

INFLUENCE OF GROUP SIZE AND HABITAT TYPE ON REPRODUCTIVE SUCCESS IN COMMON MURRES (*URIA AALGE*)

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ABSTRACT.—On Tatoosh Island, off the Olympic Peninsula in Washington, Common Murres (*Uria aalge*) nest either in small subcolonies located in crevices in vertical, rocky cliff walls, or in large subcolonies located on the island top, usually at cliff's edge. Nesting murres are subject to predatory pressure from Glaucous-winged Gulls (*Larus glaucescens*) and Northwestern Crows (*Corvus caurinus*), which are resident egg predators, as well as from Peregrine Falcons (*Falco peregrinus*) and Bald Eagles (*Haliaeetus leucocephalus*), which are transient predators on adults. Although subcolony size dilutes the effects of egg predators, the presence of raptors in the system negates this simple effect of dilution. Relative to conspecifics in crevice subcolonies, murres in cliff-top subcolonies are more likely to be attacked by raptors, as well as to temporarily evacuate the subcolony in response to the presence of raptors. During subcolony evacuations, egg predators gain unhindered access to abandoned eggs. As a result, murres nesting in cliff-top subcolonies experience both delays in phenology and lowered reproductive success relative to murres nesting in crevice subcolonies. Despite continued raptor-facilitated egg predation, the majority of the murre population nests in cliff-top subcolonies, which are less than 20 years old and are growing rapidly. This suggests that new colonists are constrained by a lack of accurate information into making incorrect decisions about which subcolonies to join. Received 7 February 1994, accepted 17 April 1994.

COLONIAL NESTING in seabirds has been cited as a behavior mitigating egg and chick predation (Furness and Monaghan 1987). As a function of size, nesting colonies dilute the risk of predation and also may provide members with early warning of predator presence (Siegel-Causey and Hunt 1981). Interactions between colonial nesters and predators on eggs and chicks have been well explored (e.g. Patterson 1965, Birkhead 1977, Brown and Brown 1987, Spear 1993), but whether colonial nesting confers advantages on the adults, with respect to predation, depends on the numerical response of predators to colony size and location. Increasing colony size may dilute the risk of predation on any single individual (Patterson 1965, Birkhead and Harris 1985; see also Alexander 1974). However, an immobile aggregation such as a nesting colony also is bound to attract predators as it is a predictable source of food (Wittenberger and Hunt 1985, Clode 1993). Should the threat of predation loom large, breeders may leave the colony, although this may entail the loss of that year's reproductive investment.

Common Murres (*Uria aalge*) breed in dense colonies of over one million birds (Nettleship and Evans 1985). Murres often nest within physical contact of their neighbors and densities of 20 pairs/m² are reported to be average (Harris and Birkhead 1985). Due to colony size

and proximity to neighbors, murres have developed a variety of behaviors mediating intraspecific aggression (Birkhead 1978). For example, parents not only care for and defend their own chick, but may also brood the chick of a temporarily absent neighbor (Birkhead and Harris 1985). Although total colony size may determine reproductive success (e.g. Hunt et al. 1986), finer-scale differences in group density (Birkhead 1978), number of immediate neighbors (Hatchwell 1991), alloparenting behavior, and subtle aspects of the physical habitat (Hatchwell 1991) also can have a pronounced effect.

On Tatoosh Island, in northwestern Washington, Common Murres nest in densely packed subcolonies, defined as a spatially distinct nesting aggregations, ranging in size from ones to several thousand. Subcolonies occur in two types of habitat. On the cliff top, murres nest on bare ground at cliff's edge. Cliff-top subcolonies are large (hundreds to thousands), bounded by vegetation (principally salmonberry, *Rubus spectabilis*) on the inland side, and exposed to attack from above. On the vertical cliff face, murres nest in natural ledges, one to two murre-body-widths deep. Crevice subcolonies are small (ones to tens) and protected, relative to cliff-top subcolonies, by the rock wall and ceiling. All subcolonies are visited by egg and chick predators:

Glaucous-winged Gulls (*Larus glaucescens*) and Northwestern Crows (*Corvus caurinus*). In addition, adult murres occasionally are attacked by Peregrine Falcons (*Falco peregrinus*) and Bald Eagles (*Haliaeetus leucocephalus*).

Colony-level processes affecting adult mortality and reproductive success, such as declining food resources and attraction of predators to the area (Brown et al. 1990), should affect the entire Tatoosh population. However, within that macroscale framework, microscale differences between subcolonies also may determine egg, chick, and adult survival. Assuming that both colonial nesting and predatory pressure are givens in this system, incoming breeders have at least two choices regarding which type of nesting subcolony to join so as to minimize predation. If dilution of the per-capita effect of predation is subcolony-size dependent (i.e. the selfish herd; Hamilton 1971), individuals should join the largest subcolonies. A second possibility is to choose according to the level of protection the habitat affords, irrespective of subcolony size. If both subcolony size and habitat type are important, incoming breeders might assort according to an ideal-free model (Fretwell and Lucas 1969), until protection levels balanced out and/or space became limiting. While these choices may seem straightforward, newly arriving murres on Tatoosh must assess subcolony quality as a function of both egg/chick and adult predation. Because murres are highly philopatric, often returning to the same location on the same subcolony year after year (Harris and Birkhead 1985), a correct initial decision is paramount to future fitness expectations.

I evaluated how well these hypotheses (group size and habitat type) explain murre distribution on Tatoosh by quantifying the interaction between nesting murres and their egg and adult predators, and estimating reproductive success for each subcolony I observed.

