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TIME-BUDGETS OF COMMON MURRES AT A DECLINING AND INCREASING COLONY IN ALASKA[1]

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Abstract: We observed Common Murres (*Uria aalge*) at two breeding sites in lower Cook Inlet, Alaska, to determine whether food availability was reflected in their time-budgets at each colony. Catches of forage fish in nets and relative biomass were greater around a murre colony that has been increasing for the past 25 years than around a colony that has been decreasing over the same time period. Murres spent much more time "loafing" on their breeding ledges at the increasing colony, particularly during the incubation period and during evening hours. However, there was little or no difference between colonies in chick feeding rates, chick growth rates, or productivity. It appears that murres at the declining colony devote more time to foraging and have less discretionary time ashore. Because this had little apparent affect on their ability to feed and rear chicks, the population decline must be due to other factors. In any case, attendance time-budgets provide a more sensitive index of food availability than other breeding parameters at murre colonies.

Key words: colony attendance, Common Murre, parental attendance, time-budgets, Uria aalge.

Common Murres (*Uria aalge*) respond in nonlinear fashion to fluctuations in prey density (Cairns 1987, Piatt 1990). As long as food abundance is above threshold levels, Common Murres can maintain high levels of productivity over a wide range of prey densities by adjusting their foraging time-budget (Burger and Piatt 1990). When prey are abundant, adult murres spend more time attending breeding sites (Furness and Barrett 1985, Burger and Piatt 1990). Conversely, when prey are scarce, murres increase the amount of time spent foraging at the expense of time spent ashore (Monaghan et al. 1994). The largest difference in murre time-activity budgets between years with varying food supply is reflected in time spent at the colony by nonbrooding adults (Uttley et al. 1994).

We investigated patterns of parental attendance at two murre colonies located about 100 km apart on opposite sides of Cook Inlet, Alaska. Murre populations have been steadily declining at one colony and increasing at the other during the past 25 years (Piatt and Anderson 1996, Zador et al. 1997). These opposing trends may be related to long-term changes in the forage fish base in the Gulf of Alaska (Piatt and Anderson 1996, Anderson et al. 1997, Bechtol 1997). We present trawl, seine, and acoustic survey data that show differences in food supply between the two colonies. We tested the hypothesis that murres in the declining colony would reflect food shortage by minimizing discretionary time spent at the colony. We expected to find higher parental attendance by murres in the expanding colony.

METHODS

We conducted our attendance study during summer 1995 at Gull and Chisik Islands in lower Cook Inlet, Alaska. Chisik Island (60°09′N, 152°34′W) is located nearshore in shallow waters (< 50 m) on the western side of Cook Inlet. The murre population there has declined by 90% since 1970 to about 2,200 individuals (Piatt and Anderson 1996, Zador et al. 1997). Gull Island (59°35′N, 151°19′W) is located nearshore on the eastern side of the inlet, in Kachemak Bay, an area with generally shallow (< 50 m) waters but some deeper channels. The murre population at Gull Island has increased by about 80% since about 1984 and presently numbers about 8,500 individuals (Piatt and Anderson 1996, Zador et al. 1997).

On Chisik Island, we conducted continuous diurnal activity watches from a blind, observing 7–11 breeding pairs of murres between 07:00 and 20:00. Observers recorded arrivals, departures, incubation and brooding shift exchanges, and food deliveries. On Gull Island, we used a high-quality time-lapse video camera (Fieldcam TLV 8-mm recorder, color CCD zoom camera from Fuhrman Diversified Inc., Seabrook, Texas) to record murre activities throughout daylight hours. Only data collected between 07:00 and 20:00 were used for analyses. We positioned the camera about 10 m from a breeding ledge to include 6–8 viewable murre nest sites within the picture frame, and the video recorder taped four frames sec^{-1}. Observers later reviewed the tapes with an editing machine and high-resolution monitor to obtain data on activities (as above).

