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Breeding success, predation and local dynamics of colonial Common Gulls *Larus canus*

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I censused colonies (15 sites) of Common Gulls in the northern Baltic, Hanko, in 1978–91. The total population in the area declined from 240 to 159 pairs. Reproductive success was low in many colonies for several years during the study period. The mean rate of fledged young per pair varied from 0.17 to 1.09 (1982–91). The reproductive failures were mainly due to predation by Mink, and Herring Gull. When Minks appeared to decline in numbers, production rose significantly. With respect to predation risk, colony sites varied very much. During 8 years (1982–89) some colonies were never subject to major disturbances, while some colonies were severely disturbed in most years. The colonies disturbed most declined rapidly, while colonies successful in most years gained pairs, inspite of a general decreasing trend. I suggest that this was due to relocation of breeders between colonies in the area. The rate of decline was also tied to the severity of the disturbance, when adults are threatened, rapid desertion of a colony site may follow, when chicks are taken, the desertion process is slower. This is likely due to the Common Gull being adapted to stable breeding environments favouring site tencity. I suggest that the colonies formed an interactive metapopulation-like system, which is significant for understanding how archipelago birds in the Baltic should best be protected.

1. Introduction

Coloniality in gulls (Larus) is often viewed upon as a powerful strategy against predation (Kruuk 1964, Veen 1977, Götmark & Andersson 1984, Burger & Gochfeld 1990). In some species, breeding colonies are stable (Southern 1977), while some species change sites frequently (Burger 1974, McNicholl 1975).

The advantages of site fidelity versus breeding dispersal in colonial birds are not fully understood (Wittenberger & Hunt 1985). For species nesting in short-lived habitats (i.e. marshes, sand bars), colony sites may or may not be available in any one year and such species may frequently change sites (McNicholl 1975). The site fidelity of species breeding in more stable habitats (i.e. cliffs, rocky islands), may be primarily affected by factors reducing adult potential survival or reproductive success (Southern 1977).

Predation in colonies may operate on eggs or young, lowering reproductive output to some extent, which is typical for non-specialized avian predatiors. Mammalian predators, or specialized avian predators may wipe out the entire pool of growing chicks (Veen 1977, Burger & Gochfeld 1990, Hario 1994). The first type is generally the most prevalent. On another level predation operates on adult birds, ending all reproductive efforts.

For long lived species one or a few lost clutches may not be a crucial loss (Coulson & Thomas 1985), but unsuccessful breeding has been shown to induce site changes in colonial Caspian Terns (*Sterna caspia*, Cuthbert 1988). Predation on adults has been shown to cause temporary abandonment of colonies in Black Skimmers (*Rynchops niger*, Burger & Gochfeld 1990).

Few studies have dealt with colony dynamics in relation to different types of predation (Burger 1984, Burger & Gochfeld 1990). In this study I will deal with colony dynamics of a population of Common Gulls (*Larus canus*) breeding at 15 sites in close proximity to each other. I will (a) identify the types of predation ocurring in these colonies, (b) establish whether sites differed in quality, and (c) discuss some behavioural and numerical responses of the gulls in the colonies over several years. Of special interest here is whether;

(a) major reproductive failures occur, and whether this leads to colony abandonment
(b) predation on adults leads to more rapid responses in numbers at a site than predation on offspring
(c) colonies interact

Anwers to these questions helps in understanding colony dynamics, which apart from having a value *per se*, also is of considerable value to conservation planning involving colonial birds.