MATERIALS AND METHODS

I collected observational data between dawn and dusk over three successive seasons (1990–1992) on Common Murres nesting on Tatoosh Island (124°45'W, 48°25'N), 0.6 km off the northwestern tip of the Olympic Peninsula, Washington. All data were collected from remote observation sites with the aid of binoculars and a spotting scope. Overlapping observations made by a remote time-lapse 35-mm camera indicated that the murres were not overtly affected by

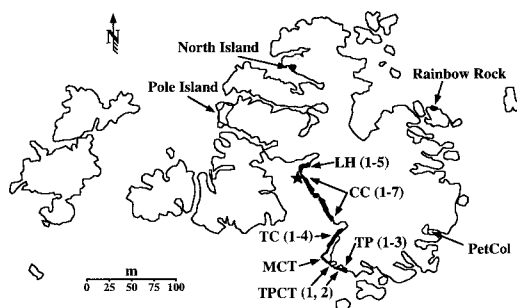


Fig. 1. Overview of Tatoosh Island showing location of murre subcolonies in 1990 through 1992. Cliff-top subcolonies shown in white and crevice subcolonies in black. Star indicates observation point from which nine crevice subcolonies (CC1–5; TC1–4) and one cliff-top subcolony (MCT) could be observed simultaneously.

researcher presence (unpubl. data). The majority of the behavioral data was collected from a single location that afforded a simultaneous view of 11 separate subcolonies (Fig. 1). The distance separating subcolonies was defined by physical barriers, such as the end of a ledge, or a rock obstruction that divided a larger ledge and blocked passage. On the cliff top, distinct subcolonies were defined by unoccupied distances of at least 5 m.

During 1990, I collected data from 6–10 July. During 1991, I made nine trips between 12 May and 11 August, and made observations on 30 days (60 h; 25 days with greater than 1 h of observation). During two trips spanning 24 August to 10 September, data on attendance and phenology were collected by R. T. Paine. In 1992, I made eight trips from 1 May through 29 August and observed murre nesting subcolonies on 27 days (80 h; 24 days with greater than 1 h of observation). Data on attendance and phenology also were collected by R. T. Paine (three trips) and B. Johnson (one trip). Although observations began and ended at haphazard times of day, all hourly intervals between dawn and dusk were sampled on at least five different days throughout each season (1991 and 1992).

I assessed subcolony attendance at least once during every trip. When calculating average annual attendance, counts were limited within season to after eggs were laid but before chicks began to fledge, and within day to after 1100 PST (because a larger percent of birds foraged early in the morning) and before dusk (when accurate counting became more difficult). For small subcolonies (e.g. <200 birds attending), direct counts were always made. For larger subcolonies, attendance was estimated by counting a subplot (usually not less than 30% of the total subcolony) and extrapolating total attendance by estimating the area of the subplot relative to the area of the entire subcolony. Occasionally, cliff-top subcolony attendance

also was evaluated by counting directly, as the murres arrived on the subcolony after a disturbance had caused them to leave.

Starting in March–April, the Tatoosh murre population followed the basic pattern of rafting (March–May) followed first by island colonization (May–June), and eventually by the initiation of reproductive activity (June–July). During the initial period of island colonization, the murres rarely remained on the cliffs throughout the day and flew off at frequent intervals. I defined stable colonization as the period starting from the date murres remained on the subcolony throughout the day, regardless of when eggs first began to appear. I also defined several phenological stages: prelaying (murres attending subcolony, but no eggs), egg (eggs first observed in subcolony), chick (chicks first observed in subcolony), and fledging (fledglings first observed leaving subcolony). The fledging period ended when no chicks remained on the subcolony. Although each stage was defined by onset, the murres were highly synchronous within subcolony, the majority of eggs being laid within a one- to two-week period. Subcolonies frequently proceeded from one stage to the next in between trips to the island. In these cases, onset was either inferred from back calculation (e.g. hatching dates from chick size) or represented by a range of possible onset dates.

In 1992, I estimated reproductive success as the number of chicks divided by average attendance. This more general measure allowed comparison of crevice subcolony success, which could be calculated as fledglings per pair, with cliff-top subcolony success, where accurate assessment of pair numbers was impossible. Reproductive success was assessed for three crevice subcolonies located on a single vertical cliff face, all within 30 m of each other (CC1–3; Fig. 1) and one crevice subcolony located along the south side of the island (TP1; Fig. 1). The number of chicks was counted when chicks were approximately one to two weeks of age and again at the onset of fledging.

Visits in previous years indicated that breeding in the cliff-top subcolonies occurred along a thin band underneath the vegetation canopy, extending out onto the bare ground. Murres along the leading (cliff side) edge rarely retained eggs, and this area was mainly used for take-off and landing. Due to inaccessibility and the destructive nature of direct visitation, reproductive success on two cliff-top subcolonies (MCT and PetCol; Fig. 1) was estimated during single visits at approximately the same phenological stage as chick counts were made in the crevice subcolonies (chicks at one to two weeks of age, scattered eggs remaining). After eggs had hatched, murres in cliff-top subcolonies could be approached from the inland (vegetated) side to within about 1.5 m. Counting all of the chicks on the subcolony was not feasible as visits in previous years had indicated that closer approach caused the adults to evacuate their nest sites, and the entire subcolony could not be seen from my position in the salmonberry. For both cliff-top subcolonies, I counted

the number of adults, eggs, and chicks within a subplot located along the inland side of the subcolony. This method of estimating reproductive success may be biased upward because nonbreeding murres may have left the subcolony, or moved away at my approach.

Egg predators always were present on or close to murre subcolonies. I defined egg-predator location with respect to a subcolony as interior (operationally defined as inside the leading edge of incubating/brooding murres) or on the periphery. Only interior locations gave egg predators access to eggs and chicks. On the half-hour during each observation period (e.g. 0600, 0630, etc.), I counted the total number of gulls and crows present on each subcolony, as well as the interior subset. Egg predators also were counted within 1 min following any temporary evacuation by part or all of a subcolony (in 1992 only). Concurrent with egg-predator counts, I estimated crude subcolony attendance (0–5, 6–50, 51–95, 96–100%).

Because the data were observational, sample sizes within cells were not equal; frequently, cells contained either zero values, single values, or zero variance. Therefore, several different univariate tests were performed, depending on the hypothesis and constraints of the data. One-way ANOVAs were used to test whether total egg-predator presence was a function of murre attendance. Significant main effects were evaluated with *a posteriori* contrasts. Chi-square tests were used to examine whether egg-predator presence was a function of reproductive stage. I used *t*-tests to examine whether the number of egg predators in the subcolony differed from background levels following a disturbance. During the egg stage, I counted the number of eggs I saw taken by invading predators.

