Costs and benefits to Red-breasted Mergansers nesting in tern and gull colonies.

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ABSTRACT

The costs and benefits to Red-breasted Mergansers (Mergus serrator) nesting in a Common Tern (Sterna hirundo) colony and a Herring (Larus argentatus) and Greater Black-backed Gull (L. marinus) colony were studied from 5 June to 17 August 1984 on islands off the east coast of New Brunswick. Merganser nests outside larid colonies were preyed upon significantly more than nests in the tern colony while no difference existed with nests in the gull colony. Nests in the tern colony were more likely to be abandoned probably due to inter- and intra-specific interaction including nest parasitism. Clumped nests in the tern colony were not initiated in greater synchrony than dispersed nests. The merganser-gull nesting association cannot be accounted for solely by an anti-predator hypothesis. It is postulated that the protective benefit for merganser nests in tern colonies accounts for the evolution and maintenance of the nesting association.

RESUME

Les coûts et bénéfices encourus par des Bec-Scies à Poitrine Rousse (Mergus serrator) nichant dans une colonie de Sternes Communes (Sterna hirundo) et dans une colonie de Goélands Argentés (Larus argentatus) et de Goélands à Manteau Noir (L. marinus) furent étudiés du 5 juin au 17 août 1984, sur des îles au large de la côte est du Nouveau-Brunswick. Les nids de Bec-Scies situés à l'extérieur des colonies de laridés ont subi une prédation significativement plus forte que les nids situés dans la colonie de sternes, alors qu'aucune différence ne fut observée pour les nids situés dans la colonie de goélands. Les nids situés à l'intérieur de la colonie de sternes avaient une plus grande probabilité d'être abandonnés, probablement à cause d'interactions inter- et intra-spécifiques, incluant le parasitisme des nids. La synchronisation des nids groupés à l'intérieur de la colonie de sternes n'est pas supérieure à celle des nids dispersés. L'association Bec-Scies-Goélands ne peut être complètement expliquée par une hypothèse d'anti-prédation. Il est postulé que la protection dont bénéficient les nids de Bec-Scies à l'intérieur des colonies de sternes explique l'évolution et le maintien de l'association en période de nidification.

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REGULATIONS ON THESIS PRESENTATION

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PREFACE

The objective of this thesis was to test *a priori* hypotheses concerning some possible anti-predator strategies used by breeding Red-breasted Mergansers. Hypotheses tested were that Red-breasted Mergansers nested 1) in association with Common Terns 2)in association with Herring and Greater Black-backed Gulls and 3) colonially as anti-predator strategies. I was unable to test an hypothesis that creching behavior in Red-breasted Mergansers serves an anti-predator function. Broods were very hard to follow over any length of time due to their great mobility and characteristics of the study area.

An original contribution of this thesis is that the anatid-larid nesting association was investigated in detail for an anatid species nesting with two separate larid species and alone.

A brief literature review is included to provide additional background information on the hypotheses in accordance with the *Guidelines Concerning Thesis Preparation*. The information in the literature review is intended to compliment that already present in the introduction and discussion of the thesis although there is some overlap of information.

Rodger Titman contributed information on the nesting conditions of Red-breasted Mergansers at Kouchibouguac National Park as well as suggestions about the study and editorial comments on earlier drafts of this manuscript. I formulated the hypotheses, designed the methodology to test them, collected, analyzed and wrote up the data.

This thesis is being submitted in the form of a manuscript intended for publication in the Auk. My thesis supervisor, Rodger Titman, will be a co-author of this manuscript.

LITERATURE REVIEW

European observers (Koskimies 1957, Hilden 1964, Newton and Campbell 1975) have reported a strong social attraction between some nesting anatids and larids. In central Scotland, Newton and Campbell (1975) found that Tufted Ducks (Aythya fuligula) nested at much greater densities in a Black-headed Gull (Larus ridibundus) colony than outside it. The attraction of Tufted Ducks to nest in larid colonies has been noted elsewhere (Durango 1954, Hilden 1964). In North America, a high incidence of nest association between Arctic Terns (Sterna paradisaea) and Oldsquaws (Clangula hyemalis) was found at Churchill, Manitoba (Evans 1970). Vermeer (1968) provides evidence that nesting Pintail (Anas acuta) and Lesser Scaup (Aythya affinis) strongly associate with Common Terns (Sterna hirundo). Among 6 small islands in central Alberta, nesting densities of 11 duck species were significantly higher on those islands inhabited by Common Terns compared to those islands without the terns (Vermeer 1970).

One reason for the observed nesting associations between waterfowl and larid species could be that waterfowl nests are provided protection from predators through the mobbing behavior of the larids (Evans 1970, Long 1970). The anatid-larid nesting association is poorly understood. When ducks nest in association with such larid species as Arctic Terns, Common Terns and Black-headed Gulls, reproductive success can increase due to the protection provided the duck nests by the larids (Long 1970, Bengtson 1972, Newton and Campbell 1975). Hatching success of Tufted Ducks, Mallards (Anas platyrhynchos), Gadwalls (A. strepera), Wigeon (A. americana) and Shoveler (A. clypeata) combined was higher in areas with Black-headed Gulls compared to areas without them (Newton and Campbell 1975). Long (1970) suggests that nest success of waterfowl was promoted by the presence of Common Terns. When ducks nest in association with one of the larid species which are serious predators upon eggs and/or young, such as California (Larus californicus), Greater Black-backed (L. marinus) and Herring (L. argentatus) Gulls, reproductive success can be reduced (Odin 1957, Choate 1967, Vermeer 1968, Dwernychuk and Boag 1972, Bourget 1973, Munro and Bedard 1977). On islands in Penobscot Bay Maine, Bouget (1973) found greater than two thirds of the Common Eider (Somateria mollissima) eggs and young lost to predation were attributed to Greater Black-backed and Herring Gulls nesting with the eiders. Vermeer (1968) and Dwernychuk and Boag (1972) found that ducks had high hatching success when nesting in association with California and Ring-billed Gulls (L. delawarensis) but fledging success declined to zero due to predation by the gulls.