2. Study area and methods

The study population of Common Gulls breeds on islands off the Hanko Peninsula, the most southwestern tip of Finland. The total area (about 200 km^2) holds some 170 islands. In all, 15 sites (1 to 55 pairs) have been monitored since 1978. The Common Gull population decreased during 1978–91 from 240 to 159 pairs, which corresponds to a

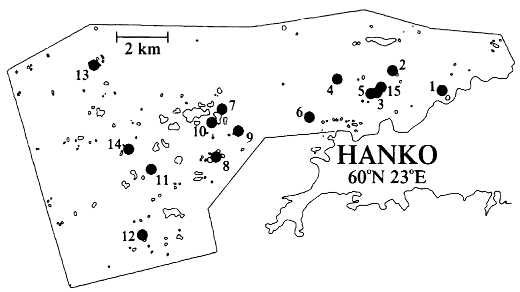

Fig. 1. Study area and studied colony sites. The numbers and names of colonies are the same as in Table 3.

rate of a 3.5 % annual decrease. The trend in numbers is significant ($r_s = -0.93$, $P < 0.01$). Thus, when discussing the changes in a colony, the expected trend during the period is stable or slightly declining. The number of occupied islands has remained the same throughout the period.

This study covers detailed colony histories during eight years (1982–89) covering annually all colonies exceeding 5 pairs (13 sites during those 8 yrs). Yearly, a few pairs (about 10) breed solitarily at sites were no colonies have existed during the period, so most Common Gulls in the area are colonial. The mean distance between nearest colony sites were 1.0 ± 0.7 km for these 13 sites (range 0.05 to 2.5 km).

The islands occupied by breeding Common Gulls off Hanko range in size from 0.2 ha to 3.8 ha. The small nesting islands and skerries are open rocky sites with small patches of low vegetation, while the largest islands (Andalsskär (no. 8), Bandskär (no. 9), Måslandet (no. 11), and Stenskär (no. 12 in Table 3, Fig. 1) have extensive vegetation of junipers (*Juniperus communis*). Judged by the type of island currently used by the gulls, there are at least 50 suitable, but unused islands in the general area.

Each year the exact number of active nests were counted during 2–3 successive counts timed to coincide with the latter half of incubation. Nests were usually marked individually. The colonies were then surveyed throughout the rearing period. The final estimate of fledgling production per pair is based on 1–3 successive counts timed 1–3 weeks after the median chick has fledged. Since all colonies are synchronous and fairly small, fledglings are easy to count accurately at the proper time.

I measured reproductive success on two levels; (1) very accurately using several counts for a number of colonies (covering all major colonies) each year (5–12 sites) to give an estimate of the average production, and (b) on a coarser level usually based on only one count of young in all colonies. The coarser level suffices for an estimate of whether serious failure occurred (defined here as a production < 0.20 fledglings per pair, including zero success). A total failure (zero years in Table 3) is easy to document, since adult birds that have lost their offspring will leave the colony about 2 weeks before normal (own data). Thus, I was not interested in occasional predation and thinning, but focused on drastic depressions in reproductive success. Judging from data on

Lesser Black-backed Gulls (*L. fuscus*) a production of less than 0.2 fledglings per pair is clearly below what is required for a stable population, and associated with drastic population decline (Hario 1990, 1994). It is worth noting that production figures cannot strictly be compared between years, since my checking intensity varied in terms of pairs checked each year (Table 2). However, even if a lower proportion of all pairs were checked in detail in some years, all pairs were still checked roughly. This means that if production would have been good in comparision to the intensively checked colonies, I would have detailed it, but low production colonies were sometimes only scanned through and entered as having lowered reproductive output.. The mean estimates of fledging success are thus conservative in favour of a higher fledging success.

Potential predators on chicks and adults include Great Black-backed Gulls (*L. marinus*), Herring Gulls (*L.argentatus*), Eagle Owls (*Bubo bubo*), Red Fox (*Vulpes vulpes*), Raccoon Dog (*Nyctereutes procyonoides*), Badger (*Meles meles*) and Mink (*Mustela vison*). Man also occasionally constitutes a threat. Though living on the larger islands in the study area, Badgers, Red Fox and Eagle Owls have never been seen preying on chicks or adults of colonial Common Gulls. Predation type affecting the colony was identified by either direct observations on the predator, identifying the predator from the remains of prey left in the colony, and inspecting remains at nests of large gulls. Minks in the colonies also almost invariably killed female Common Eiders (*Somateria mollissima*), if not leaving any other signs of their presence.