The murres had a graded set of responses to potential threats ranging from alarm calling and head bobbing (for complete description, see Birkhead 1977) to all members leaving the subcolony for the water. A disturbance event was defined as any occurrence causing the murres to leave the subcolony temporarily, either in total or in part. Where possible, the source of disturbance was noted. For the purposes of this analysis, I classified murre disturbance, by subcolony, as: (1) no response, if the murres remained in the subcolony, regardless of the amount of head bobbing, etc.; (2) partial evacuation, if a proportion of the murres left the subcolony; and (3) total evacuation, if all of the murres left the subcolony. If any subcolony responded by leaving, either in part or in whole, I recorded the response of all other observable subcolonies. I also noted the response of all subcolonies whenever eagles flew over the area. *G*-tests for goodness-of-fit (log-likelihood ratio; Zar 1974) were used to determine whether the distribution of subcolony response was a function of habitat type (cliff top or crevice), where one comparison was made for each reproductive stage (prelaying, egg, and chick). *G*-tests also were used to determine whether the distribution of subcolony response, within each habitat

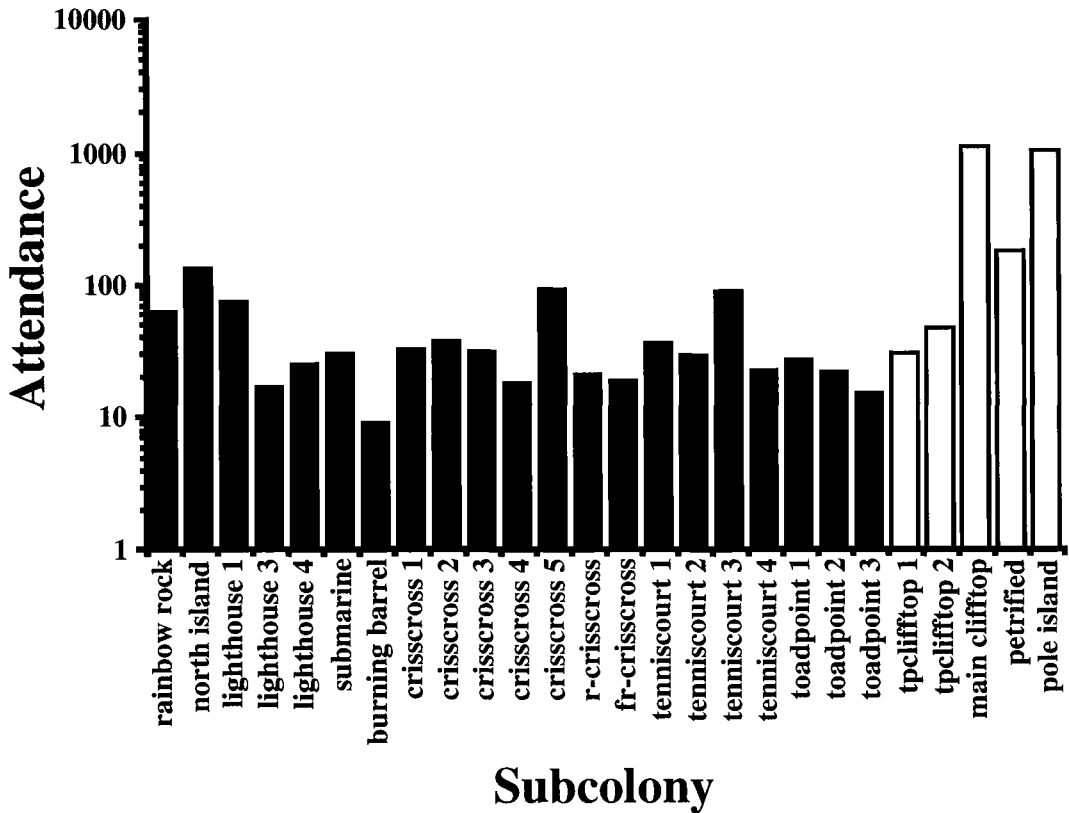


Fig. 2. Average attendance by subcolony (1992) calculated from period after eggs were laid, but before fledging onset. Cliff-top subcolonies shown in white and crevice subcolonies in black. Total island attendance was 3,228.

type, varied across reproductive stage. Finally, these tests were used to determine whether the MCT responded to eagles differently than they responded to other predators.

When the murres left the subcolony, they either flew to the water in front of the subcolony and rafted, or they circled in front of the subcolony and immediately relanded. I counted the number of times the murres either rafted or relanded as a function of the total number of observed disturbance events created by eagles and egg predators, respectively. I calculated a raft-to-reland ratio as a function of predator and reproductive stage (prelaying and egg). Once murres began to reland, I documented the time course of resettlement until the subcolony was full (96–100% attendance), another disturbance event occurred, or darkness and/or weather precluded continuing observation.

RESULTS

Population numbers. — On Tatoosh Island, Common Murres nest in 28 spatially separate

subcolonies, principally located in crevices on the west- and south-facing cliffs (Fig. 1). Crevice attendance (1992) ranged from an average of 3 to 134 birds (Fig. 2). Although the majority of the subcolonies are contained in crevices (80%), most of the murres on the island nest in five much larger subcolonies located along the perimeter of the island top. In 1992, the cliff-top subcolonies accounted for approximately 75% of the Tatoosh population (Fig. 2). One of these subcolonies, Pole Island, is composed of a series of broad benches interspersed by spires and arches carved out by the weather, creating a series of “open rooms” within which murres, cormorants (*Phalacrocorax pelagicus*, *P. penicillatus*), and Glaucous-winged Gulls nest. The remaining four subcolonies are flat expanses of bare earth sandwiched inbetween stands of salmonberry and the cliff’s edge, and located on the southwest- and south-facing cliffs. Regardless of subcolony size, murres nested shoulder-to-shoulder. The largest subcolony (MCT)