Beyond the benefit of two or more species nesting together, colonial nesting has certain anti-predator benefits of its own. In colonially nesting species, reproductive synchrony could be increased through social stimulation. Eggs and young would thus be produced over a shorter period of time. This predator swamping effect may reduce total predation as was first suggested by Darling (1938) and supported by Patterson (1965) working on the Black-headed Gull. Colonial nesting may reduce the risk for an individual nest hidden in the colony (Hamilton 1971). Assuming that Hamilton's selfish herd theory applies, peripheral nests in colonies should be preyed upon in greater proportion than more centrally located nests as was found for nesting colonies of Black-headed Gulls (Patterson 1965, Sandwich Terns (Sterna sandvicensis, Fuchs 1977, Veen 1977) and Bank Swallows (Riparia riparia, Hoogland and Sherman 1976).

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INTRODUCTION

Two or more bird species may nest together due to similar habitat preferences, food information sharing or predator avoidance (Erwin 1979). Several waterfowl species nest in association with larids in Europe (Koskimies 1957, Hilden 1964, Newton and Campbell 1975) and North America (Vermeer 1968,1970, Evans 1970, Long 1970, Dwernychuk and Boag 1972). Hilden (1964) found a positive correlation between the occurrence of nesting Red-breasted Mergansers (*Mergus serrator*) and the density of nesting larids.

Nests of one bird species may be provided protection when they are associated with those of a more aggressive protector species which actively defends its own nest (Clark and Robertson 1979, Wiklund 1979, Gotmark and Anderson 1980, Slagsvold 1980, Dyrcz *et al*. 1981, Ericksson and Gotmark 1982). For example, waterfowl nests may be provided protection when they are associated with nests of aggressive larid species (Koskimies 1957, Evans 1970). Incubating females could also use the warning calls of the larids as an early warning to cover their nests and leave before the arrival of a predator. This has been reported for grebes nesting with larids (Nuechterlein 1981, Burger 1984).

The protective benefit of the anatid-larid nesting association has been documented in anecdotal fashion (Vermeer 1968, Evans 1970, Dwernychuk and Boag 1972) and a few authors have provided quantitative analysis (Olsson 1951 cited by Bourget 1973, Bengston 1972, Newton and Campbell 1975).

Costs associated with mixed species nesting associations may cancel (Kruuk 1964) or outweigh the protective benefits (Vermeer 1968, Dwernychuk and Boag 1972). Kruuk (1964) reported that costs are involved when the protector species itself is a predator upon eggs. From their studies, Vermeer (1968) and Dwernychuk and Boag (1972) believed that costs resulting from duckling mortality by gulls nesting with ducks exceeded the benefits of nest protection.

In colonially nesting species, increased reproductive synchrony could produce eggs and young over a shorter period of time. A "predator swamping" effect would result and may reduce overall predation (Darling 1938). Colonial nesting may also reduce the risk for an individual nest hidden in the colony (Hamilton 1971).

Hypotheses formulated were that Red-breasted Mergansers nested 1) in association with Common Terns (Sterna hirundo), 2) in association with Herring (Larus argentatus) and Greater Black-backed (L. marinus) Gulls and 3) colonially as anti-predator strategies. Predictions arising from the first two hypotheses were that a greater proportion of nests preyed upon would be outside the larid colonies and that larids would actively mob and exclude potential predators from their colonies. In relation to the third hypothesis, I predicted that clumped nests would be initiated in greater synchrony than more dispersed nests and that peripheral nests of colonially nesting mergansers should have the highest predation rate.

STUDY AREA AND METHODS

The study was conducted in Kouchibouguac National Park, on the east coast of New Brunswick, Canada. Red-breasted Mergansers nested throughout a colony of 12,000 Common Tern pairs on Tern Island (46^{o} 47' N, 64^{o} 52' W), on the periphery of a Herring and Greater Black-backed Gull colony of approximately 130 and 5 pairs, respectively, and solitarily away from larid colonies on Dune Island (46^{o} 45' N, 64^{o} 47'W) (Fig. 1). Nests in the tern colony, gull colony and solitary sites were compared to determine the effect that larids had on nesting. Comparisons were made between the densely concentrated nests in the tern colony (11.6 nests/ha), with the more dispersed nests in the gull colony, and solitary nests on Dune Island (0.35 nests/ha) to determine the effect of clumped versus dispersed nesting on nesting success.

Tern and Dune Islands are barrier islands composed of sand and stabilized by Marram Grass (*Ammophila breviligulata*, McCann *et al.* 1973, Greenwood and Davidson-Arnott 1977). Tern Island consisted of 3 areas separated at high tide by water. Merganser nests were quite often located in Marram Grass on elevated areas. Potential nest predators on the study area included Crows (*Corvus brachyrhynchos*), Ravens (*Corvus corax*), and Herring and Greater Black-backed Gulls.

Nest searching and monitoring was conducted from 5 June to 17 August, 1984. Each area was visited every 7-9 days between 0900 and 1600 hours. Nest visits did not take place on rainy days and were done at the same time of the day in each area. Nests were located while walking by looking in the grass so that all parts of the ground were covered systematically. When a nest was located it was marked with a green lathe placed 4m north of the nest bowl. The lathes were usually shorter than the surrounding vegetation in order to minimize the attraction of avian predators (Picozzi 1975). The approximate position of the nest was recorded on a 1:2,000 scale aerial photograph. Besides noting the number of eggs and whether eggs were warm or cold, a plastic field candler (Young in prep.) modified from Sobkowiak and Bird (1984) was used to determine the stage of embryo development of 3-7 eggs from each nest. More eggs were candled from a nest where development stages varied. The above data were collected when the nest was first found and on subsequent visits every 7-9 days until the nest either hatched or was considered unsuccessful. All eggs remaining in a nest that hatched or failed were candled. Unknown dates of clutch initiation were determined by back dating. Embryo mortality in the egg was determined by candling 3-7 eggs every visit over the life of the nest. A "new egg" was any egg added to the clutch when the other eggs were at least 6 days developed in order to insure incubation had begun. An "unhatched but developed egg" was alive but not developed enough to hatch when the hen and brood left the nest.

