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SPATIOTEMPORAL PREDICTABILITY OF SCHOOLING AND NONSCHOOLING PREY OF PIGEON GUILLEMOTS

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Abstract. Low spatiotemporal variability in the abundance of nonschooling prey might allow Pigeon Guillemots (*Cepphus columba*) to maintain the high chick provisioning rates that are characteristic of the species. We tested predictions of this hypothesis with data collected with beach seines and scuba and hydroacoustic surveys in Kachemak Bay, Alaska, during 1996–1999. Coefficients of variability were 20–211% greater for schooling than nonschooling prey on day, seasonal, and km scales. However, the proportion of schooling prey in chick diets explained relatively little variability in Pigeon Guillemot meal delivery rates at the scale of hours ($r^2 = 0.07$) and weeks ($r^2 = 0.19$). Behavioral adaptations such as flexible time budgets likely ameliorate the negative effects of high resource variability, but we propose that these adaptations are only effective when schooling prey are available at distances well below the maximum foraging range of the species.

Key words: Cepphus, *demersal, foraging, pelagic, provisioning, quality–variability trade-off, seabirds.*

Previsibilidad Espacio-Temporal de Presas que Forman y No Forman Cardúmenes de *Cepphus columba*

Resumen. La baja variabilidad espacio-temporal en la abundancia de presas que no forman cardúmenes podría permitir que *Cepphus columba* mantenga las altas tasas de aprovisionamiento de los pichones que caracterizan a esta especie. Evaluamos las predicciones de esta hipótesis con datos colectados mediante redes barredoras de playa y buceo y muestreos hidro-acústicos en la Bahía Kachemak, Alaska, durante 1996–1999. Los coeficientes de variabilidad fueron 20–211% mayores para las presas que forman cardúmenes que para las que no forman cardúmenes a las escalas diaria, estacional y de km. Sin embargo, la proporción de presas que forman cardúmenes en la dieta de los pichones explicó relativamente poca variabilidad en las tasas de entrega de alimento de *C. columba* a la escala de horas ($r^2 = 0.07$) y semanas ($r^2 = 0.19$). Las adaptaciones de comportamiento como presupuestos de tiempo flexibles probablemente corrigen los efectos negativos de la alta variación de recursos, pero proponemos que estas adaptaciones son sólo efectivas cuando las presas que forman cardúmenes están disponibles a distancias bien por debajo del rango máximo de forrajeo de la especie.

Cepphus guillemots are the only auks (Alcidae) that raise two chicks to near-adult weight in the nest (Sealy 1973). *Cepphus* guillemots also have shorter foraging ranges than other auks (typically <10 km), and feed on a higher proportion of demersal fishes and benthic invertebrates than other members of the family (Gaston and Jones 1998). These prey contain less lipid than the pelagic fishes and crustaceans that dominate the diets of most auks, and are therefore lower in energy density (kJ g^{-1}; Norrbin and Båmstedt 1984, Anthony et al. 2000). The higher energy density of pelagic prey results in increased chick growth rates and reproductive success for Pigeon Guillemots (*Cepphus columba*) that feed their chicks these prey (Golet et al. 2000, Litzow et al. 2002). However, in spite of these benefits of pelagic prey, *Cepphus* guillemots often feed chicks mostly demersal fishes, even when pelagic prey are apparently abundant (Cairns 1987, Golet et al. 2000,

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Litzow et al. 2000). The answer to this paradox may lie in differences in dispersion of demersal prey, which are typically nonschooling, and pelagic prey, which are exclusively schooling. Kuletz (1983) and Cairns (1987) proposed that nonschooling fishes are spatially and temporally more predictable than schooling fishes, and that this predictability offsets the disadvantage of lower energy density by allowing *Cepphus* guillemots to maintain the high provisioning rates necessary to raise two chicks to near-adult weight. This ''quality–variability trade-off'' hypothesis fits with the general view that distributions of schooling fishes and crustaceans are spatially and temporally more heterogeneous than those of nonschooling taxa (Valiela 1995), and the recognition that high variability of schooling prey is an important constraint on seabird foraging success (Lack 1968, Ashmole 1971). Schooling prey are more variable than nonschooling prey on interannual time scales, both in the environment (Litzow and Piatt 2003) and in Pigeon Guillemot diets (Golet et al. 2000). However, we are not aware of previous studies that have compared variability in abundance of the two prey groups at scales (days, weeks, and km) that match the temporal and spatial scales of *Cepphus* foraging during chick rearing. Such a comparison may shed light on factors shaping the foraging ecology and life history of seabirds feeding on these two prey types.