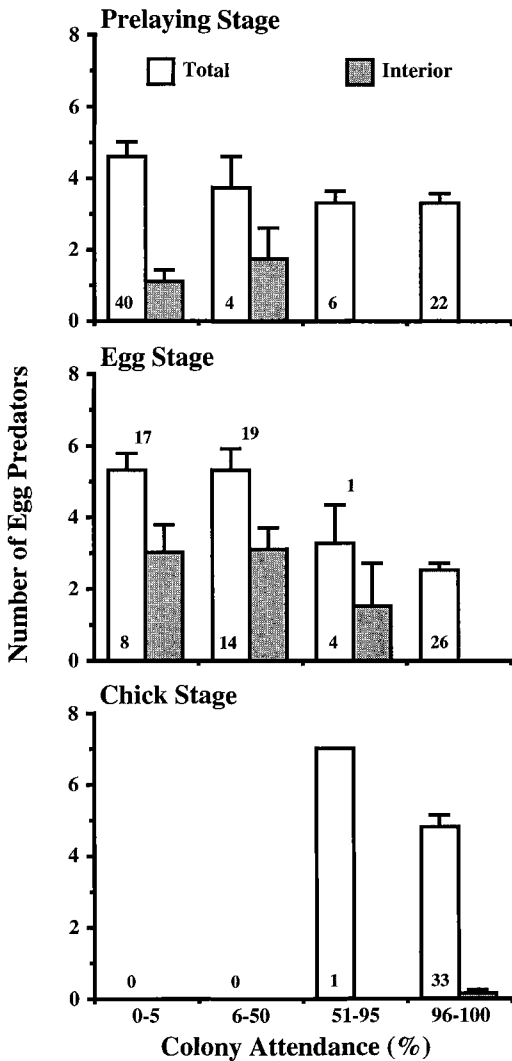


Fig. 3. Average number of egg predators on main cliff-top subcolony (MCT) as function of murre phenology (prelaying, egg, and chick stages) and murre attendance ($\bar{x} \pm SE$), sampled on the half hour during observation periods. Open bar indicates all egg predators and stippled bar the subset in interior of murre subcolony (i.e. those with potential access to eggs or chicks). Number in each open bar indicates sample size. Values above bars in center panel are number of eggs I witnessed being taken by egg predators.

is the only cliff-top subcolony, which can be observed in full and, therefore, has been the most intensively studied. Photographs taken from 1968 through 1980 show that, prior to 1980, salmonberry and grass hummocks grew to the cliff's edge and that, as the MCT subcolony increased in size, the grass and salmonberry died

back exposing bare ground (Parrish and Paine unpubl. manuscript). Thus, unlike the crevice subcolonies, cliff-top subcolonies are not space limited.

Interactions with egg predators.—Two species of egg predators nest on Tatoosh. Glaucous-winged Gulls have numbered in the low thousands since at least 1959 (1986–1988, $\bar{x} = 3,800$; Paine et al. 1990). Northwestern Crows also nest on the island (estimated population 8–30 birds in 1986–1988; Paine et al. 1990). These species were constantly seen in the vicinity of both crevice and cliff-top subcolonies. In the five most easily observed crevice subcolonies (CC1–5; Fig. 1), the average number of egg predators per attending murre was consistently higher than on the cliff-top subcolonies (CC1–5, egg stage, 7.8×10^{-3} , and chick stage 6.8×10^{-3} ; MCT, egg stage, 2.1×10^{-3} , and chick stage, 4×10^{-3}). However, on the crevice subcolonies, all of these predators stayed at the periphery of the subcolonies. On only one occasion did I witness an egg predator, a crow, gain access to the interior of a crevice subcolony; this occurred after a disturbance event during which approximately 25% of the murrees were flushed. The remaining adult murrees were able to prevent the crow from removing chicks or eggs.

By comparison, cliff-top subcolonies were regularly invaded by both gulls and crows throughout the nesting season. Cliff-top subcolonies usually had gull nests located at the periphery (MCT, PetCol, TPCT1–2) or interspersed with groups of nesting murrees (Pole Island). The number of egg predators regularly observed on the MCT varied as a function of both murre presence and reproductive stage. Early in the season, during the prelaying period, the number of egg predators visiting the MCT declined as murre attendance increased, although this trend is not statistically significant (one-way ANOVA, $F = 2.27$, $df = 3$, $P = 0.09$; Fig. 3). After eggs appeared, however, the number of egg predators became dependent on murre attendance (one-way ANOVA, $F = 13.65$, $df = 3$, $P < 0.001$). When subcolony attendance was at or below 50%, there were significantly more egg predators on the MCT than when more than 50% of the murrees were present (*a posteriori* contrast, $F = 20.57$, $P < 0.001$; Fig. 3). Once eggs began to hatch, murrees were never observed leaving the subcolony, and on only one occasion was attendance below 96–100% (Fig. 3).

Even if egg predators managed to land on the MCT, this did not necessarily indicate that they would be successful because only those predators gaining access to the interior of the subcolony could steal eggs. When the MCT was 96–100% occupied, gulls and crows almost always were found only on the periphery, regardless of reproductive stage or relative predatory pressure (measured as total number of predators present; Fig. 3). Therefore, aggregation was an effective behavioral strategy for keeping egg predators away from the nests in a subcolony.

However, the MCT was often partially empty (i.e. <96% occupied). The numbers of egg predators gaining access to the interior of the subcolony during the prelaying and egg stages were highly dependent on subcolony attendance (chi-squared tests; H_0 , that distribution of egg predators inside subcolony was not different from uniform distribution across subcolony attendance; prelaying stage, $X^2 = 70.7$, $df = 3$, $P < 0.001$; egg stage, $X^2 = 26.5$, $df = 3$, $P < 0.001$). Although this pattern was similar across all reproductive stages, the causal factors were different. During the prelaying period, egg predators had no food available to them and rarely entered the interior of the MCT, even when the murres were absent (Fig. 3). The presence of a few egg predators during this period suggests that these birds were continually checking for the presence of eggs. Once eggs appeared, the number of egg predators invading the interior of the MCT increased dramatically when the subcolony was less than 51% occupied. During the chick stage, the murres no longer left the subcolony en masse.

In 70 h (over 28 days) of observation during the MCT egg stage (1991–1992), I witnessed 37 eggs being stolen from the MCT (34 by gulls, 3 by crows). All but one were taken when the subcolony was less than 51% occupied (Fig. 3). This total is conservative, as observations were made during only 9% of the total daylight hours (based on egg stage of 11 June through 30 July; 16 h of light per day). I also collected 266 destroyed eggs, the vast majority of which were found on a horizontal intertidal bench 40 m below the MCT. These eggs were destroyed in two different ways. Egg predators, trying to break open an egg and/or carry it away, often inadvertently rolled eggs off the cliff. However, many of these eggs were destroyed by the murres themselves. When the murres left the

subcolony in response to a disturbance, eggs located nearest the leading edge rolled off the cliff as a result of the panicked, forward movement of so many birds. Therefore, egg predators were both directly (predation) and indirectly (breakage) responsible for egg loss in the murre subcolonies.