In order to observe if terns and gulls were mobbing potential avian predators, 26 and 4 total hours of observation were done on the Tern and Dune Islands, respectively, from 6 June to 17 July from 0800 to 2130. Observation periods varied from 1 1/2 to 3 hours. A 3 meter high observation tower was constructed on 5 June on Tern Island while an elevated hill was used on Dune Island. A 20-45 power zoom telescope and 8 power binoculars facilitated observation which were recorded on tape.

Reproductive synchrony of Tern Island and Dune Island nests were compared by examining the skewness, variance and kurtosis of the distributions of nest initiation dates for the 2 islands. The Chi-square test (2x2 contingency table) was used to compare the response of incubating merganser females to the investigator's presence for the tern colony, gull colony and solitary nests (Daniel 1978). The Chi-square test was also used to compare the proportions of different egg fates from Tern Island with those from Dune Island. The Fisher exact test was chosen to compare the proportion of the different fates for nests from the tern colony, gull colony and solitary sites (Daniel 1978) because of small expected frequencies in the 2x2 contingency table. A 0.05 level of significance was used for all tests.

To determine whether mergansers were using the alarm calls of terns and gulls as an early warning for their own escape (Nuechterlein 1981, Burger 1984) the frequency of flushing a female from her nest was compared to the number of times she had already gone and/or had already covered up her nest in response to observer visits to the nests. Only visits during incubation were used because females were rarely at the nest during the laying period and only visits when eggs were warm are included to prevent including a female as having gone in response to larid calls when she had left the nest before the visit.

In an unsuccessful attempt to study creching behavior in Red-breasted Mergansers, females were caught during the last 1-4 days of incubation with either a hand held net or an automatic nest trap (Weller 1957). Patagial tags were applied and enabled the recognition of females during the brood rearing period. Unfortunately it appeared that a total of 31 females abandoned their nests due to this process. These nests were thus considered successful in data analysis (see Appendix). This is a reasonable assumption since the nests had survived most of the nesting period and were within 1-4 days of hatching. No nest losses occurred during this time period for any of the other nests (although one nest was preyed upon 6 days before hatch). In fact, no other nest losses occurred within 2 weeks of hatching. Abandonment would be unlikely during this period due to the female's strong attachment to the nest. Since the predation rate (1/160) was very low on nests on the Tern Island it is unlikely that a Tern Island nest would have been lost to predation at this time. There was a greater possiblity that loss might have occurred in the 4 Dune Island nests which were abandoned due to tagging because the predation rate (5/22) was much higher there. Although this is still unlikely given that 4 nests were exposed to predation for only 3-4 days each out of a 41 day nesting period.

RESULTS

Nest fates

The proportions of successful, abandoned and preyed upon nests in the tern colony, gull colony and solitary sites are shown in Figure 2. A significantly (p=0.00068) greater proportion of solitary nests was preyed upon than tern colony nests. No significant difference was found in the proportion of preyed upon nests from the gull colony compared with the tern colony (p=0.115) or solitary nests (p=0.249). A significantly (p=0.00000011) greater proportion of nests was abandoned from tern colony nests compared to the gull colony while there were no significant differences in the proportion of abandoned nests in the tern colony and solitary nests (p=0.106), gull colony and solitary nests (p=0.104) or the tern colony compared with the gull colony and solitary nests combined (p=0.059). No significant differences existed between the proportion of successful nests from the gull colony compared to the tern colony (p=0.34), solitary and tern colony nests (p=0.141) or solitary and gull colony nests (p=0.156).

Abandonment accounted for 89.5% (51/57) of total nest mortality, while predation comprised only 10.5% (6/57) of total nest mortality. Thirty-eight and 13 nests were abandoned during laying and incubation, respectively. Nest loss, due mainly to abandonment was usually greatest during 4 day periods when the percent of nests initiated was highest (Fig. 3).

All 6 events of nest predation, most likely by Crows and/or Ravens, occurred between 17 June and 29 June. Nests that were preyed upon had no eggs remaining in them and about half of the nest bowl torn out.

According to Rearden (1951) these are signs of crow predation. Crows often take the eggs away and eat them in another place (F. Gotmark, pers. comm.). Herring and Greater Black-backed Gulls, the other potential nest predators on the study area, tend to eat them on the spot (Tinbergen 1953, Bourget 1973), but this was not observed.

Mobbing behavior

During 26 hours of observation on the Tern Islands 7 events of tern flocks ie. greater than 40 individuals, mobbing a single Crow were recorded. Terns were also seen mobbing a male Marsh Hawk (*Circus cyaneus*), an Osprey (*Pandion haliaetus*) and a Short-eared Owl (*Asio flammeus*). While nest searching, 2 more events of terns mobbing a single Crow were observed, 4 events of terns mobbing a Short-eared Owl and 1 mobbing event of a Barred Owl (*Strix varia*) were observed. Red-breasted Merganser females were also mobbed by tern flocks on 8 occasions while coming to or leaving a nest. On 3 occasions during nest initiation, females were forced off the vegetated area of the island and onto the sand by mobbing terns. During 1 of these events the female flew around the island 3 times and landed back where she had taken off. Female mergansers were often mobbed by terns after being released from tagging.

