Predator-prey interactions of adult and pre-fledgling Bank Swallows and American Kestrels. Condor 77:359–361.

YOM-TOV, Y. 1975. Synchronization of breeding and intraspecific interference in the Carrion Crow. Auk 92:778–785.

ZAR, J. H. 1974. Biostatistical analysis. Prentice Hall, Englewood Cliffs, New Jersey.

# APPENDIX I

## CLUTCH SIZE, AND HATCHING AND FLEDGING FREQUENCIES OF CLAM ISLAND HERRING GULLS

| | 1976 | | | | 1977 | | | | 1978 | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Hatched | | Fledged | | Hatched | | Fledged | | Hatched | | Fledged | |
| Clutch size[1] | No.[2] | Freq. | No. | Freq. | No. | Freq. | No. | Freq. | No. | Freq. | No. | Freq. |
| One | 0 | 1 | | | 0 | 1 | | | 0 | 13 | | |
| (N = 30) | 1 | 6 | 0 | 5 | 1 | 4 | 0 | 1 | 1 | 5 | 0 | 5 |
| | | | 1 | 1 | | | 1 | 3 | | | 1 | 0 |
| Two | 0 | 0 | | | 0 | 3 | | | 0 | 20 | | |
| (N = 125) | 1 | 7 | 0 | 4 | 1 | 8 | 0 | 0 | 1 | 9 | 0 | 5 |
| | | | 1 | 3 | | | 1 | 8 | | | 1 | 4 |
| | 2 | 17 | 0 | 9 | 2 | 28 | 0 | 10 | 2 | 33 | 0 | 9 |
| | | | 1 | 4 | | | 1 | 8 | | | 1 | 14 |
| | | | 2 | 4 | | | 2 | 10 | | | 2 | 10 |
| Three | 0 | 0 | | | 0 | 19 | | | 0 | 35 | | |
| (N = 925) | 1 | 49 | 0 | 22 | 1 | 32 | 0 | 6 | 1 | 36 | 0 | 16 |
| | | | 1 | 27 | | | 1 | 26 | | | 1 | 20 |
| | 2 | 84 | 0 | 19 | 2 | 79 | 0 | 10 | 2 | 100 | 0 | 39 |
| | | | 1 | 41 | | | 1 | 29 | | | 1 | 31 |
| | | | 2 | 24 | | | 2 | 40 | | | 2 | 30 |
| | 3 | 92 | 0 | 13 | 3 | 208 | 0 | 18 | 3 | 191 | 0 | 31 |
| | | | 1 | 33 | | | 1 | 34 | | | 1 | 60 |
| | | | 2 | 31 | | | 2 | 81 | | | 2 | 56 |
| | | | 3 | 15 | | | 3 | 75 | | | 3 | 44 |
| Number of nests | 256 | | | | 382 | | | | 442 | | | |

[1] N = number of nests with that clutch size.

[2] Number of eggs that hatched.

No. 21. **Social Organization and Behavior of the Acorn Woodpecker in Central Coastal California,** by Michael H. MacRoberts and Barbara R. MacRoberts. 1976. $7.50 ($6.00 to AOU members).

No. 22. **Maintenance Behavior and Communication in the Brown Pelican,** by Ralph W. Schreiber. 1977. Price $6.50 ($5.00 to AOU members).

No. 23. **Species Relationships in the Avian Genus *Aimophila*,** by Larry L. Wolf. 1977. Price $12.00 ($10.50 to AOU members).

No. 24. **Land Bird Communities of Grand Bahama Island: The Structure and Dynamics of an Avifauna,** by John T. Emlen. 1977. Price $9.00 ($8.00 to AOU members).

No. 25. **Systematics of Smaller Asian Night Birds Based on Voice,** by Joe T. Marshall. 1978. Price $7.00 ($6.00 to AOU members).

No. 26. **Ecology and Behavior of the Prairie Warbler *Dendroica discolor*,** by Val Nolan, Jr. 1978. Price $29.50.

No. 27. **Ecology and Evolution of Lek Mating Behavior in the Long-tailed Hermit Hummingbird,** by F. Gary Stiles and Larry L. Wolf. viii + 78 pp., 26 text figures. 1979. Price $8.50 ($7.50 to AOU members).

No. 28. **The Foraging Behavior of Mountain Bluebirds with Emphasis on Sexual Foraging Differences,** by Harry W. Power. x + 72 pp., color frontispiece, 12 text figures. 1980. Price $8.50 ($7.50 to AOU members).

No. 29. **The Molt of Scrub Jays and Blue Jays in Florida,** by G. Thomas Bancroft and Glen E. Woolfenden. 1982. Price $8.00 ($6.50 to AOU members).

No. 30. **Avian Incubation: Egg Temperature, Nest Humidity, and Behavioral Thermoregulation in a Hot Environment,** by Gilbert S. Grant. ix + 75 pp., 35 text figures. 1982. Price $9.00 ($7.00 to AOU members).