In order to assess the immediate response of egg predators to changes in murre attendance, I compared the number of egg predators in the subcolony within 1 min of a disturbance event causing murres to leave, to the "background" egg-predator pressure as assessed by the half-hour samples (i.e. Fig. 3). As would be expected, the number of egg predators on the subcolony increased significantly (t -tests on prelaying and egg stages combined; total number of egg predators, $t = -2.742$, $df = 51$, $P = 0.008$; egg predators in subcolony interior, $t = -4.823$, $df = 51$, $P < 0.001$; Fig. 4), suggesting that egg predators made active and immediate use of the subcolony evacuations.

Interactions with eagles.—During the prelaying stage, murres frequently left their subcolonies for the water. As the nesting season progressed, these mass exoduses decreased in frequency, presumably due to both learning what constituted a threat and increasing reproductive investment. The source of these disturbances varied, but most often was attributable to the presence of eagles, either flying over a subcolony, or actually attacking the murres.

During the 1990–1992 nesting seasons, several raptors (principally juvenile Bald Eagles and female Peregrine Falcons) stooped on murres in the cliff-top subcolonies (Table 1). However, during 160 h of observation, I witnessed only 39 attacks, only one of which was successful (Table 1) and all of which were perpetrated on cliff-top nesters. In 1991 and 1992, 21 partially riddled adult murre carcasses were found on the island (Table 1). In general, raptors posed only a minor threat to individual murres. Raptors were never observed attacking, or landing on, the crevice subcolonies, although they frequently flew over the cliffs containing these subcolonies. Although raptors were only infrequently observed attacking, they were constantly present on the island. Both juvenile and adult eagles flew by the MCT and nearby crevice subcolonies on their way to and from frequently used perches in snags or rocky outcroppings several times each day.

In the presence of predators, murres in both

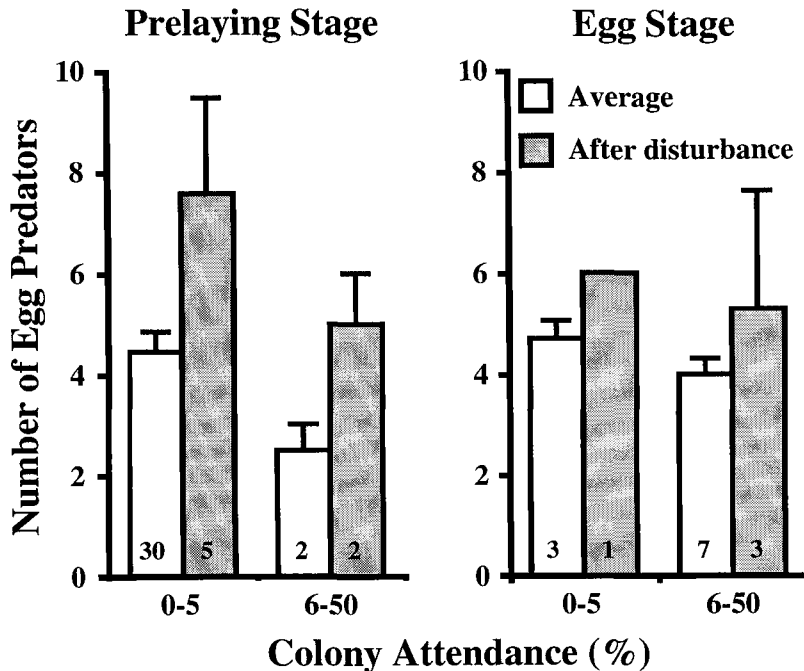


Fig. 4. Average number of egg predators on main cliff-top subcolony (MCT) as function of murre phenology (prelaying and egg stages) and murre attendance ($\bar{x} + SE$) in 1992. Open bars indicate average number of egg predators present (see Fig. 3) and stippled bars average number of egg predators present immediately following disturbance event. Number within each bar indicates sample size.

habitat types (crevice and cliff top) responded with alarm behavior ranging from no response to subcolonywide temporary evacuation. However, the average level of response was always higher for murres in the MCT compared to birds in the adjacent crevice subcolonies (Fig. 5). During both the prelaying and egg stages, the difference in response was significant (log-likelihood goodness-of-fit G -test; prelaying stage, $G = 73.18$, $df = 2$, $P < 0.001$; egg stage, $G = 19.6$, $df = 2$, $P < 0.001$). However, this difference

between the level of response in the two habitat types was dampened as the nesting season progressed such that by the chick stage there was not a statistical difference in the distribution of responses by murres in the two habitat types ($G = 0.23$, $df = 2$, $P > 0.75$). This convergence was due to murres in the MCT exhibiting lower levels of response as the season progressed (log-likelihood goodness-of-fit G -test; MCT response as function of reproductive stage, $G = -25.4$, $df = 4$, $P < 0.001$).

TABLE 1. Strikes on adult Common Murres nesting on Tatoosh Island (successes/attempts). Raptors were never observed attacking crevice-subcolony residents.

| | 1990 | 1991 | 1992 |
|-----------------------|------|------|------|
| Juvenile Bald Eagle | 0/8 | 0/9 | 0/2 |
| Adult Bald Eagle | — | 0/1 | 1/3 |
| Peregrine Falcon | 0/4 | 0/5 | 0/7 |
| Total | 0/12 | 0/15 | 1/12 |
| No. hours observation | 20 | 60 | 80 |
| Body count | — | 9 | 12* |

* Includes witnessed eagle kill.

Murre response was not only a function of habitat type and reproductive stage, but also of predator species (Fig. 6). During the prelaying stage, the sudden appearance of any predator could provoke an evacuation by the MCT murres. Eagles produced the majority of these responses (Fig. 6), even though egg predators were constantly at the subcolony (Fig. 3). Once eggs were laid, only eagles caused murres to leave the subcolony (Fig. 6). However, the response to eagles during the egg stage was dampened relative to the prelaying stage (log-likelihood goodness-of-fit G -test; $G = 10.64$, $df = 2$, $P < 0.005$).