3. Results

3.1. Predators

Identified predators in the colonies included Mink, Herring- and very infrequently Great Black-backed Gulls, Raccoon dog and humans. The large species of gulls breed in many of the Common Gull colonies studied, Great Black-backs as solitary pairs, annually on the average in 5 ± 0.7 colonies, potentially affecting 55 ± 8% of all pairs and Herring Gulls either as solitary pairs, or colonially annually on the average in 7 ± 1.6 colonies covering 72 ± 14% of the population (Table 1). Mink occurred on the average annually in 2 ± 2.1 colonies, potentially affecting 27 ± 23% of all nesting common gulls. Raccoon dog occurred only in one year, and human interference was occasional.

Minks took both young and adult Common Gulls, while the gulls (primarily Herring Gull, see discussion) took young of all ages prior to fledging. Herring Gull interference was of two types, young of Common Gulls were taken as prey and killed at territories.

The proportion of the the Common Gull population potentially affected by both Herring and Great Black-backed Gulls remained roughly at the same level all years. The proportion of the Common Gull population affected by Minks decreased ($r_s = -0.85$, $n = 8$ yrs, $P = 0.01$), either because minks decreased, or because of a redistribution of birds between colonies, or both.

3.2. Predation rates

During 104 colony years, 38 (36.5%) severe colony-specific reproductive failures occurred. Mink was the main cause in 16 of these failures

Table 1. The number of pairs, and the proportion potentially at risk in colonies with documented nesting of other gulls and occurrence of mink. The number of study sites is 13 sites throughout (1982–89 data).

Year	Pairs	% of pairs affected by Mink (no. colonies)		% of pairs affected by Herring Gull (no. colonies)		% of pairs affected by Great Black-backed (no. colonies)	
1982	207	52%	(3)	67%	(5)	48%	(5)
1983	210	36%	(3)	78%	(6)	57%	(6)
1984	210	62%	(6)	42%	(5)	41%	(5)
1985	190	29%	(4)	74%	(7)	61%	(6)
1986	160	21%	(1)	75%	(7)	49%	(5)
1987	180	0%	(0)	71%	(8)	61%	(6)
1988	170	0%	(0)	77%	(10)	56%	(5)
1989	152	13%	(1)	91%	(7)	66%	(4)

(42%), gulls accounted for 19 cases (50%) while three cases (8%) were due to humans and Raccoon Dog. Minks affected proportionally more breeding pairs than did Herring Gulls, since total failures due to Herring Gulls occurred in only 2 colonies with no more than 25% of all pairs. Minks killed the offspring of up to 50% of all pairs in some years, and in up to 6 colonies annually.

The proportion of all pairs subject to a severe failure ranged from 0% (1988) to 52% in 1982, averaging 32 ± 17%. This proportion varied, but did not show a significant change over time ($r_s = 0.52$, $n = 8$ yrs, $P > 0.05$). The annual mean production per colony however, increased over the period studied ($r_s = 0.76$, $n = 8$ yrs, $P < 0.05$), from a low of 0.17 ± 0.24 in 1982 to 1.05 ± 0.93 fledged young per pair in 1988 (Table 2). Production was thus depressed in the beginning of the study period.

Over the entire period 1982–91, the mean number of failed colonies per year was 2.9 ± 2.4. The data in Tables 1 and 2 indicates that once Mink predation decreased, mean production rates rose.