During 4 hours of observation on the Dune, 2 events of a Greater Black-backed and 1 of a Herring Gull diving at a single Crow were observed. A Herring Gull was observed diving at and chasing a single Crow off the Dune.

Female response

The number of times a female had already left the nest out of 491 visits during incubation depended on whether the nest was located in the tern colony, the gull colony or a solitary site (Table 1). The proportion of females that had already left the nest was significantly (X^2=5.48,$0.025<p<0.01$) greater for nests within the tern colony than for solitary nests. Gull colony and solitary nest (X^2=1.91,$p>0.10$) and tern colony and gull colony comparisons (X^2=1.04,$p>0.10$) were not significantly different.

Nest initiation dates

Comparison of the distribution of nest initiation dates from Tern Island with Dune Island revealed that the former nests were not initiated in greater synchrony than the latter nests. The variance of Tern Island nests initiation dates (var.=163) was greater than Dune Island initiation dates (var.=90). The distribution of Dune Island initiation dates was slighlty more peaked (kurtosis = 2.36) than the Tern Island distribution (kurtosis=1.93), although both were relatively flat. Mean date of nest initiation was 10-11 June for Tern Island and 7-8 June for Dune Island.

Intra-specific nest parasitism

It was difficult to determine the extent of nest parasitism and the degree to which it affected nesting and hatching success. Nest parasitism was more frequent in the densely concentrated Tern Island nests than in the more dispersed Dune Island nests. Tern Island nests had an average clutch size of 11.4 for 125 incubated nests, 37 of which had greater than 12 eggs. A total of 34 new eggs were introduced into nests during incubation and there were 8 instances of a laying rate greater than 1 egg per day. The Dune Island nests had an average clutch size of 8.1 for 19 incubated clutches with none having greater than 12 eggs, no nests receiving new eggs and no instances of a laying rate more than 1 egg per day.

The effect of parasitism during the laying period was especially hard to determine. One nest with a laying rate of greater than 1 egg per day was abandoned prior to incubation, likely due to parasitic intrusions. Parasitism may also have caused some desertions during incubation. Of the 12 Tern Island nests deserted during incubation, 3 had no change in egg numbers but 9 had a total of 11 new eggs added and 29 eggs disappeared. In 3 of the nests receiving new eggs, 1 or more new eggs were found in the abandoned nests.

Incubated Tern Island clutches had a significantly (X^2=5.75,0.025<p<0.01) greater proportion of eggs that died during embryo development (84/1419, 5.9%) than did the Dune Island clutches (2/154, 1.3%). The number of incubated Tern Island clutches with 14 or more eggs with at least 1 egg mortality was significantly (X^2=7.79,0.01<p<0.005) greater than clutches having less than 14 eggs. The hatching success of Tern Island nests (729/911, 80%) was not lower than that of Dune Island nests (66/84,76%). Unhatched but developed eggs made up the greatest proportion of eggs that failed to hatch on Tern Island (13%) and Dune Island (15%).

DISCUSSION

Nest protection

The island nesting habit of waterfowl provides nest protection from mammalian predators (Hammond and Mann 1956, Duebbert 1966). Anatids nesting in association with larids on islands may be provided additional protection from avian predators by the mobbing behavior of the larids (Evans 1970). Koskimies (1957) suggested how such a nesting association could evolve. Waterfowl young imprint on the larids and the young from successful nests in larid colonies return to the breeding area using the larids as a cue for recognition of nesting habitat.

Few studies have provided quantitative evidence of the protective benefit. Olsson (1951, cited by Bourget 1973) reported that Common Eiders (Somateria mollissima) nesting on islands with Herring and Greater Black-backed Gulls had a lower percentage of nests preyed upon by Hooded Crows (Corvus corone cornix) than those nesting on islands without gulls. Bengtson (1972) found that hatching success of Greater Scaup (Aythya marila) and Tufted Duck (A. fuligula) nests was higher in Black-headed Gull (Larus ridibundus) and Arctic Tern (Sterna paradisaea) colonies than in nests not associated with the larids. Finally, Newton and Campbell (1975) recorded that nesting Tufted Ducks had higher hatching success and densities within than outside a Black-headed Gull colony.

In this study, the highest proportion of nests preyed upon were solitary nests, next lowest were nests in the gull colony and then nests in the tern colony, indicating that merganser nests were better protected from avian predators when located in tern and gull colonies.

Observations of terns and gulls mobbing and effectively repelling potential nest predators further showed that terns and gulls do act indirectly as protectors for merganser nests in their colonies. The aggressive, densely concentrated terns appear to have provided better protection for merganser nests in their colony than the more widely spaced nesting gulls. Terns had an effective communal mobbing system, often mobbing avian predators in great numbers and chasing the predator quite a distance from the colony. Gull defensive efforts were by solitary individuals, most often confined to the individual's territory. Mergansers nested throughout the tern colony but only on the periphery of the gull colony where fewer gulls were available to repel predators. Herring and Greater Black-backed Gulls are known to prey heavily on waterfowl nests in some areas (Choate 1967, Bourget 1973). The gulls were not serious predators on merganser nests but kept out those that were. Tern and gull nests may act as a buffer for merganser nests during avian predation. The presence of many exposed tern and gull eggs could be favored by avian predators over the well concealed merganser eggs, especially when the predator's search time is limited by mobbing harassment from terns and gulls.