Evacuating murres would either join rafts lo-

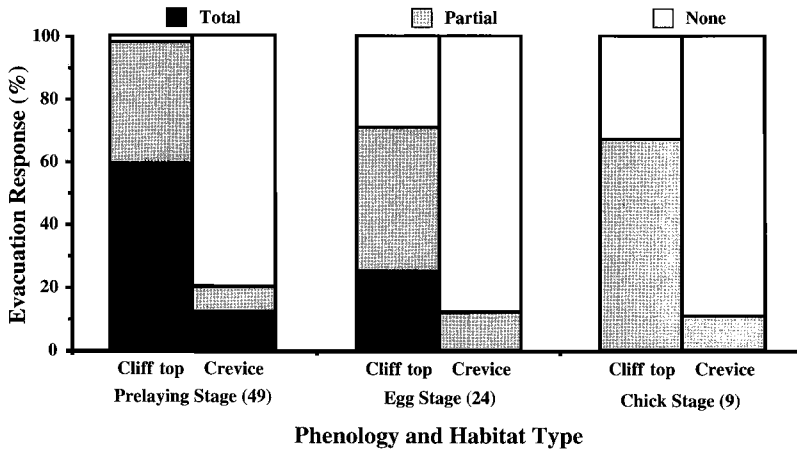


Fig. 5. Level of evacuation of murre nesting subcolonies in response to perceived threats (percent of total observations) categorized by habitat type (cliff top [MCT] and crevice [CC1-5; TC1-4]) and reproductive stage (prelaying, egg, and chick stages). Total and partial evacuation most often elicited by presence of raptors. Sample sizes in parentheses.

cated within sight of the subcolony or circle around and immediately reland. Both the initial response decision (i.e. leave or stay), as well as the subsequent behavior (raft or reland) can be used as indicators of perceived risk. During the prelaying period, where the response to the appearance of a predator was at least a partial evacuation of the subcolony, the MCT murre always rafted (raft-to-reland ratio, 9:0 for total evacuation; 1:0 for partial evacuation). By comparison, birds in the crevice subcolonies not

only responded more frequently with a partial evacuation, but rarely rafted (raft-to-reland ratio, 2:2 for total evacuation; 1:5 for partial evacuation). Thus, the length of time crevice subcolonies stood empty was small compared to the MCT.

Following an evacuation, individuals from the resulting raft eventually would begin to fly back over the subcolony, without landing (flyby). This behavior would lead to a single bird briefly touching down (bounce land), followed by a

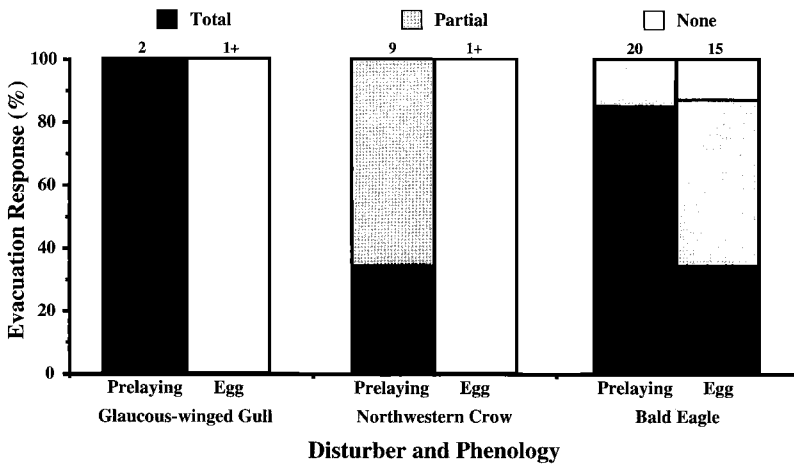


Fig. 6. Level of evacuation of murre nesting in MCT subcolony in response to perceived threat (percent of total observations) categorized by reproductive stage (prelaying and egg stages) and assumed source of threat (gulls, crows, or eagles). Sample sizes given above each bar. During egg stage, murre did not respond (None) to either gulls or crows on subcolony.

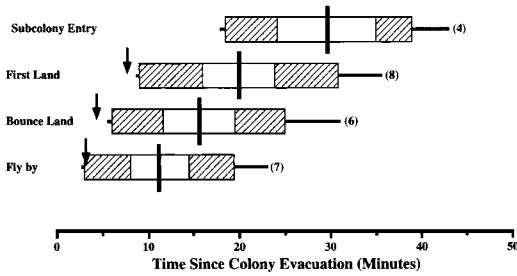


Fig. 7. Timing of resettlement of main cliff-top subcolony (MCT) following eagle-induced total evacuation (1991 and 1992). For prelaying stage, vertical lines are means, open bars standard errors, hatched bars standard deviations, and horizontal lines ranges. Arrows indicate mean or single point of resettlement timing during egg stage.

single bird landing and remaining at the subcolony (first land). On the MCT, first landers remained on the extreme edge of the subcolony outside the boundary of the nesting area, close to the cliff edge. If not disturbed, the first bird was soon followed by the arrival of the rest of the murres. Once attendance was above 30 to 50%, these murres would move into the nesting area (subcolony entry).

Rafting murres often remained on the water for up to several hours and frequently overnight if darkness fell before resettlement had started. This was particularly true in cases where the predator remained on the cliff top or a second disturbance happened before resettlement was complete. During the prelaying stage, resettlement was gradual, lasting more than 0.5 h from evacuation to subcolony entry (Fig. 7). Once eggs were laid, resettlement happened much more quickly, although low sample sizes preclude statistical comparisons (Fig. 7). Given no secondary disturbance, the first murre landed after only 7 min and the subcolony was completely occupied (i.e. 96–100%) after 20 min.

