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PREY DENSITY AND THE BEHAVIORAL FLEXIBILITY OF A MARINE PREDATOR: THE COMMON MURRE (*URIA AALGE*)

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Abstract. Flexible time budgets allow individual animals to buffer the effects of variable food availability by allocating more time to foraging when food density decreases. This trait should be especially important for marine predators that forage on patchy and ephemeral food resources. We examined flexible time allocation by a long-lived marine predator, the Common Murre (*Uria aalge*), using data collected in a five-year study at three colonies in Alaska (USA) with contrasting environmental conditions. Annual hydroacoustic surveys revealed an order-of-magnitude variation in food density among the 15 colony-years of study. We used data on parental time budgets and local prey density to test predictions from two hypotheses: Hypothesis A, the colony attendance of seabirds varies nonlinearly with food density; and Hypothesis B, flexible time allocation of parent murres buffers chicks against variable food availability. Hypothesis A was supported; colony attendance by murres was positively correlated with food over a limited range of poor-to-moderate food densities, but independent of food over a broader range of higher densities. This is the first empirical evidence for a nonlinear response of a marine predator's time budget to changes in prey density. Predictions from Hypothesis B were largely supported: (1) chick-feeding rates were fairly constant over a wide range of densities and only dropped below 3.5 meals per day at the low end of prey density, and (2) there was a nonlinear relationship between chick-feeding rates and time spent at the colony, with chick-feeding rates only declining after time at the colony by the nonbrooding parent was reduced to a minimum. The ability of parents to adjust their foraging time by more than 2 h/d explains why they were able to maintain chick-feeding rates of more than 3.5 meals/d across a 10-fold range in local food density.

Key words: behavioral flexibility; chick-feeding rates; colony attendance; Common Murre; hydroacoustic surveys; marine predators; prey density; seabird; time budget; time buffer; Uria aalge.

Introduction

The extent to which individuals can adjust their time–activity budgets differs among species, and understanding this flexibility is important for interpreting species-specific responses to changing environments. Flexible time budgets allow some animals to buffer the effects of variable food availability. Individuals may allocate more time to foraging when food density is low, whereas when food is abundant, they may allocate more time to other activities such as rest, play, or courtship (e.g., Hixon et al. 1983, Davies and Lundberg 1985). This type of behavioral plasticity is a useful trait for marine predators living in a variable environment characterized by patchy and ephemeral food resources.

Although the time budgets of several marine species have been shown to vary in relation to food availability (e.g., Boyd 1999, Litzow and Piatt 2002), little is known about the form and function of this relationship because the foraging behavior and food supplies of marine predators are notoriously hard to measure (Grémillet et al. 2004). Seabirds are an attractive group of animals with which to examine functional relationships because they are easy to observe where they breed on land or forage at sea, and they often feed on dense aggregations of schooling fish that may be quantified with hydroacoustics (Piatt 1990, Mehlum et al. 1999). In an effort to clarify the response of seabirds to varying food availability, Cairns (1987) hypothesized that the amount of time spent at a colony by breeding seabirds would vary nonlinearly with food availability. Cairns predicted that time spent at a colony should be minimal when food supplies are low and foraging time is high, but that

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colony time should increase rapidly over moderate-to-good food availabilities until reaching a plateau at some optimal level of colony attendance.

Flexibility of parental time budgets has been well studied in the Common Murre (*Uria aalge* Pontoppidan), a highly colonial seabird species that breeds in large colonies on narrow cliff ledges or flat islands (Harris and Birkhead 1985). Because they nest at high densities, breeders compete to occupy and maintain breeding sites (Birkhead 1985) and individuals that lose a breeding site may not breed in the following year (Harris et al. 1996). In addition to constraints associated with colonial living (Birkhead 1985), murres are central-place foragers (Orians and Pearson 1979), with time allocation influenced by the distance parents must travel between their feeding grounds and the breeding colony (Houston et al. 1996). Parents must share incubation and brooding duties (see Plate 1), and the single chick needs to be brooded constantly to protect it from predators (Harris and Birkhead 1985). In spite of these many constraints on their activities, off-duty parents can increase foraging time in exchange for time at the colony when prey is scarce (Burger and Piatt 1990, Uttley et al. 1994, Zador and Piatt 1999). Alternatively, more time can be spent at the colony when food is abundant and foraging time is minimal.

Burger and Piatt (1990) hypothesized that flexible time allocation was a mechanism by which adult murres could buffer chicks against variability in food supply. They further predicted a nonlinear relationship between provisioning rates and local food density: parents should be able to maintain adequate chick-feeding rates over a broad range of food availabilities, but should be unable to compensate fully when food is very scarce. This prediction has been supported to some extent by observations of murres made during a few years with extremely poor food supplies (Monaghan et al. 1994, Uttley et al. 1994).