The proportion of successful nests was slightly higher in the gull colony than in the tern colony but the difference was not significant. Based on nest densities, Tern Island provided the optimal nesting habitat (Bengtson 1972) and should have produced the greatest proportion of offspring. The gull colony nests were at much lower density. Nesting success in the gull colony did not account for duckling mortality due to predation by the gulls themselves. Vermeer (1968) and Dwernychuk and

Boag (1972) presented evidence for a seemingly paradoxical situation of ducks nesting with gulls (*Larus californicus* and *L. delawarensis*) where the costs of duckling mortality exceeded the benefits of nest protection. Dwernychuk and Boag (1972) suggested that this nesting association began when ducks initially nested with non-predatory Common Terns and then the islands were colonized by predatory gulls. The association is maintained by the annual recruitment of yearling and adult females to the traditional nesting islands and these returning females do not discriminate between terns and gulls.

In this study, survival of ducklings from merganser nests in the gull colony relative to other nests was difficult to determine due to the large temporal and spatial separation of hatching nests, the great brood mobility and creching behavior. Any difference in mortality of ducklings from nests in the gull colony with other nests would be apparent only immediately after the ducklings left the islands. During this critical period, duckling survival from nests in the gull colony may have been reduced due to the close proximity of numerous breeding and non-breeding gulls and their young. Herring and Greater Black-backed Gulls are notorious predators of waterfowl young (Bourget 1973, Munro and Bedard 1977, Braun *et al.* 1980). This may also help to explain why nests in the gull colony were more successful than those in the tern colony and yet had a much lower density. After leaving the islands, broods moved quickly to the mainland shore, where all broods would be equally likely to encounter a predatory gull.

Based on nest densities, Red-breasted Mergansers seemed to prefer nesting with gulls to nesting solitarily. There was suitable unused nesting habitat adjacent to the gull colony. The Red- breasted Merganser-gull nesting association could be partially maintained by the return of females to the gull colony if benefits of nest protection were greater than the costs of duckling mortality. The nesting of mergansers with gulls cannot be accounted for solely by an anti-predator hypothesis because there was no significant difference in the number of nests preyed upon in the gull colony and solitary nests.

Early warning system

A bird species may use the warning calls of a nesting associate to avoid predators. Grebes nesting in association with larids respond to the warning calls of the larids by covering up their nest and leaving the nest before a predator arrives (Nuechterlein 1981, Burger 1984). Palmer (1976) stated that some Red-breasted Mergansers nesting in gulleries and terneries react to their warning calls. During some nest visits in this study, incubating female mergansers reacted to the warning calls of terns and gulls in response to the approaching investigator by leaving their nests early. However, even for nests in the tern colony where the response of females was greatest, just over half of hens not responding to the warning calls of the terns were flushed from a short distance. Hence, Red-breasted Mergansers and grebes do not seem to respond in the same way to the warning calls of larids, perhaps due to a difference in their predators. Grebes faced with mammalian predators may need to escape beforehand to avoid predation. Red-breasted Mergansers, receiving most predation from egg predators such as Crows and Ravens may be better served by remaining to defend the nest against the predator. A female nesting solitarily apparently tried unsuccessfully to defend her nest; the remains of numerous merganser feathers and a corvid feather were found beside a nest that had been preyed upon. A Mallard (Anas platyrhynchos) hen has been observed defending her nest against Crows (Hammond and Mann 1956). Milne (1974) suggests that the Common Eider's habit of remaining at the nest during the nesting period may have developed in order to protect the eggs from crows and gulls. Similar behavior may function to protect eggs of the Greater Snow Goose (Chen hyperborea, Lemieux 1959).

Colonial nesting

In colonial nesting associations, breeding may be more synchronous due to intra-specific social stimulation resulting in production of eggs and young over a shorter period of time. This predator swamping effect may reduce overall predation (Darling 1938). Examination of the nest initiation dates from the densely concentrated nesting mergansers on Tern Island with the more dispersed nesting mergansers on Dune Island showed that the colony nests were not initiated in any greater synchrony than the solitary nests. Nest losses were usually greatest during periods when the greatest percentage of nests was initiated (Fig. 4). Thus colonial nesting in this species probably does not function to produce a predator swamping effect and thus reduce overall predation. Colonial nesting may reduce the risk for a nest hidden in the colony (Hamilton 1971). If Hamilton's theory of the selfish herd applies, the predation rate should be highest on peripheral nests (Patterson 1965, Fuchs 1977, Veen 1977). This prediction could not be tested due to the low predation rate on clumped Tern Island nests. Interestingly, both the 1 nest and the 1 incubating hen preyed upon were located on the very periphery of the Tern Island. The nest distribution pattern on Tern Island seemed to reflect the availability of suitable nesting cover rather than selection for nests to be hidden in the colony.

Abandonment

Abandonment was the greatest single cause of nest loss in this study. McLaughlin and Grice (1952) documented that the rate of nest desertion in Wood Ducks (Aix sponsa) was density dependent. Bengtson (1972) reported that hatching success in Barrows Goldeneye (Bucephala islandica) was significantly lower at high nesting densities due to a greater proportion of deserted nests. Duebbert et al. (1983) and Lokemoen et al. (1984) found an above average abandonment rate was the major cause of egg failure of densely nesting Mallards and Gadwalls (Anas strepera) on an island in North Dakota. They suggested that the high nesting densities of ducks may have increased intra-specific aggression and resulted in a higher rate of nest desertion. Lokemoen et al. 1984 believed that thick nesting cover was important to nesting hens because it screened hens on nests from harassment by other conspecific nesting hens. Red-breasted Mergansers preferred to nest in thick vegetation which may have acted as a screen for nesting mergansers, as well as providing shelter for female mergansers being mobbed by terns. Alternatively, movement in thickly vegetated areas was restricted to well defined pathways and tunnels where intra-specific conflicts may have been intensified, thus increasing the rate of abandonment. Nests in the tern colony had approximately 3 times the proportion of abandoned nests compared with those in the gull colony and twice that in solitary nests. Nests in the tern colony were also by far the most densely concentrated of the 3 nesting conditions, leading to increased frequency of intra-specific conflicts and thus the frequency of abandonment. Vigorous mobbing attacks by terns upon nesting female mergansers may have caused some abandonments. Nest parasitism may also have caused some abandonments, but this will be discussed shortly.