Murre reproduction.—Because murres on the MCT continued to respond to eagles by leaving, early eggs were eaten or lost, and the subcolony did not become stable (i.e. when birds remain on cliff throughout day) or lay the majority of its eggs until one to several weeks later than the crevice subcolonies (Fig. 8). The same pattern was evident in all years. The longer time period over which new eggs appeared on the MCT could have been due to both delays in laying (because females were on the water instead of in subcolony), as well as re-laying for

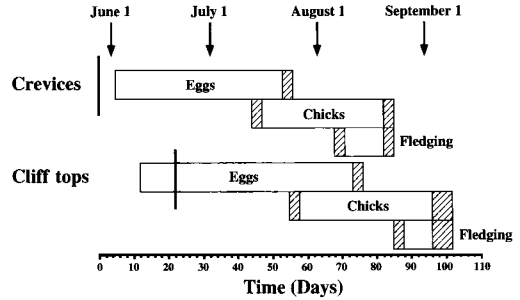


Fig. 8. Phenology of murres nesting on Tatoosh (1991), categorized by habitat type (crevice and cliff top). Bars indicate range of each reproductive stage. Hatched bars indicate range within which onset or cessation fell. Vertical lines indicate day after which murres remained on subcolony throughout day (stable colonization).

those individuals losing early eggs. In general, chicks hatched on all cliff-top subcolonies later than they hatched on crevice subcolonies (Fig. 8). At the time fledging started on the MCT, it was completed in the crevice subcolonies (Fig. 8).

Egg loss, delays in phenology, and loss of synchrony probably all contributed to lowered reproductive success in cliff-top subcolonies relative to crevice subcolonies (Table 2). In 1990, nesting murres had deserted two of the five cliff-top subcolonies (MCT, TPCT2) prior to any chick hatching, a total reproductive failure. In 1992, crevice-subcolony reproductive success was at least twice that of sampled cliff-top subcolonies (Table 2). Reproductive success was not calculated in 1991 due to the effects of an oil spill during the nesting season.

DISCUSSION

Many seabird studies have shown that, with respect to predation, reproductive success increases as a function of group size (see review by Wittenberger and Hunt 1985). On Tatoosh, murre reproductive success is not associated with subcolony size, but instead with habitat type (see also Siegel-Causey and Hunt 1981, Hatchwell 1991). If predator success increased with the number of predators per murre, or per murre egg, reproductive success should have been higher in the cliff-top subcolonies compared to the crevice subcolonies. In fact, the opposite was true. In 1990, two cliff-top subcolonies failed

totally, and in 1992 reproductive success in all subsampled cliff-top subcolonies was less than one-half that in the sampled crevice subcolonies (Table 2).

Although the differences in reproductive success between cliff-top and crevice subcolonies are definitely a consequence of egg-predator pressure, habitat type (specifically, differences in degree of exposure to eagles) is the mediating factor allowing the island's egg predators differential access. Because disturbance by eagles regularly caused all or most of the murre in the cliff-top subcolonies to leave, egg predators that had been held at bay were able to gain access to previously well-defended eggs (Fig. 3). That egg predators used the murre's response to raptors to their advantage is supported by the finding that, immediately following a partial or total subcolony evacuation, the number of egg predators in the subcolony increased dramatically (Fig. 4). An extreme social response, such as a mass exodus resulting from the appearance of an eagle, may protect adult murre, but is clearly deleterious to short-term reproductive success (Emlen et al. 1966).

The indirect effect of disturbance by eagles facilitating egg predation by gulls and crows not only lowered reproductive success (Table 2), but also extended the reproductive season of cliff-top subcolonies relative to crevice subcolonies (Fig. 8). Delays in phenology resulted in MCT chicks fledging after all murre in crevice subcolonies had left for the year (Fig. 8). Later fledging is generally associated with a lowered chance of survival (Harris and Birkhead 1985), although I do not have evidence that this is the case on Tatoosh.

Given the low number of eagle attacks on murre and the extremely small number of witnessed predation events relative to the total murre population, why did the murre consistently leave the cliff-top subcolonies when eagles appeared? Although the realized risk to cliff-top nesters was small, the perceived risk, reflected in the murre's response, was large. During the prelaying stage, eagle overflights caused consistent evacuations by birds in cliff-top subcolonies, and occasional evacuations by those in crevice subcolonies as well (Fig. 5). However, the initial perception of high risk (i.e. a threat dire enough to cause individuals to leave their subcolony for the relative safety of the water) was reevaluated by crevice dwellers while still on the wing. Thus, crevice nesters

TABLE 2. Reproductive output of select subcolonies in 1992.

| Subcolony | Chicks per pair | Chicks per mean attendance |
|--------------------------|-----------------|----------------------------|
| Crevice habitat | | |
| CC1 | 0.76-0.87 | 0.44 |
| CC2 | 0.94-1.00 | 0.50 |
| CC3 | 0.73-0.89 | 0.28 |
| TP1 | 0.82-0.90 | 0.50 |
| Cliff-top habitat | | |
| PetCol | — | 0.23 |
| MCT | — | 0.18 |

circled in front of the subcolony and relanded while cliff-top nesters rafted, leaving their subcolony empty for minutes to hours.

If reproductive investment is low (no eggs or nest material), subcolony exodus may be the most advantageous response even if the threat is minimal. Until reliable information can be gathered about threat sources, over-response can be safer in the long run (see Helfman 1989). For long-lived seabirds with low clutch size, loss of a single year's investment is a minimal cost relative to personal injury or death. Furthermore, because murre are gregarious birds, the decision to leave by some individuals may quickly be adopted by neighbors who suddenly risk exposure on an unprotected flank (Hamilton 1971). Thus, temporary evacuation by the entire subcolony may actually be a wave of individual decisions as each "layer" becomes exposed (Pulliam 1971). Once eggs have been laid, parents faced with the risk of eagle attack may be forced to make a choice between protecting their investment and protecting themselves. During the egg stage, murre in both crevice and cliff-top subcolonies were less responsive to the appearance of eagles (Fig. 6), indicating that investment level may mediate response. However, the apparent risk to cliff-top inhabitants was still higher than that to crevice dwellers.