All studies of parental time budgets to date have used categorical data on prey abundance, either comparing one or more years at the same colony, or two colonies with contrasting food availability (e.g., Zador and Piatt 1999). Hypotheses about the form (Cairns 1987) and function (Burger and Piatt 1990) of flexible time allocation in seabirds remain untested because they require continuous data collected over a broad range of prey densities (Piatt 1990). One must obtain an adequate number of data points above *and* below threshold values in order to define the form of nonlinear functional relationships (Hassell and May 1974). This presents practical problems in designing a study. It may take decades for prey abundance to fluctuate over the extreme range needed to resolve functional relationships at a single colony. Furthermore, surveys of marine fish are logistically complicated and expensive, and therefore difficult to sustain over long time periods. To avoid these pitfalls, we designed a five-year study of parental time budgets at three separate colonies with highly contrasting oceanographic conditions and levels of prey abundance (Piatt and Harding 2007). Annual seine, trawl, and hydroacoustic surveys revealed 1–2 orders of magnitude variation in food density among the 15 colony-years of study (Robards et al. 1999, Abookire and Piatt 2005, Speckman et al. 2005).

In this paper, we use these data to test two hypotheses: (A) colony attendance of seabirds varies nonlinearly with food density and (B) flexible time allocation of parent murres buffers chicks against variable food supplies. We used a modeling approach to test predictions from these two hypotheses. From the first hypothesis, we predicted that time spent at a colony should be minimal when food density is low, but should increase rapidly over moderate levels of food abundance until reaching a plateau over a broad range of high food densities (Cairns 1987). We tested two predicted relationships from hypothesis B: (1) chick-feeding rates should remain relatively constant over a wide range of moderate-to-high prey densities, but should be reduced under very poor foraging conditions (Burger and Piatt 1990), and (2) there should be a nonlinear relationship between provisioning rates and colony attendance; i.e., chick meal deliveries should be maintained at a relatively high and constant rate by flexible time allocation, but should be reduced once parents fall below a critical minimum of time spent at the colony. We expected this behavioral threshold to be near a point where chick-feeding rates could only be maintained if both parents foraged simultaneously, leaving the chick without any parental attention and at risk of predation.

Materials and Methods

Study sites and rationale

This study was conducted during five consecutive seasons (1995–1999) at three seabird colonies in Lower Cook Inlet, Alaska (Fig. 1), providing us with 15 colony-years of data. The colonies are separated from each other by ~100 km and are in oceanographically distinct habitats (Robards et al. 1999, Speckman 2004, Abookire and Piatt 2005). Chisik Island is adjacent to stratified, relatively warm estuarine waters with low primary productivity; Gull Island is adjacent to relatively cool, stratified, and highly productive waters that are fed by cold currents from the south; and the Barren Islands are surrounded by mixed, cold oceanic waters that result from upwelling of Gulf of Alaska water as it enters Cook Inlet (Speckman et al. 2005). The area around the Barren Islands (within the 50-km foraging range of the murre) is moderately productive relative to the other two colonies.

By including three colonies with order-of-magnitude differences in food density (grams per cubic meter) in the waters around them (*Results*; see Robards et al. 1999, Abookire and Piatt 2005, Speckman et al. 2005), our study constitutes a natural experiment to resolve the relationship between seabirds and their food supply (Piatt and Harding 2007). This approach added some

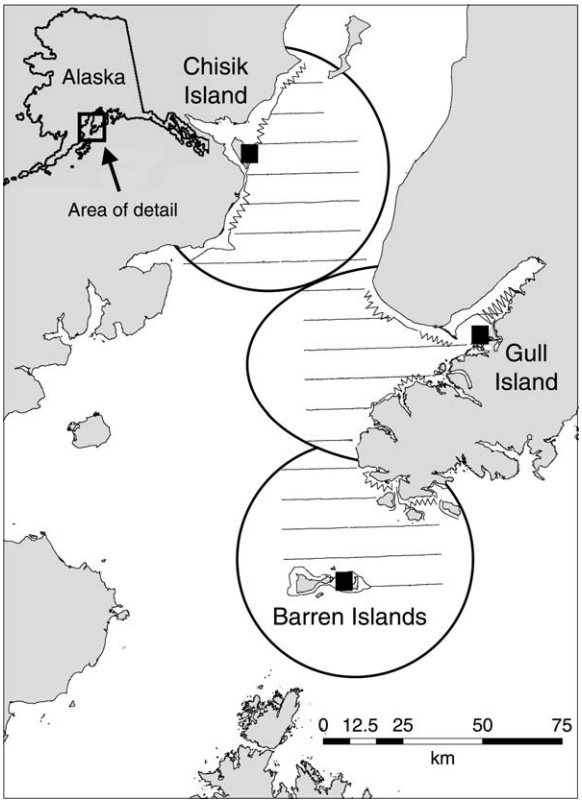


FIG. 1. Map showing location of the three Common Murre colonies and the areas and transect lines that were surveyed for fish in Lower Cook Inlet, Alaska, USA.