Although merganser nests on the Tern Island received the greatest amount of protection from avian predators, inter- and intra-specific competition on the island may have increased the number of females abandoning nesting attempts. The nesting success of an individual female in the tern colony may be higher than indicated by the overall rate of abandonment due to successful renesting attempts. The second phase of nest initiation (Fig. 4) may represent renesting attempts or be partly due to delayed nesting to reduce intraspecific strife as was suggested by McKinney (1965) for densely nesting Mallards.

Intra-specific nest parasitism

The degree of intraspecific parasitism appears to be density dependent in waterfowl (Weller 1959, Hilden 1964). Intra-specific parasitism by the Red-breasted Merganser is fairly common (see Hilden 1964). Parasitism was more frequent among the densely concentrated Tern Island nests than in the more dispersed Dune Island nests. Weller (1959) pointed out that one response of the nesting host female to continuous parasitic intrusion is desertion and that this is most likely to occur early in the laying stage when the females' attachment to the nest site is weakest. Jenkins et al. (1975) found that nest losses due to desertion in densely nesting Shelducks (Tadorna tadorna) were high and attributed some of these desertions to intra-specific parasitism.

Pienkowski and Evans (1982) reported that at least one third of the densely nesting Shelduck clutches studied were the product of more than 1 female. They reported that desertion in these multiple clutches was significantly greater than in those laid by a single female. Detecting the effects of parasitism on nest abandonment is difficult. One nest with a laying rate of greater than 1 egg per day may have been abandoned during laying as a result of parasitism. Most of the Tern Island nests abandoned during incubation had new eggs introduced or eggs lost from the clutch. Some of these females very likely deserted in response to parasitic intrusions.

Nest parasitism can reduce hatching success through embryo mortality due to eggs broken during normal nest movements on a large nest or inefficient incubation of a large clutch leading to chilling of some eggs (Weller 1959). Embryo mortality was higher on Tern Island than that on Dune Island and was more frequent in clutches containing greater than 14 eggs. A higher incidence of embryo mortality on the Tern Island and in larger clutches was probably the result of intra-specific nest parasitism. Hatching success of successful Tern Island clutches was not greatly affected by embryo mortality because it comprised a small percentage of unhatched eggs.

CONCLUSION

Red-breasted Mergansers derived a protective benefit by nesting in a Common Tern colony compared to nesting solitarily. Merganser nests in a Herring and Greater Black-backed Gull colony were provided a level of protection between that provided by the tern colony and solitary nests. The merganser-gull nesting association cannot be accounted for by an anti-predator hypothesis alone. Nests in the tern colony were more likely to be abandoned probably due to the increased interaction between mergansers and terns at high nesting densities. Nest parasitism was greater in the tern colony and very likely caused some nest desertions and reduced hatching success. Nesting synchrony was not increased by clumped nesting in the tern colony and therefore probably does not function to produce a predator swamping effect and reduce overall predation. Clumped nesting seemed to reflect the availabilty of suitable nest sites in preferred nesting habitat of the tern colony rather than selection for nests to be hidden in the aggregation of merganser nests. Nests in the gull colony may have experienced a higher duckling mortality as a result of predation by the gulls themselves. The protective benefit of the merganser-tern nesting association exceeded the observed costs. The protective benefit for merganser nests in a tern colony appears to account for the evolution and maintenance of the nesting association. Red-breasted Mergansers preferred to nest in the tern colony, as their nest density there was very high. Bengtson (1970) stated that the highest densities are found in the optimal habitats. If this is true, Tern Island provided optimal nesting habitat for Red-breasted Mergansers while the gull colony and solitary nesting conditions on Dune Island are suboptimal.