No. 31. **The Native Forest Birds of Guam,** by J. Mark Jenkins. x + 61 pp., color frontispiece, VI color plates, 24 text figures. 1983. Price $9.00 ($7.00 to AOU members).

No. 32. **The Marine Ecology of Birds in the Ross Sea, Antarctica,** by David G. Ainley, Edmund F. O'Connor, and Robert J. Boekelheide. x + 97 pp., 42 text figures. 1984. Price $9.00 ($8.00 to AOU members).

No. 33. **Sexual Selection, Lek and Arena Behavior, and Sexual Size Dimorphism in Birds,** by Robert B. Payne. viii + 52 pp., 12 text figures. 1984. Price $8.00 ($6.50 to AOU members).

No. 34. **Pattern, Mechanism, and Adaptive Significance of Territoriality in Herring Gulls (*Larus argentatus*),** by Joanna Burger. xii + 92 pp., 30 text figures. 1984. Price $9.00 ($7.00 to AOU members).

Like all other AOU publications, *Ornithological Monographs* are shipped prepaid. Make checks payable to "The American Ornithologists' Union." For the convenience of those who wish to maintain complete sets of *Ornithological Monographs* and to receive new numbers immediately upon issue, standing orders are encouraged.

Order from: **Frank R. Moore, Assistant to the Treasurer AOU, Department of Biology, University of Southern Mississippi, Southern Station Box 5018, Hattiesburg, Mississippi 39406.**

# ORNITHOLOGICAL MONOGRAPHS

No. 1. **A Distributional Study of the Birds of British Honduras,** by Stephen M. Russell. 1964. $7.00 ($5.50 to AOU members).

No. 2. **A Comparative Study of Some Social Communication Patterns in the Pelecaniformes,** by Gerard Frederick van Tets. 1965. $3.50 ($2.50 to AOU members).

No. 3. **The Birds of Kentucky,** by Robert M. Mengel. 1965. $15.00 ($12.50 to AOU members).

No. 5. **A Comparative Life-history Study of Four Species of Woodpeckers,** by Louise de Kiriline Lawrence. 1967. $6.00 ($4.50 to AOU members).

No. 6. **Adaptations for Locomotion and Feeding in the Anhinga and the Double-crested Cormorant,** by Oscar T. Owre. 1967. $6.00 ($4.50 to AOU members).

No. 7. **A Distributional Survey of the Birds of Honduras,** by Burt L. Monroe, Jr. 1968. $14.00 ($11.00 to AOU members).

No. 9. **Mating Systems, Sexual Dimorphism, and the Role of Male North American Passerine Birds in the Nesting Cycle,** by Jared Verner and Mary F. Willson. 1969. $4.00 ($3.00 to AOU members).

No. 10. **The Behavior of Spotted Antbirds,** by Edwin O. Willis. 1972. $9.00 ($7.50 to AOU members).

No. 11. **Behavior, Mimetic Songs and Song Dialects, and Relationships of the Parasitic Indigobirds (*Vidua*) of Africa,** by Robert B. Payne. 1973. $12.50 ($10.00 to AOU members).

No. 12. **Intra-island Variation in the Mascarene White-eye *Zosterops borbonica*,** by Frank B. Gill. 1973. $3.50 ($2.50 to AOU members).

No. 13. **Evolutionary Trends in the Neotropical Ovenbirds and Woodhewers,** by Alan Feduccia. 1973. $3.50 ($2.50 to AOU members).

No. 14. **A Symposium on the House Sparrow (*Passer domesticus*) and European Tree Sparrow (*P. montanus*) in North America,** by S. Charles Kendeigh. 1973. $6.00 ($4.50 to AOU members).

No. 15. **Functional Anatomy and Adaptive Evolution of the Feeding Apparatus in the Hawaiian Honeycreeper Genus *Loxops* (Drepanididae),** by Lawrence P. Richards and Walter J. Bock. 1973. $9.00 ($7.50 to AOU members).

No. 16. **The Red-tailed Tropicbird on Kure Atoll,** by Robert R. Fleet. 1974. $5.50 ($4.50 to AOU members).

No. 17. **Comparative Behavior of the American Avocet and the Black-necked Stilt (Recurvirostridae),** by Robert Bruce Hamilton. 1975. $7.50 ($6.00 to AOU members).

No. 18. **Breeding Biology and Behavior of the Oldsquaw (*Clangula hyemalis* L.),** by Robert M. Alison. 1975. $3.50 ($2.50 to AOU members).

No. 19. **Bird Populations of Aspen Forests in Western North America,** by J. A. Douglas Flack. 1976. $7.50 ($6.00 to AOU members).

No. 20. **Sexual Size Dimorphism in Hawks and Owls of North America,** by Noel F. R. Snyder and James W. Wiley. 1976. $7.00 ($6.00 to AOU members).

(*Continued on inside back cover*)