uncertainty to our measurements because these colonies presumably differed in other ways as well. For example, parental time allocation of seabirds may be affected by colony differences other than prey density, such as colony size (Lewis et al. 2001, Davoren and Montevecchi 2003) or distance to foraging grounds (Davoren and Montevecchi 2003). In our study, however, intercolony differences in prey density far outweighed other colony-specific factors. Although the size of each Cook Inlet murre colony differed (Chisik Island ~2200, Gull Island ~8500, Barren Islands ~51 600; Zador and Piatt 1999; D. G. Roseneau and A. B. Kettle, *unpublished data*), the colonies most similar in size (less than twofold difference between Gull and Chisik) exhibited the biggest contrast in density of prey in adjacent waters (>10-fold) and in time allocation. Similarly, there were differences among colonies with respect to distance to foraging grounds (Speckman 2004), accounting for some of the difference in foraging trip duration among colonies (ANOVA: $F_{2,200} = 28.92$, $P < 0.001$; Chisik, 229 ± 10.97 min (mean ± SE); Barren Islands,174 ± 14.50 min; and Gull Island, 137 ± 12.20 min; J. F. Piatt and A. B. Kettle, *unpublished data*). However, variation in prey density among colonies (CV = 0.69) far exceeded intercolony variation in foraging trip duration (CV = 0.26).

Similarly, we recognize that differences in chick diet composition among colonies will contribute to noise in our measurements of delivery rates (e.g., Wanless et al. 2005), but we believe that these effects are relatively minor compared to the overall effect of variability in prey density among colonies. For example, we identified thousands of murre chick meals (J. F. Piatt and A. B. Kettle, *unpublished data*) in 1995–1999 at Chisik (n = 1846), Gull ($n = 1175$), and Barren ($n = 1640$) islands. In all years, osmerids (mostly capelin [*Mallotus villosus*], 20.6 kJ/g dry mass; Anthony et al. 2000), Pacific sand lance (*Ammodytes hexapterus*, 20.0 kJ/g dry mass), and Pacific herring (*Clupea pallasii*, 17.8 kJ/g dry mass) comprised the majority of chick diets at Chisik (80.4%), Gull (89.5%), and Barren (95.6%) islands. Juvenile salmon and gadoids comprised most of the remainder of diets, but even including these less nutritious prey (17–18 kJ/g dry mass), prey quality (i.e., energy content) varied little (CV = 0.082) among colonies.

The size of prey delivered is also an important source of variability in food delivery, especially for single-prey loaders such as murres (e.g., Wilson et al. 2004). We were able to make visual calibrations of prey size by estimating prey length relative to bill length of birds carrying fish at Gull ($n = 1031$ prey) and Chisik ($n = 1796$ prey) islands, and found that there was minimal variability in the annual mean lengths of chick prey delivered at both colonies (CV = 0.038) and minimal among-year variability in prey length within each colony (CV = 0.022–0.070). There was also a similar level of among-colony variability in size of capelin (*Mallotus villosus,* CV= 0.060) and Pacific sand lance (CV = 0.089) captured in mid-water trawls around all three colonies in Cook Inlet (Speckman 2004).

In summary, neither prey quality nor size varied much among colonies, allowing us to use the common currencies of meal delivery rate at colonies and average prey density at sea to examine functional relationships between murre behavior and fluctuations in food supply.

Local prey density

We measured local fish densities around each of the three seabird colonies by conducting hydroacoustic surveys on a grid of transects arranged in most years as shown in Fig. 1, within a roughly 50 km radius of each site (details are found in Speckman 2004, Speckman et al. 2005). Although Common Murres may sometimes forage at greater distances from their colonies (Cairns et al. 1990), most forage within ~50 km of Cook Inlet colonies during chick-rearing (Speckman 2004). Distances surveyed among areas were similar, and averaged ~1100 linear kilometers of transects for all areas combined in each year except for 1995 (820 km surveyed with fewer transects, but similar geographic range) and 1996 (2020 km surveyed over a much larger area, with a subset of ~1100 km used here for analysis) (Speckman 2004; J. F. Piatt, *unpublished data*). Hydroacoustic surveys were conducted during a three-week

period in each year (1995, 10–23 August; 1996, 14–31 July; 1997, 19 July–8 August; 1998, 21 July–12 August; 1999, 25 July–16 August). Mean Common Murre hatch date over all colony years was 10 August (J. F. Piatt and A. B. Kettle, *unpublished data*).