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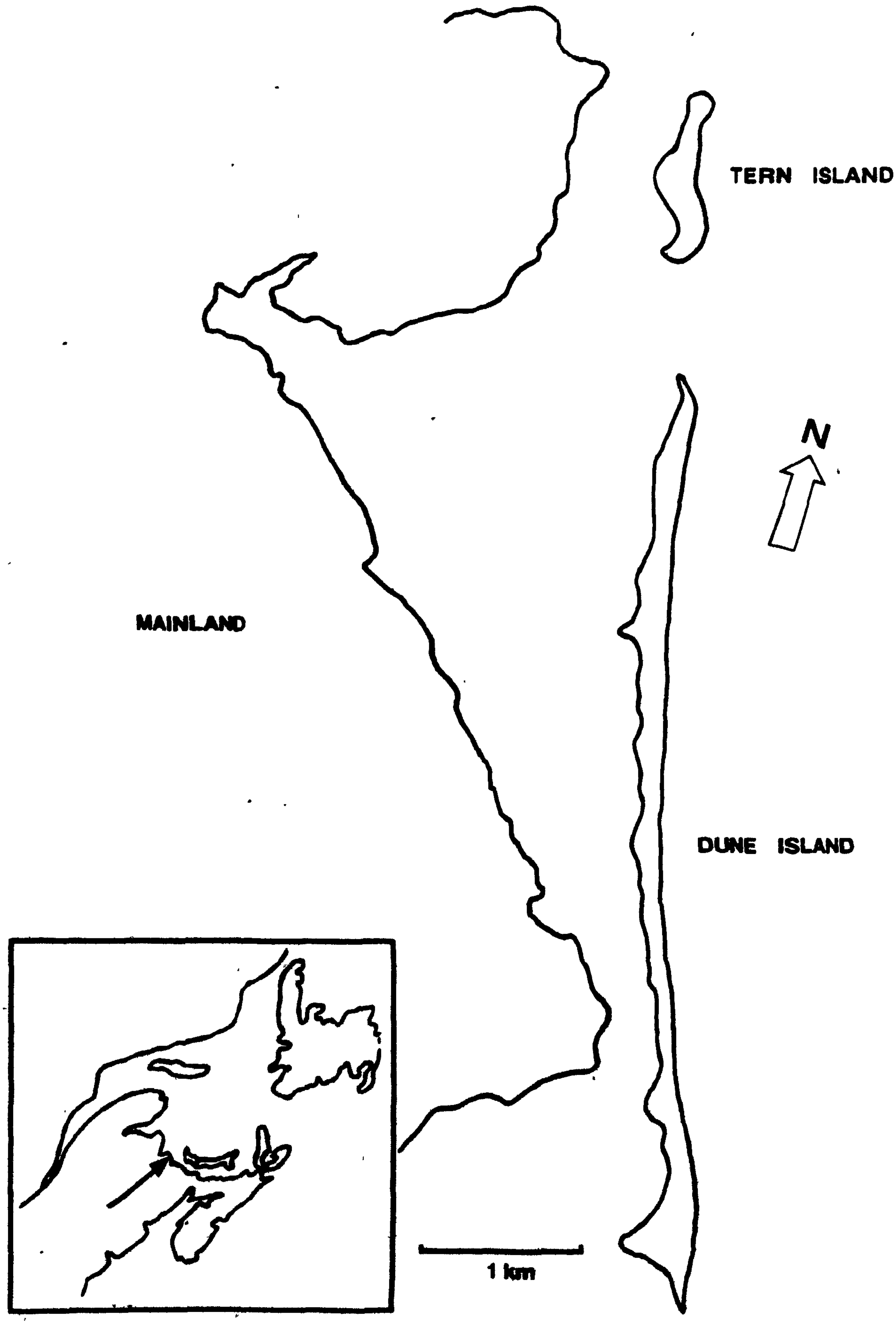
Table 1. Number of times an incubating female had already left the nest or flushed during visits of tern colony, gull colony and solitary nests of Red-breasted Mergansers.

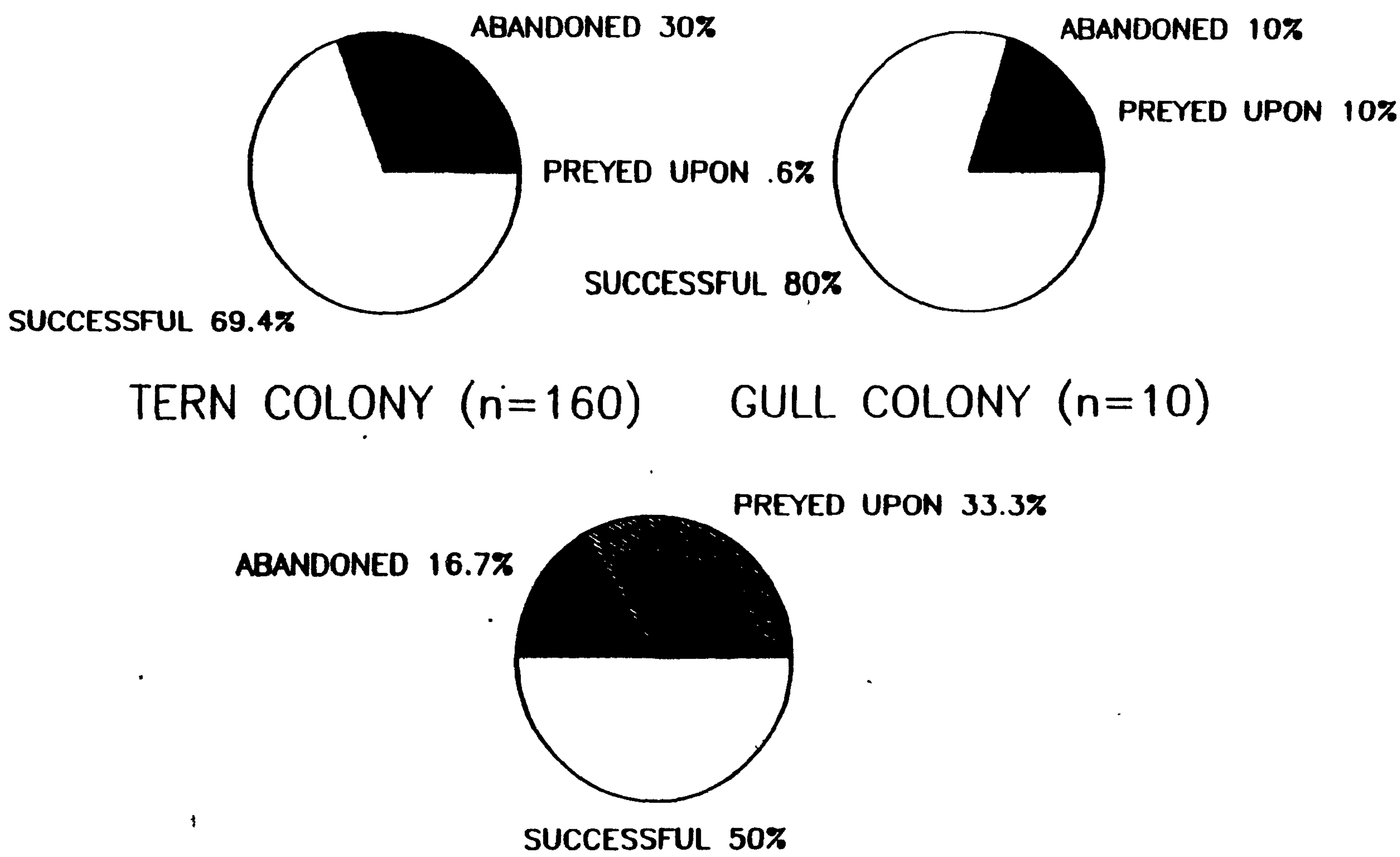
	Tern Colony	Gull Colony	Solitary
female already left nest	202	14	4
female flushed from nest	232	23	16
TOTAL	434	37	20

Figure 1. Map of the study area in Kouchibouguac National Park, New Brunswick.