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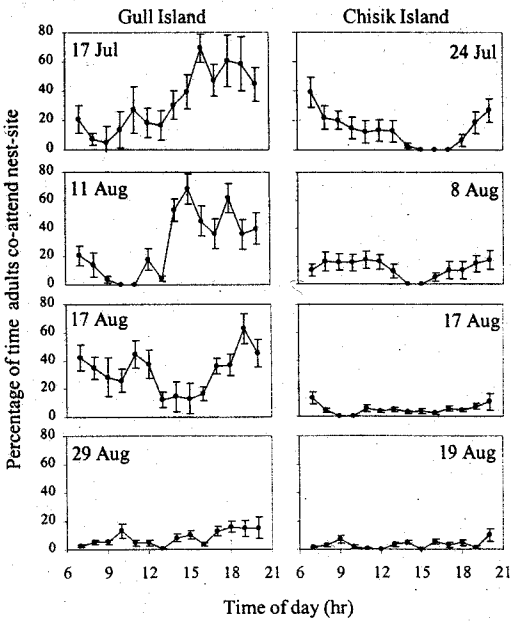

FIGURE 1. Diurnal attendance patterns of Common Murres at nest sites on Gull and Chisik Islands during early incubation (17–24 July), late incubation (8–11 August), early chick-rearing (17–19 August), and late chick-rearing (29 August). Values indicate the proportion of time (mean % ± SE) that both adults of a breeding pair were present together at a nest site.

We conducted watches at each island once during early/mid incubation (July) and once during late incubation (early August). During the chick-rearing stage (late August), we conducted watches twice at Gull Island and three times at Chisik Island. Breeding phenology was similar among colonies, with mid-hatching on about 15 August. For statistical analyses of attendance, we used data calculated in bird-minutes of attendance. For example, 75 bird-min hr^{-1} of attendance would correspond to a 1-hr period in which one mate was present at the nest for the entire hour (always the case), while the other mate attended for 15 min of that hour (60 + 15 = 75). Thus, attendance data could range only between 60 and 120 bird-min hr^{-1}. We present hourly (Fig. 1), daily, and seasonal attendance data as the percent of time that both adults of a nesting pair were together at a nest site (i.e., 25% [15/60] in the example above). We did not include exchanges between adults that occurred in less than 1 min as additional site attendance. We calculated the duration of adult foraging trips from the time elapsed between departures and arrivals at each site. We calculated feeding rates as the mean number of food deliveries per chick per hour.

Murre productivity was monitored using standard protocols (Birkhead and Nettleship 1980) on four plots at Chisik Island which included a total of 106 nest sites. Nest-site status was recorded every 2–3 days to estimate phenology and hatching success. Work on Chisik ended before fledging, however, so no final measure of breeding success was possible. On Gull Island, murres were not monitored through the breeding season. However, on 28 August, we obtained an index of productivity by counting the ratio of chicks to adults (breeding status not known) on five different plots. Chicks were captured on both islands to measure body condition, calculated as average mass (g) divided by wing length (mm) for chicks obtained during the linear phase of growth (wing lengths 21–50 mm; Harris and Wanless 1988).

In 1995, hydroacoustic surveys for fish were conducted within a 45-km radius of Chisik and Gull islands using a BIOSONICS DT4000 digital echosounder. Few mid-water trawls were conducted in 1995, and so acoustic signals could not be identified. However, relative fish biomass was calculated from each area by echo-integration of acoustic signal on transects into 10 m depth and ca. 300 m (1 min of transect) distance strata (Piatt et al. 1990). About 200 linear km of transects were surveyed hydroacoustically in each area. We conducted more mid-water trawls during July of 1996 from a 22-m stern trawler (Alaska Department of Fish and Game, *R/V Pandalus*) within 45 km of each colony. Fish were sampled using a modified herring trawl with a 9 m opening and lined with a 3 mm cod-end and collecting bucket. Nearshore fish communities were sampled using a 44-m long variable-mesh beach seine at Chisik Island during July and August of 1996 and in Kachemak Bay during May to September of 1996.

All statistical analyses were performed using SAS for Windows (SAS Institute 1998) and SigmaStat (v. 2.0, Jandel Scientific Software). Differences in attendance between colonies and breeding sites were tested by using analysis of variance (ANOVA). Where differences between breeding sites were insignificant, data were pooled and ANOVA, Kruskal-Wallis ANOVA on ranks, and Pearson correlations were calculated to examine diurnal and seasonal attendance patterns. Differences between colonies in average feeding rates and foraging trip durations per site were tested using independent two-tailed *t*-tests. All means are reported ± SE.

RESULTS

Seasonal attendance of adults at nest sites differed markedly between colonies ($F_{1,21}$ = 11.2, $P < 0.01$; Fig. 1). On Chisik Island, breeding pairs (n = 10 sites) were present together at nest sites only 8.2% of daylight hours through incubation and chick-rearing, compared to 24.2% of the time on Gull Island (n = 12 sites).