Hydroacoustic data were collected with a single-beam 120-kHz BioSonics DT4000 system (BioSonics, Seattle, Washington, USA) with a 6° beam angle. Before each cruise, the acoustic system was calibrated using a 33.2-mm tungsten carbide sphere with expected target strength of −40.6 dB. To identify acoustic signals and measure the size of individual fish, we conducted 163 mid-water trawls (see Abookire and Piatt 2005, Speckman et al. 2005). Acoustic data were analyzed using SonarData Echoview software (Version 2.10.48, SonarData, Hobart, Tasmania, Australia) and were integrated with a minimum threshold of −70 dB to obtain relative measures of acoustic biomass, S_A, which is a measure of area scattering (rather than volume scattering) in units of square meters per square nautical mile [1 nautical mile = 1.852 km] (a proxy for fish biomass). These were converted to absolute estimates of fish density (number of fish per cubic meter) by dividing S_A by σ (backscattering cross-sectional area of single prey) for species with the following known target strengths (TS) and body length (L, in centimeters): walleye pollock (*Theragra chalcogramma*) $TS = 21.1 \log(L) - 70.5$; herring $TS = 202.0 \log(L) - 67.6$; and capelin $TS = 28.4 \log(L) - 81.8$ (all from Gauthier and Horne 2004); sand lance $TS = 20.0 \log(L) - 80$ (Thomas et al. 2002); and Pacific cod (*Gadus macrocephalus*) $TS = 20.0 \log(L) - 65$ (Rose and Leggett 1988). (The equations yield the amount of scattering per individual fish; the sum of the scattering from a given area is divided by the amount of scattering expected per individual to estimate the total number of fish in that area.) These species accounted for 99.2% of all fish caught. The proportion of catch, expressed as Catch Per Unit Effort (CPUE), standardized to number of fish captured per kilometer trawled, was used to convert acoustic backscatter to species-specific fish density (in fish per square meter) (Speckman 2004). Geometric mean acoustic densities were calculated from transformed data as mean ($\log x + 1$) values, and then were transformed back to original density units (Johannesson and Mitson 1983). We used a two-way ANOVA to examine differences in food density (in grams per cubic meter) among colonies and years (using SPSS; George and Mallery 2002).

Species composition was determined from 163 mid-water trawls (see Robards et al. 1999, Abookire and Piatt 2005). The most abundant taxa caught in mid-water trawls were forage fish <200 mm in length (Abookire and Piatt 2005). Although 39 species were caught in 163 mid-water trawls conducted in waters adjacent to all three colonies during 1996–1999 (Abookire and Piatt 2005), catches consisted largely of only four taxa: Pacific sand lance (71% of the catch, length 71.8 ± 13.4 mm (mean ± SD), $n = 7976$ fish lengths); Pacific herring (17.7%, 74.4 ± 42.5 mm, $n = 2873$); juvenile gadoids such as walleye pollock (8.8%, 54.8 ± 12.3 mm, $n = 5146$); and osmerids such as capelin (1.7%, 88.3 ± 18.9 mm, $n = 1731$) (Abookire and Piatt 2005).

Parental behavior

We measured parental time spent at the colony and chick-feeding rates of Common Murres during each of the 15 colony-years. Data were collected by direct observations of murres on Chisik Island, and indirectly, using a time-lapse video camera, on Gull Island (details in Zador and Piatt 1999). Murres at the Barren Islands were observed directly in 1995 and by time-lapse video in 1996–1999.

Birds at each colony were observed on plots containing 7–12 breeding pairs of murres from sunrise to sunset (about 07:00 to 21:00 hours in late August at Gull Island). To standardize comparisons among colony-years in this analysis, we selected data collected between 07:00 to 20:00 hours Alaska Daylight Time on three observation days during the chick-rearing phase at each colony (except for two days at Barrens in 1995). We observed the same nest sites within each summer, although failed nests were replaced in later watches. Observation days were scheduled to sample the early, middle, and late parts of the chick-rearing phase to control for any change in provisioning behavior with chick age (Birkhead and Nettleship 1987).

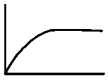
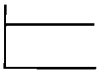
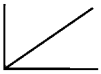
We noted each parent's arrival and departure time at the colony and the time of food delivery to chicks. Attendance was measured in bird-minutes per hour. For example, where one brooding parent attended its nest for a full hour, and the off-duty partner attended for half of that hour, we calculated 90 bird-minutes of attendance for that hour. Fewer than 60 bird-minutes of attendance would mean that the egg or chick was left unattended for some period of time. Nest site was a sample unit, with mean colony attendance calculated per nest from data pooled over the chick-rearing period. Chick-feeding rates (number of feeds per hour) per nest were also calculated from data pooled over the chick-rearing period.