Colonies were at different risk for failure, and subject to different predation pressure (Table 3). Two colonies were never seriously disturbed, while one failed during 6 years out of 8 in the period with coherent data (1982–1989). The two colonies with the highest rate of severe failure (Måslandet, 7 out of 8 and Bandskär with 6 failures out of 8) were effectively raided by minks in 1982–1986. Långgrund, on the other hand, experienced 3 zero years in 1986–1989 due to predation by (apparently) just one pair of Herring Gulls breeding in the colony. Stenskär (5 disturbed years), Andalsskär (4) and Trean (5) experienced a mixture of gull and (mostly) Mink predation. Måsgrund suffered from a prolonged human disturbance (campers) in one year. The incidence of a severe reduction in breeding success (< 0.2 per pair) appears to be linked to population size ($r_s = 0.54$, $n = 13$ colonies, $P < 0.05$) measured as mean colony size over the period 1978–91. However, this is possibly a site-effect (see Discussion).

3.3. Response of Common Gulls to disturbance

Colonies experiencing a high rate of breeding failures seem to have different long-term trends (Table 3). The number of zero production years (in 1982–89) is correlated with a decrease in number of pairs ($r_s = -0.53$, $n = 13$ colonies, $P < 0.05$) over the period 1978–91. Totally, only 5 colonies out of 15 show an increase in population size. The increased colonies (4) among the set of 13 studied in detail, suffered only 4 severe failures in 32 colony years (12.5%), while decreased (9) colonies suffered 34 failures in 72

Table 2. Proportion of all common gull pairs loosing all young in 1982–89, and the mean production of fledged young per pair measured accurately in 5–12 colonies annually. Note that the zero-production colonies are included in the means.Means should not be directly compared between years, but taken as indicative only.

Year	Pairs	% pairs lost all young (colonies)		Mean production (range) and number of monitored pairs (colonies)			
1982	207	52	(3)	0.17	(0–0.4)	156	(5)
1983	210	30	(2)	0.45	(0–0.9)	148	(6)
1984	210	42	(4)	0.27	(0–0.7)	161	(7)
1985	190	28	(3)	0.18	(0–0.5)	105	(6)
1986	160	49	(4)	0.38	(0–1.7)	120	(7)
1987	180	19	(1)	0.85	(0.1–2.0)	120	(12)
1988	170	0	(0)	1.05	(0.1–2.5)	149	(9)
1989	152	13	(1)	0.63	(0–1.5)	135	(9)
1990	–	–		1.09	(0–2.1)	47	(3)
1991	159	5	(1)	0.53	(0–1.9)	115	(9)

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colony years (47.2%, χ^2 (with Yates correction) = 10.1, P = 0.001).

Pair numbers in the colonies have changed rapidly in some cases, and more gradually in others (Table 3).

The largest colonies in 1978–83 dwindled in the late 1980s; Bandskär from 50 pairs to 9 pairs, Måslandet from 50 pairs to 11 pairs, Andalsskär from 35 to 1 pair, and Långgrund, from 39 to 8 pairs. Stora Vädergrund has grown rapidly from 15 to 55 pairs. A drop over two years at Måsgrund from 28 pairs to 6 pairs, was immediately followed by a sudden establishment of a colony at Lilla Måsgrund from 1 pair to 16 pairs close nearby (50 meters). This is the only direct evidence of a sudden change certainly caused by immigration, based on a few identifiable individuals. It is not known, whether any emigration out of the area occurred.

Two colonies were reduced to single pair sites during the period 1982–89. At one site (Flintskärsgrund), disturbance was extreme, as a Mink nested within the colony, and managed to kill at least 5 adults prior to laying in one year, causing desertion in that year with no recovery. At the other site (Andalsskär) the reason was unknown. The other cases (3) of predation prior and during the laying period resulted in a sudden drop of pair numbers from the previous season (Flintskär from 10 pairs to 1, Måsgrund 13 to 5, Bandskär 38 to 12 and Måslandet 36 to 12). In each of these cases Minks managed to kill a few adults, but the mink did not reside on the colony island, and the disturbance was not continuous. When predation affected only chicks (5 colonies), the decrease in colony size was gradual and did not lead to complete colony abandonment.