TERN ISLAND
N
MAINLAND
DUNE ISLAND
1 km

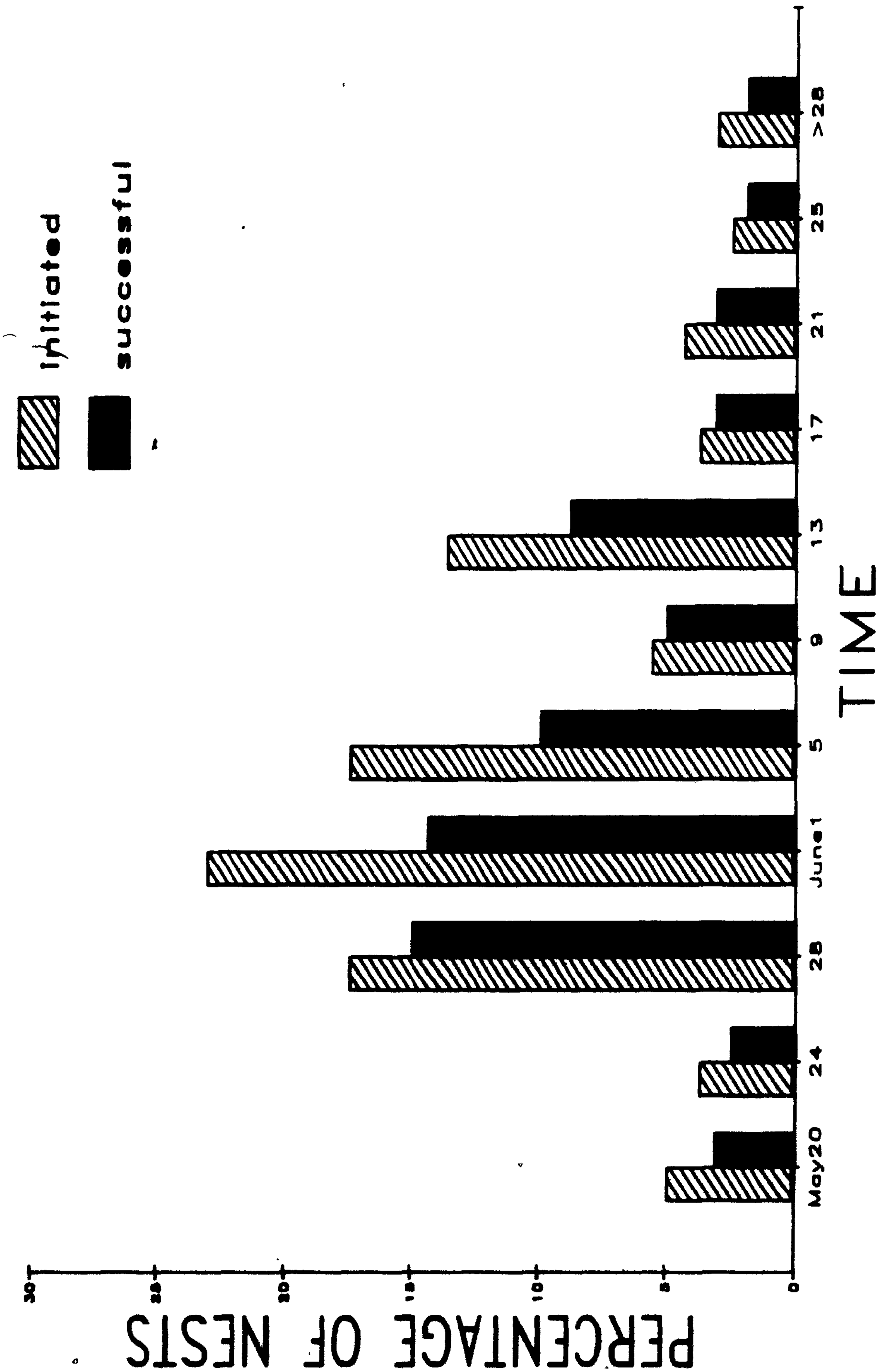
10

Figure 2. Percentage of preyed upon, successful and abandoned nests for tern colony, gull colony and solitary nests.



SOLITARY (n=12)

Figure 3. Percentage of total Tern Island nests initiated and subsequently successful during the nesting season.


initiated
successful
PERCENTAGE OF NESTS
0
5
10
15
20
25
30
TIME
May20
24
28
June1
5
9
13
17
21
25
>28

APPENDIX

If the 31 nests that were abandoned following the marking of hens are excluded from data analysis, the proportions of nest fates from the 3 sites would be biased. These nests were very likely to have been successful because they were abandoned 1-2 days prior to hatching. The exclusion of the 31 nests would result in unrealistically low percentages of successful nests and unrealistically high percentages of preyed upon and abandoned nests from 3 sites. For comparison, the percentage of preyed upon, successful and abandoned nests from tern colony, gull colony and solitary sites are considered (Table 2), including and excluding the late abandoned nests.

Table 2. Nest fate percentages for the 3 study sites if the 31 nests abandoned following the marking of hens just prior to hatching are included (I) and excluded (E).

	Tern colony		Gull colony		Solitary	
	I	E	I	E	I	E
successful	69.4	63.0	80.0	75.0	50.0	40.0
preyed upon	0.6	0.8	10.0	12.5	33.3	40.0
abandoned	30.0	36.2	10.0	12.5	16.7	20.0
TOTALS	100.0	100.0	100.0	100.0	100.0	100.0