Hypotheses

We used data on parental time budgets and local prey density to test predictions from two hypotheses (Table 1): Hypothesis A, the colony attendance of seabirds varies nonlinearly with food density; and Hypothesis B, flexible time allocation of parent murres buffers chicks against variable food availability.

Hypothesis A.—We compared the fit of our data to three models (Table 1). The first of these models assumes the predicted nonlinear relationship between food density and time spent at the colony (Cairns 1987), with colony attendance increasing over a limited range of poor-to-moderate food densities, but constant over a broad range of higher densities. The second model (null) assumes no relationship between food density and

TABLE 1. Two major hypotheses (A, B) on the flexibility of parental time budgets of Common Murres with three separate predicted relationships tested by comparing the fit of colony-mean annual values to the models using Akaike's information criterion.

			Predicted models evaluated								
											
	Relationships		Nonlinear			Null			Linear-positive		
Hypothesis	x-axis	y-axis	ΔAIC_c	w	r^2	ΔAIC_c	w	r^2	ΔAIC_c	w	r^2
A1	food density	colony attendance	**0.00**	**0.71**	**0.65**	8.80	0.01	0.0	1.85	0.28	0.49
B1	food density	chick-feeding rate	2.86	0.12	0.15	0.74	0.36	0.0	**0.0**	**0.52**	**0.12**
B2	colony attendance	chick-feeding rate	**0.0**	**0.87**	**0.53**	4.30	0.10	0.0	6.63	0.03	0.06

Notes: Hypothesis A: The colony attendance of seabirds varies nonlinearly with food density (Cairns 1987). Hypothesis B: The flexible time allocation of parent murres buffers chicks against variable food availability (Burger and Piatt 1990). The best-fitting model for each predicted relationship is boldfaced; w is the Akaike weight. Model-averaged fits to the data for each prediction are shown in Fig. 2.

colony attendance. This relationship might exist if our study only encompassed high levels of food density. The third model assumes a positive, linear relationship between food density and colony attendance, the response predicted if food were limited to a range of poor densities.

Hypothesis B.—We tested two predicted relationships. (1) We examined the relationship between provisioning rates and prey density to test the prediction that chick-feeding rates remain relatively constant over a wide range of moderate-to-high prey densities, but are reduced under very poor foraging conditions (Burger and Piatt 1990). This prediction can be mathematically depicted as a nonlinear model (Table 1). We contrasted the fit of our data to this predicted nonlinear relation model to the fit of a model with no relation (null), and to the fit of a model with a linear relationship between food density and chick-feeding rates. If foraging conditions encountered in this study were limited to either a relatively low or high range of density, we predicted data to best fit either a linear increase or a null model, respectively. (2) We examined the relationship between provisioning rates and colony attendance to test the assumption that flexible time allocation is the behavioral mechanism for buffering chicks against variable food availability. We predicted that chick meal deliveries should be maintained at a relatively high and constant rate by flexible time allocation, but would be reduced once parents fell below some critical minimum amount of time spent at the colony (i.e., our data would best fit the nonlinear model; Table 1). We compared the fit of our data to this predicted nonlinear model with that of a model with no relation (null) and a linear model where chick-feeding rates increase with increased time spent at the colony. Similar to other predictions, we predicted that a null or linear increase model would be supported if the range of food availabilities encompassed in the 15-colony-year study were limited to either a low or high range of prey densities.

We tested each of these predictions by comparing the fit of the models depicted in Table 1 to colony mean values using the Akaike information criterion, adjusted for finite sample size (AIC_c; Burnham and Anderson 2002). Each model was statistically represented with a least-squares regression model in which the error sums of squares, sample size, and number of estimated parameters all influenced the AIC_c calculation (Burnham and Anderson 2002:60–66). The model with the lowest AIC_c best represented the data. The nonlinear model can be described as a quadratic with plateau as it represents a joint, or piecewise model (Toms and Lesperance 2003) in which the first piece represents a quadratic function, the second piece represents a flat asymptote or plateau of zero slope, and the two pieces intersect at a point that their functions have in common (SAS Institute 1990:1162). We provide initial values and ranges for the parameters to be estimated and then the maximum likelihood algorithm searched for parameter values that minimized residuals while also satisfying the conditions just described concerning a quadratic shape joined with a flat asymptote (SAS Institute 1990:1162). For each model we also present an AIC_c weight that reflects the relative likelihood of that model being the best-fitting model among those considered, and where all AIC_c weights within an analysis sum to 1. These AIC_c weights enabled us to employ model-averaging procedures, which allow one to spread inference among competing models in an appropriately weighted fashion rather than focusing on the single best model (Burnham and Anderson 2002).