4. Discussion

Veen (1977) identified three immediate responses to predators in colonial Sandwich Terns (*Sterna sandvicensis*), depending on the type of the predator. When the predator is a danger only to the brood, the adult sits on the nest and threathens, if the predator also threatens the adult, the adult will fly up and sometimes attack, and if the predator is mainly a threath to the adult, escape behaviour is observed. Common Gulls in my study area will respond vigorously to stuffed Minks and Herring Gulls. Minks kill adults, but Herring Gulls apparently do not, though fledged young may be taken (own data). In Ring-billed

Table 3. Trends in all 15 study colonies from 1978 to 1991. Given are mean sizes of the colony, range, the coefficient of variation (*CV*), number of census years, and the Spearman rank correlation coefficient for the trend, where (*) denotes $P < 0.05$. Zero years, and total number of years with a serious reduction in reproduction (less than 0.2 fledged / pair) also given.The main agent of reproductive failures is indicated (M = Mink, HG = Herring Gull). The numbering corresponds with Fig. (1).

Colony	Mean size (range)	*CV*	Census years	r_S-value	Zero years	Total
Långboda (1)	17.7 (7–27)	25.0%	14 yrs	0.62*	0	1
Trean (2)	8.1 (4–15)	42.7%	13 yrs	– 0.75*	3	5 M
Måsgrund (3)	18.0 (6–28)	46.8%	11 yrs	– 0.87*	0	2
Långskär (4)	26.5 (8–39)	39.5%	13 yrs	– 0.46	3	4 HG
Hästklobb (5)	3.0 (1–6)	64.5%	9 yrs	0.68*	0	0
Vädergrund (6)	35.5 (15–55)	41.7%	9 yrs	0.82*	0	1
Långkobb (7)	5.1 (1–9)	60.3%	8 yrs	0.84*	0	1
Andalskär (8)	12.5 (1–35)	88.9%	10 yrs	– 0.44	1	4 M
Bandskär (9)	24.6 (9–50)	59.8%	11 yrs	– 0.88*	5	6 M
Backasgr. (10)	2.2 (0–6)	95.3%	11 yrs	– 0.50	1	1
Måslandet (11)	27.7 (11–50)	55.9%	11 yrs	– 0.88*	6	7 M
Stenskär (12)	6.0 (3–10)	43.6%	8 yrs	– 0.23	4	5
Trehålsland (13)	7.5 (5–10)	35.6%	8 yrs	– 0.67	?	?
Flintskär (14)	3.7 (1–13)	116.2%	13 yrs	– 0.82*	1	2 M
L.Måsgr. (15)	5.7 (0–16)	132.9%	13 yrs	0.78*	0	0

Gulls (*L. delawarensis*) Conover (1987) found an enhanced mobbing response when the experimentor carried a dead adult, implicating that gulls are able to react to the killing of conspecific colony members. In the cases of adult killing early in the season I observed, colony abandonment for that particular year occurred, showing an immediate respons to a predator affecting survival of adults. Clearly Common Gulls seem able to identify predators and possibly the degree of threat they represent. However, events leading to abandonment are scarce, and it is difficult to obtain sufficient data. Andersson (1992) discusses major decreases and large-scale shifts from old sites in archipelago bird species in the archipelago of Stockholm, Sweden, attributable to Mink predation, but the frequency of census was too low to allow for a detailed account of the swiftness of the decline.

Extended over consecutive seasons, the three types of immediate responses would result in (1) stable colonies when threats are only on offspring, and can be deterred or reduced by mobbing so that production is not affected heavily, and (2) heavy turnover at colonies where the entire offspring production is threatened, and/or adults killed. Essentially, colonies disturbed occasionally should remain stable or grow, those affected by predation on chicks decline gradually, and those affected by predation on adults should decline rapidly. My limited observations suggest this pattern.

Hario (1990, 1994) documented steep declines of colonies of both Lesser Black-backed and Common Gulls in the Gulf of Finland following very heavy predation on chicks by Herring Gulls.