Daily attendance (n = 48 site-days) at Chisik Island decreased (r = −0.3, $P < 0.03$) as the season progressed (Kruskal-Wallis, H = 12.1, $P < 0.02$). Daily average co-attendance of both adults at sites declined from 11–13% during incubation to only 3–5% during early chick-rearing. Attendance (n = 31 site-days) also varied through the season at Gull Island ($F_{4,30}$ = 4.41, $P < 0.01$), and co-attendance of adults hovered around 28–32% during incubation and early chick-rearing, but declined to only 7.8% during late chick-rearing.

Diurnal attendance patterns changed through the

season and varied among colonies (Fig. 1). During incubation and early chick-rearing at Gull Island, average co-attendance was much higher and more variable in the latter half of the day (Fig. 1). Diurnal patterns at Chisik were quite different during these periods, showing only slight elevations in co-attendance during morning and evening hours. During the late chick-rearing stage (29 August) at Gull Island and early incubation (17–19 August) at Chisik Island, co-attendance of adults was low at all hours of the day.

We detected no significant differences between islands in the average rates at which chicks were fed ($P = 0.09$) or the duration of foraging trips ($P = 0.12$). Chicks at Gull Island were fed 0.37 ± 0.05 fish hr^{-1} ($n = 9$ sites), whereas those at Chisik Island were fed 0.29 ± 0.03 fish hr^{-1} ($n = 7$ sites). The composition of meals delivered to chicks was not quantified, but casual observations suggest that osmerids such as capelin (*Mallotus villosus*), sand lance (*Ammodytes hexapterus*), and juvenile gadids including pollock (*Theragra chalcogramma*) were most common in chick diets at both colonies. Murres at Gull Island left their breeding sites for 128 ± 14 min $trip^{-1}$ ($n = 9$ sites), whereas those at Chisik Island left their breeding sites for 167 ± 19 min $trip^{-1}$ ($n = 7$ sites).

Murres at Chisik Island had a minimum hatching success of 0.67 ± 0.11 chicks $pair^{-1}$ ($n = 4$ plots). Assuming fledging success of 95% (Harris and Wanless 1988, unpubl. data), overall breeding success may have been as high as 0.64 chicks $pair^{-1}$. At Gull Island, we observed a ratio of 0.44 ± 0.06 chicks $adult^{-1}$ ($n = 5$ plots, 337 adults) during late chick-rearing. Given that only about 70% of adult murres on ledges at that time were likely breeders (Hatch and Hatch 1990, unpubl. data), and about 8% of those were second members of a pair in attendance (Fig. 1), then breeding success was about 0.61 ± 0.08 chicks $pair^{-1}$. We detected no significant difference ($P = 0.07$) in growth among chicks from Chisik (3.71 ± 0.15 g mm^{-1} of wing length, $n = 36$) and Gull Island (4.17 ± 0.16 g mm^{-1}, $n = 16$).

Average forage fish catches in mid-water trawl nets were much higher in offshore waters around Gull Island (345 fish set^{-1}, $n = 16$ sets) than Chisik Island (92 fish set^{-1}, $n = 6$ sets). Similarly, average nearshore catches of forage fish in beach seines near Gull Island were much higher (511 fish set^{-1}, $n = 238$ sets) than those near Chisik Island (33 fish set^{-1}, $n = 30$ sets). Owing to high variability in catches, however, these differences were not statistically significant. Sand lance (*Ammodytes hexapterus*), gadids (mostly *Theragra chalcogramma*), and smelts (mostly *Mallotus villosus*) were the most common fish caught in seines and trawls. Relative acoustic biomass of fish at 0–50 m depth was an order of magnitude higher ($t_{1242} = 6.13$, $P < 0.001$) around Gull Island (9.15 ± 1.30 units) than Chisik Island (1.00 ± 0.27 units).

DISCUSSION

In light of the 90% decline in murre populations at Chisik and the 80% increase at Gull Island, it seemed reasonable to assume that forage fish have been relatively scarce and abundant, respectively, around these islands during the past 25 years (Cairns 1987, Piatt and Anderson 1996). Fish sampling and hydroacoustic surveys conducted over two years confirmed that prey are less available to birds at the declining colony at Chisik Island than at the increasing colony at Gull Island. A major shift in the composition and abundance of forage species during the late 1970s in Cook Inlet and the Gulf of Alaska probably contributed to contrasting ecological conditions at these colonies (Piatt and Anderson 1996, Anderson et al. 1997, Bechtol 1997).