RESULTS

Local food density

Mean prey density varied among the 15 colony-years: overall 0.0353 ± 0.006 g/m^3 (mean $\pm$ SE), CV = 0.69, minimum = 0.0078 g/m^3, maximum = 0.0899 g/m^3). Mean prey densities per colony-year differed significantly among the three colonies (ANOVA: $F_{2,8} = 5.38$, $P = 0.033$), but did not differ among years (1995–1999; ANOVA: $F_{4,8} = 0.73$, $P = 0.594$). Prey density was significantly higher at Gull Island than either Chisik Island or the Barren Islands (Tukey's multiple compar-

ison test, $P < 0.05$; Chisik = 0.0138 ± 0.002 g/m^3; Barren = 0.0383 ± 0.008 g/m^3; Gull = 0.0540 ± 0.012 g/m^3).

Hypothesis A: the colony attendance of seabirds varies nonlinearly with food density.—Time spent at the colony by Common Murres varied nonlinearly with food availability (Table 1, Fig. 2). Overall, the nonlinear model best fit the data ($\Delta AIC_c > 1.0$ for competing models), with time at the colony reaching a plateau of 72.1 bird-min/h over conditions of moderate-to-high food abundance. This equated to 12 bird-min/h spent at the nest site by the nonbrooding parent; equivalent to 3 h of colony time in a 15-h day (the average number of daylight hours from hatching to fledging). Time spent at the colony was only correlated with changing food density over the poor-to-moderate range of prey densities, and was independent of food density above 0.058 g/m^3. The relationship between food density and colony attendance differed among colonies, reflecting the contrasting prey densities of each colony. The relationship was linear at Chisik Island (the colony characterized by the lowest food density) and almost null at the colony with the highest food density (Gull Island).

Hypothesis B: the flexible time allocation of parental murres buffers chicks against variable food availability.—

1. *Relationship between chick-feeding rate and food density*.—Annual mean chick-feeding rates ranged from 0.15 to 0.36 meals/h, or 2.3 to 5.4 meals per 15-h day. Overall, the data were best described by a linear model, with chick-feeding rates increasing with food density (Table 1, Fig. 2). The nonlinear model fit the data poorly ($\Delta AIC_c = 2.9$, AIC_c weight = 0.12).

2. *Relationship between chick-feeding rate and colony attendance*.—Overall, the nonlinear model best fit the data ($\Delta AIC_c > 4.0$ for competing models); with ~0.27 meals/h (translating to 4.1 meals per 15-h day) delivered over a 4 h/d range in the amount of time the nonbrooding parent spent at the colony (Table 1, Fig. 2). Chick-feeding rates sharply declined when parents spent less than 63 bird-min/h (sum of time for both parents) at the colony. This transition point translated to less than 3 min/h or 45 min in a 15-h day spent at the colony by the off-duty parent.

Discussion

Hypothesis A: the colony attendance of seabirds varies nonlinearly with food density

The amount of time seabirds spend at their colony represents a balance between competing needs to maintain a nest site at the colony and to acquire food at sea. Cairns (1987) proposed that time spent at the colony should rise rapidly with increasing prey density until birds exceed some threshold that satisfies their minimum need to attend the colony. We provide the first empirical evidence in support of Cairn's hypothesis: colony attendance by murres at colonies in lower Cook Inlet, Alaska, increased rapidly over a limited range of