Despite the depressed reproduction in the cliff-top subcolonies, murre numbers on Tatoosh have been steadily increasing, at least doubling within the last decade (Paine et al. 1990). The majority of this population increase is due to the birth and rapid expansion of cliff-top subcolonies (Parrish and Paine unpubl. manuscript). Such a large and sustained annual

increase suggests that Tatoosh is not a closed system, but that immigration probably is augmenting the return of first-time native breeders. Wilson (1991) has documented a concomitant, precipitous decline in murre-colony numbers on the outer coast of Washington (exclusive of Tatoosh). Thus, it is possible that adult murrens have immigrated to Tatoosh (see also Halley and Harris 1993). On what basis do immigrants make decisions about which subcolony to join?

Although crevice-subcolony size is limited relative to cliff-top subcolonies, there are unoccupied crevices on the island. Several of these potential nesting sites have been prospected late in the season (a behavior attributed to inexperienced breeders), but none have been settled (pers. obs.). Thus, incoming breeders settle differentially on cliff tops rather than crevices, even though future reproductive success of cliff-top settlers will be low to nonexistent. Brown et al. (1990) suggested four explanations for the observed differences in bird-colony size, three of which are potentially applicable to murrens on Tatoosh: (1) ideal-free assortment; (2) individually-based optima; and (3) constraints on ability to gather information. If subcolony size is an indicator of relative quality, immigrants should select the largest aggregation in which there is space available (i.e. ideal-free assortment). Although this mechanism would explain the settlement pattern on Tatoosh, subcolony size is not a good measure of relative quality. With perfect knowledge, immigrants instead should choose to settle in occupied crevices, followed by unoccupied but suitable crevices. Only when all crevice habitat is filled should individuals add themselves to cliff-top subcolonies. Thus, it appears that immigrants do not have sufficient information about subcolony quality to make accurate decisions when they settle.

There are many interacting factors affecting future expectation of reproductive success of colonial seabirds (Brown et al. 1990, Clode 1993). Seemingly simple choices about group size or habitat type may be obscured by changes in the balance of forces (e.g. predator pressure versus food availability) as a consequence of annual variation, as well as directional change. On Tatoosh, the rapid expansion of the murre population into novel habitat (the cliff top) and the resultant eagle and murre interaction is creating a new set of subcolony optima to which the population has yet to respond.

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LITERATURE CITED

- ALEXANDER, R. D. 1974. The evolution of social behavior. *Annu. Rev. Ecol. Sys.* 5:325-384.
- BIRKHEAD, T. R. 1977. The effect of habitat and density on breeding success in the Common Guillemot (*Uria aalge*). *J. Anim. Ecol.* 46:751-764.
- BIRKHEAD, T. R. 1978. Behavioral adaptations to high density nesting in the Common Guillemot *Uria aalge*. *Anim. Behav.* 26:321-331.
- BIRKHEAD, T. R., AND M. P. HARRIS. 1985. Ecological adaptations for breeding in the Atlantic Alcidae. Pages 205-231 in *The Atlantic Alcidae* (D. N. Nettleship and T. R. Birkhead, Eds.). Academic Press, New York.
- BROWN, C. R., AND M. B. BROWN. 1987. Group-living in Cliff Swallows as an advantage in avoiding predators. *Behav. Ecol. Sociobiol.* 21:97-107.
- BROWN, C. R., B. J. STUTCHBURY, AND P. D. WALSH. 1990. Choice of colony size in birds. *Trends Ecol. & Evol.* 5:398-403.
- CLODE, D. 1993. Colonially breeding seabirds: Predators or prey? *Trends Ecol. & Evol.* 8:336-338.
- EMLEN, J. T., D. E. MILLER, R. M. EVANS, AND D. H. THOMPSON. 1966. Predator-induced parental neglect in a Ring-billed Gull subcolony. *Auk* 83:677-679.
- FRETWELL, S. D., AND LUCAS, H. L. 1969. On territorial behavior and other factors influencing habitat distribution in birds. *Acta Biotheor.* 19:16-36.
- FURNESS, R., AND P. W. MONAGHAN. 1987. Seabird ecology. Chapman and Hall, New York.
- HALLEY, D. J., AND M. P. HARRIS. 1993. Intersubcolony movement and behaviour of immature Guillemots *Uria aalge*. *Ibis* 135:264-270.
- HAMILTON, W. D. 1971. Geometry for the selfish herd. *J. Theor. Biol.* 31:142-159.
- HARRIS, M. P., AND T. R. BIRKHEAD. 1985. Breeding ecology of the Atlantic Alcidae. Pages 164-171 in *The Atlantic Alcidae* (D. N. Nettleship and T. R. Birkhead, Eds.). Academic Press, New York.
- HATCHWELL, T. J. 1991. An experimental study of the effects of timing of breeding on the repro-

- ductive success of Common Guillemots (*Uria aalge*). *J. Anim. Ecol.* 60:721-736.
- HELFMAN, G. S. 1989. Threat-sensitive predator avoidance in damselfish-trumpetfish interactions. *Behav. Ecol. Sociobiol.* 24:47-58.
- NETTLESHIP, D. N., AND P. G. H. EVANS. 1985. Distribution and status of the Atlantic Alcidae. Pages 54-155 in *The Atlantic Alcidae* (D. N. Nettleship and T. R. Birkhead, Eds.). Academic Press, New York.
- PAINE, R. T., J. T. WOOTTON, AND P. D. BOERSMA. 1990. Direct and indirect effects of Peregrine Falcon predation of seabird abundance. *Auk* 107:1-9.
- PATTERSON, I. J. 1965. Timing and spacing of broods in the Black-headed Gull *Larus ridibundus*. *Ibis* 107: 433-459.
- PULLIAM, H. R. 1971. On the advantages of flocking. *J. Theor. Biol.* 38:419-422.
- SPEAR, L. B. 1993. Dynamic and effect of Western Gulls feeding in a subcolony of Guillemots and Brandt's Cormorants. *J. Anim. Ecol.* 62:399-414.
- WILSON, U. W. 1991. Responses of three seabird species to El Niño events and other warm episodes on the Washington coast, 1979-1990. *Condor* 93: 853-858.
- WITTENBERGER, J. F., AND G. L. HUNT. 1985. The adaptive significance of coloniality in birds. *Avian Biol.* 8:1-78.
- ZAR, J. H. 1984. *Biostatistical analysis*, 2nd ed. Prentice Hall, Englewood Cliffs, New Jersey.