Jehl and Chase (1987) found rapid relocation of pairs of California Gulls (*L. californicus*) following predation on both chicks and adults by Great Horned Owls (*B. virginianus*). In many species of terns (see Väisänen 1970, Burger 1984) and gulls of the "black-headed"-type (Burger 1974) rapid relocations of large groups of birds are known. The tendency of many birds to relocate as a unit (group adherence, McNicholl 1975) is partly an adaptation to rapidly changing habitats, but partly influnced by breeding success (Väisänen 1973, Cuthbert 1985). Such relocations obviously affect the local populations very rapidly. In gulls of the "white-headed"-type (such as Common Gulls) site stability seems to be the general rule (Burger 1974, McNicholl 1975, Southern 1977). My results show that site-tenacity may be reduced following heavy predation (see also Jehl & Chase 1987).

Since my population is not marked, I cannot demonstrate shifts of sites directly. But, it is likely not due to chance that the few colonies never experiencing serious reproductive failures during the study period, should also be the only colonies showing a net rate of increase in 1978–91. The decrease of the entire population was less dramatic than the most drastic annual fluctuations on colony level.

This set of data clearly demonstrated that the colonies were at considerable risk of facing severe predation, and that the gulls to some extent were able to react to predation in a way consistent with predictions about costs and benefits of site fidelity. Colony site abandonment is the only way of reducing the risk of total reproductive failure when predation is frequent over the years. The gulls faced at least two predators superior in the sense that they cannot be deterred. Minks operate at night, and gulls seem to lack an effective defence against nocturnal predation (Southern et al. 1982). Herring gulls may specialize as predators on chicks (Southern & Southern 1984, Hario 1990, 1994), and smaller gulls seem uncapable of deterring them. Both predators may also be recruitable, and hence larger colonies may be more at risk. Habitat differences at sites may also affect predation, more sheltered habitats appear more attractive to minks, and hence colonies on islets with much vegetation (Andalsskär, Bandskär, Måslandet) may have been more frequently at risk (see also Andersson 1992). The sole Herring Gull specialist found in my area apparently preyed only in the colony it resided in (Långgrund). The other pair of Herring Gulls causing some losses in one year (Långboda) killed chicks apparently in response to territorial intrusion.

Why then, is the response to seriously reduced reproductive success so slow? If a few consecutive years of failure are needed to trigger a relocation, this may be because predation upon offspring is generally a rare event. In long-lived species breeding in stable environments one or two losses of all offspring may not be disastrous, and could be outweighed by the long-term benefit of breeding in a familiar colony, instead of risking a shift to another site where recruitment may be difficult (Cadiou et al. 1994, Porter 1991, Porter & Coulson 1987). Rattiste and Lilleleht (1987) state that Common Gulls in Estonian colonies produce relatively few young in their first 1–4 breeding attempts and that they may frequently change sites. Older breeders are more site tenacious, and only 5% of all pairs relocate in the next year if the colony is undisturbed.

If adults are under direct threath, the response should be faster, which also seemed to be the case.The overall pattern of high site persistance, however, supports the notion that Common Gulls are adapted to stable breeding environments, where site tenacity is of considerable fitness value.

When colonies of Common Gulls are strongly affected by predation and large variation in colony site quality, the outcome seems to be a patch-specific rate of change depending on the nature of the adversity. However, the result suggests that dynamics in one patch affects other patches as well, leading to essentially a metapopulation situation, where occupied patches affect one another (Harrison 1991). To fully understand Common Gull population dynamics (or any other colonial species) in any one area, we would need to know the mechanism by which intercolony recruitment is achieved, and the geographical extent of what effectively constitutes a population of interacting colonies. From a conservation standpoint information on which factors affect colony dynamics locally and regionally is also essential. It is at least evident from this study, done within quite a small area, that from a conservation point of view, many colonies is a much better option than just a few. In local conservation schemes it would also pay off to protect potential sites known to have been occupied at some point in time, rather than to focus on a few currently used sites.This of course applies to a number of colonial species in the Finnish archipelago.

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