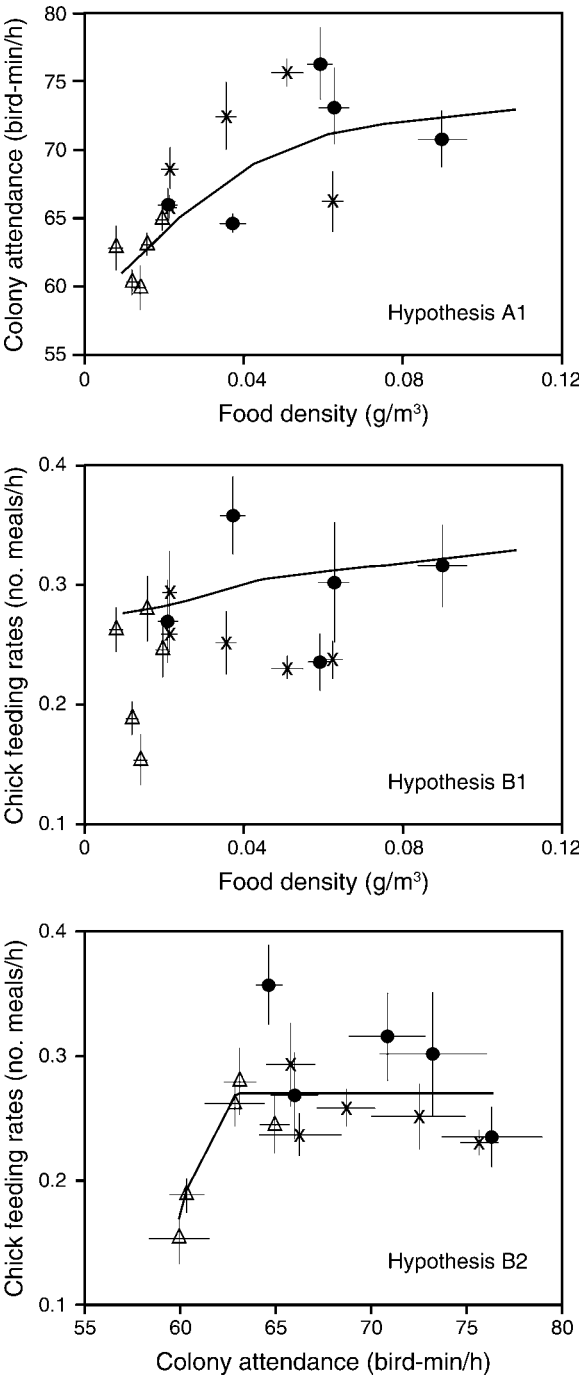


FIG. 2. For each hypothesis and predicted relationship depicted in Table 1, we show the data and the fitted line of predicted values from regression equations. Each fitted line was derived by using weighted averages of predicted values arising from the three contrasted models, where weights were the AIC_c weights. Values (mean ± SE) from the three colonies are identified by different symbols: solid circles for Gull Island, crosses for the Barrens, and open triangles for Chisik Island.

PLATE 1. A breeding pair of Common Murres attend to their chick at the nest site. One adult invariably attends the chick, but the amount of time that both adults can attend together varies with local food availability. Photo credit: M. T. Schultz.

poor-to-moderate prey densities, and then leveled off to become independent of food at high prey densities. The only reason that we could characterize this nonlinear relationship was because we designed the study around three adjacent murre colonies with highly contrasting environmental conditions (Piatt and Harding 2007). If prey densities had been restricted to only one end of the spectrum (e.g., because we studied only one colony with limited variability over 15 years), we might have falsely concluded that there was a linear or null response to prey density.

Colony attendance was independent of prey density over a broad range of moderate-to-high food densities, and that plateau in attendance (at ~3 h/d) presumably reflects a trade-off between the costs (e.g., adult predation risk, a limit on available foraging time) and benefits (e.g., pair bonding, defending nest sites, allopreening) of time spent at the colony (Cairns 1987, Jones et al. 2002, Davoren and Montevecchi 2003). Parents may also prioritize time at the colony in order to secure future reproductive success over increased provisioning rates once chicks have received the minimum quantity of food needed for survival. Some of the variation in attendance around the asymptote probably resulted from differences in colony size, breeding density and predation pressure, which in turn could affect nest-site competition and the relative importance of time spent at the colony (Parrish et al. 2001, Jones et al. 2002, Davoren and Montevecchi 2003). Variation in time spent together at the colony may also reflect variation in

pair quality (Lewis et al. 2006), with highly efficient foragers able to spend more time at the colony. Time allocation may also be affected by other extrinsic factors such as weather (Birkhead 1977, Finney et al. 1999), daylight hours (a function of latitude; Jones et al. 2002), and interspecific competition for food associated with colony size (Lewis et al. 2001, Jones et al. 2002). Although we believe that our study had a sufficiently representative sample to determine the relationship between food density and the parental behavior of murres, we acknowledge that simultaneous daily measures of food density and parental behavior at each colony may have determined this relationship to a greater degree of accuracy. Although daily hydroacoustic surveys are rarely possible, alongside daily observations on parental behavior they would provide an insight into the daily variation of prey availability and the response of a marine predator.

The functional response of predators to increasing prey density is usually nonlinear and asymptotic (Holling 1959, Goss-Custard 1970, Hassell and May 1974, Murdoch and Oaten 1975). Direct measures of the functional response parameters, such as prey consumption rate, are hard to obtain in the marine environment. Indirect measures of foraging behavior such as numerical aggregation, biomass accumulation, or reproductive success have been used as proxies to characterize the functional response of marine predators to variation in prey abundance (e.g., Piatt 1990, Piatt and Methven 1992, Philips et al. 1996, Anker-Nilssen et al. 1997, Essington and Hansson 2004). To this suite of parameters, we can add attendance time-budget data as an indirect proxy of foraging behavior.