Whatever the cause, we predicted correctly that murres breeding in the declining colony at Chisik Island would reflect chronic food shortage by minimizing time spent at the colony. Breeding pairs co-attended nest sites at Chisik only 8% of the time during incubation and chick-rearing compared to 24% of the time at Gull Island, whereas food abundance varied about 10-fold between the colonies. In the Shetland Islands, Uttley et al. (1994) found a similar difference in co-attendance of adult Common Murres at Sumburgh Head between poor (2.4%) and good (40%) years when food abundance varied 40-fold. At Witless Bay, Newfoundland, Common Murre co-attendance varied during four years of study between about 20–40%, when prey abundance varied 10-fold (Burger and Piatt 1990). In Norway, Thick-billed Murres (*Uria lomvia*) spent 53% of the day together at nest sites in a year when prey were "superabundant" (Furness and Barrett 1985). In contrast, Thick-billed Murres at Prince Leopold Island, Canada, co-attended nest sites only 4% of the day because of the great foraging distance to food supplies (Gaston and Nettleship 1982). Although time spent at the colony is not a direct (inverse) measure of foraging effort, it is a direct measure of time not devoted to foraging (Monaghan et al. 1994). Our data suggest that murres breeding at Gull Island devoted less time to foraging, and had more discretionary time ashore, than those at Chisik Island. This "loafing" time was apparently re-allocated to foraging when chick food demands increased late in the chick-rearing period.

Consistently low attendance at Chisik Island suggests that these birds were approaching a limit in foraging effort similar to that observed at Sumburgh Head during the poor food year (Monaghan et al. 1994, Uttley et al. 1994). Despite the poor food supply near Chisik Island, murres were able to provision chicks at a rate similar to that on Gull Island by adjusting their time budgets and working harder. In turn, neither chick growth rates nor overall breeding success differed between islands. Similarly, chick growth rates and breeding success did not vary among years of study at Sumburgh Head or Witless Bay—murres were able to adjust for interannual fluctuations in prey abundance (Burger and Piatt 1990, Monaghan et al. 1994, Uttley et al. 1994). In all studies, foraging trips were longer when food was scarcer, but differences were significant at Sumburgh Head only. Similarly, chick feeding rates did not vary among four years at Witless Bay, varied marginally in our study ($P < 0.10$), and were significantly different for murres at Sumburgh Head. In addition, chicks at Sumburgh Head fledged earlier and at a lighter mass during the food-poor year. Taken together, these data suggest that murres can buffer against a wide range of prey fluctuations as indicated

by the range of times (2–53% of daylight hours) nonbrooding adults have been observed "loafing" at nest sites. Effects of food shortage on other breeding parameters do not appear until co-attendance rates fall below about 10%, but even at lesser rates no significant variability in breeding success has been demonstrated.

We anticipated that murres on Chisik would not only exhibit lower attendance, but also would suffer low productivity—which was not the case. This raises the obvious question: if murres at Chisik are able to produce chicks in spite of food shortage, why have populations declined by 90% during the past 25 years? The decline may result from poor adult survival. Costs of rearing chicks under chronically poor feeding conditions may cause a significant reduction in overwinter survival of adults (Golet 1995). Alternatively, survival and recruitment of juveniles may be reduced if fledglings leave the colony early or in poor condition (Uttley et al. 1994). The relative importance of these factors deserve more study.

Attendance behavior is a useful parameter to measure in monitoring seabirds, particularly murres. *Uria* species are widely used as indicators of ecosystem health and as samplers of fish stocks in both the North Pacific and North Atlantic, and a wealth of data have been collected on breeding parameters such as chick growth rate and breeding success. Ironically, these parameters have proven to be least sensitive (varying at most 1.2-fold) to fluctuations in prey abundance (up to 40-fold) in studies that have included concurrent measures of prey abundance (Burger and Piatt 1990, Uttley et al. 1994, this study). In contrast, time budgets of attendance by breeding pairs of murres varied about 20-fold among studies. Time budget data are relatively easy to collect and should be added to routine monitoring studies of seabirds at their colonies.

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