From the ecological standpoint, nonlinearity in the response of coexisting predators that feed on shared prey may allow specialization of predators on differing densities of shared prey (Piatt 1990, Piatt and Methven 1992). At the ecosystem scale, this type of nonlinearity results in dynamic predator–prey relationships and contributes to the propensity for biological components of marine ecosystems to undergo rapid step-like changes, or so-called "regime shifts" (Hare and Mantua 2000, Hsieh et al. 2005).

Knowledge of the form or shape of functional relationships is also essential for interpreting species-specific responses to their changing environment. For example, the nonlinearity in the functional relationship between murre time allocation and prey density introduces an on–off quality into the use of parental time budgets as an indicator, with attendance only serving as a useful indicator of change in the marine ecosystem over a limited range of poor-to-moderate food densities (Piatt and Harding 2007).

Hypothesis B: the flexible time allocation of parental murres buffers chicks against variable food availability

Our study provided strong evidence that the flexible time allocation of parent murres buffers chicks against variable food availability. We examined two predicted relationships underlying the buffering hypothesis. The first prediction is that provisioning would be maintained at a relatively high and constant rate over a broad range of food densities and would be reduced only when food resources were extremely scarce (Burger and Piatt 1990). This assumption was supported to some extent because chick-feeding rates were fairly constant over a wide range of food densities, and only dropped below 0.23 meals/h at extremely low prey densities. Furthermore, the three highest provisioning rates observed at Gull Island may be inflated by the fact that foraging grounds were closer for this colony than for the others (Speckman 2004), and more trips were possible within the same time budget. Although the linear response model provided the best fit to the data, a wholly linear relationship is not possible: feeding rates cannot intercept the y-axis at the point suggested in the graph because parents would be unable to provision their chicks when food density was zero. It is more plausible that we are lacking in data at the extreme low end of prey density with which to resolve the relationship, and it is actually nonlinear like the others. Indeed, the data do indicate a tendency for chick-feeding rates to drop at the low end of prey density.

Finally, the prediction that provisioning rates should be a nonlinear function of colony attendance was well supported. Chick-feeding rates plateaued at 4.1 meals per 15-h day over a wide range in the amount of time parents spent at the colony. Only when attendance dropped below 63 bird-min/h, equivalent to the non-brooding parent spending less than 45 min/d at the colony, did the provisioning rate diminish. The maximum extent to which parents can buffer their chick against adverse foraging conditions is constrained by the need for at least one parent to constantly brood the chick. Parents cannot allocate more time to foraging when attendance falls below 60 bird-min/h without leaving the chick unattended. This will usually result in chick mortality from predation, exposure, or falling from the cliff, the alternative being that provisioning rates will decline and chicks may fledge in poor condition (Monaghan et al. 1994, Uttley et al. 1994, Davoren and Montevecchi 2003). This lower threshold also may be partly driven by reproductive costs, with parents of long-lived species being expected to invest less heavily in reproduction by reducing their provisioning rate and eventually abandoning the breeding attempt when food is limited (Drent and Daan 1980, Erikstad et al. 1998, Golet et al. 2004).

These findings are supported by the literature, in which chick feeding rates of Common Murres rarely drop below 3 meals/d except in the most extreme of poor food years (Harris and Wanless 1988, Burger and Piatt 1990, Uttley et al. 1994), whereas discretionary time spent at the colony has varied from ~2.4% to 40% of daylight hours among studies to date (Zador and Piatt 1999).

Although Common Murres in our study demonstrated strong buffering capacity, other sympatric species have less behavioral flexibility. For example, species with specialized feeding habits, expensive food-searching techniques, or small body size, such as Common Terns (*Sterna hirundo* Linnaeus), may have little flexibility in their time budgets and are more vulnerable to breeding failure in response to food shortage than are murres (Pearson 1968, Monaghan et al. 1989).

In summary, our study identified two important behavioral thresholds in the flexibility of parental time allocation: (1) nonbrooding adults spend no more than about 3 h/d (equivalent to 72 bird-min/h) at the colony, regardless of foraging conditions, and (2) below 45 min/d (equivalent to 63 bird-min/h) of colony attendance by the nonbrooding adult, provisioning of chicks becomes difficult. These behavioral thresholds represent an upper and lower limit to the flexibility of parental time allocation, and define the window of buffering capacity for Common Murres. The ability of murres to adjust their foraging time by more than 2h/d explains why parents were able to maintain chick-feeding rates at over 3.5 meals/d across a 10-fold range in food densities. Murres live in a marine environment characterized by patchy and ephemeral food availability, and this buffering capacity may partly explain why murres are so successful at fledging chicks throughout their circumpolar range.

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