In this paper we compare the spatial and temporal variability of schooling and nonschooling prey of Pigeon Guillemots at these finer scales, using data on prey abundance that were collected in Kachemak Bay, Alaska, during 1996–1999 with beach seines, scuba transects, and hydroacoustic surveys. We also use data from all-day watches of Pigeon Guillemot chick provisioning to relate the proportion of schooling prey in the diet to variability in meal delivery rates. Our objectives were to test two predictions of the quality–variability trade-off hypothesis: (1) schooling prey species are spatially and temporally more variable in abundance than nonschooling prey species; and (2) meal delivery rates are more variable when schooling prey dominate diets.

METHODS

Kachemak Bay (59°35′N, 151°19′W) is located on the east shore of lower Cook Inlet, Alaska. Pigeon Guillemots nest in approximately 30 small colonies of 2–15 nests each and in numerous solitary sites on the south shore of Kachemak Bay, and approximately 500–600 adults are present in the area during the nesting season. Chick diets at some colonies are dominated by a pelagic schooling fish, Pacific sand lance (*Ammodytes hexapterus*), while diets at other colonies are dominated by a variety of nonschooling demersal fishes and hermit crabs (*Pagurus* spp.; Litzow et al. 1998, 2000).

We used catch per unit effort (with units of number of fish set^{-1}) data from beach seines to measure seasonal and km-scale variability in prey abundance (see Abookire et al. 2000, Litzow et al. 2000 for detailed methods). We fished with a 44-m-long net at 11 stations every 2 weeks during June, July, and August of 1996–1999 ($n = 231$ sets). Stations were separated by 1.5–16 km over 44 km of shoreline (straight-line distance), and sets were made within one hour of spring low tides. Beach seines sample the shallow (≤5 m) nearshore waters where Pigeon Guillemots in the study area mostly forage (Litzow et al., unpubl. data). Fish were identified to species, except for snake pricklebacks (*Lumpenus sagitta*) and slender eelblennys (*L. fabricii*), which could not be reliably distinguished in the field. We were only interested in studying fishes that were important prey for guillemots and that were caught often enough in beach seines to generate accurate abundance estimates. We therefore limited our analysis to taxa with catch per unit effort ≥1 fish set^{-1} and those documented as major prey of Pigeon Guillemots in Alaska (i.e., ≥1% of meals in a colony-year; Golet et al. 2000, Litzow et al. 2000).

We used repeated scuba and hydroacoustic surveys to measure among-day variability in prey abundance during July 1999. Scuba and hydroacoustic transects were set in areas where radio-tagged Pigeon Guillemots had been observed foraging on nonschooling fishes and sand lance, respectively (Litzow and Piatt 2003). All surveys were conducted within 1 hr of low tide. Scuba transects were 60–100 m long and took place in 5–11 m of water. Transect depth was held constant ±1 m. We counted all demersal fishes and hermit crabs in a 2-m swath along the transect and identified prey to the lowest possible taxonomic level. Nonschooling prey abundance was defined as the number of prey items in taxonomic groups consumed by Pigeon Guillemots (Arctic shanny [*Stichaeus punctatus*], flatfish [Pleuronectidae], gunnels [Pholidae], pricklebacks [*Lumpenus* spp.], rockfish [*Sebastes* spp.], ronquils [*Bathymaster signatus* and *Ronquilus jordani*], sculpins [Cottidae], and hermit crabs). Three transects (separated by 0.5 to 11 km) were each surveyed two to three times at intervals of 1–2 days ($n = 7$ total replicates).

Hydroacoustic surveys were conducted from an 11-m boat. Six transects were each surveyed on 3 consecutive days ($n = 18$ total replicates). Transects were 100 m long, ran perpendicular to the shore beginning in 3-m-deep water, and were separated by >200 m. Hydroacoustic data were collected with a single-beam 120-kHz Biosonics DT4000 transducer with a 6° beam angle (Biosonics, Inc., Seattle, Washington). Data were analyzed with Echoview (Sonar Data Proprietary Ltd. 2000). Species composition could not be determined during our hydroacoustic surveys, so we used relative acoustic biomass (mean backscattering m^{-2}), and did not attempt to estimate actual biomass using species-specific target strengths. We calculated relative acoustic biomass with binned cells (5 m × 1 min blocks) with an integration threshold of -68 dB and bottom blanking at -1 m, and values were averaged for each transect. Midwater trawls in Kachemak Bay indicate that the pelagic fish community is dominated by sand lance, with an order of magnitude less Pacific herring (*Clupea pallasi*), capelin (*Mallotus villosus*), juvenile walleye pollock (*Theragra chalcogramma*), and juvenile Pacific cod (*Gadus macrocephalus*; Robards et al. 1999; Abookire et al., unpubl. data), so we assumed that sand lance comprised the majority of acoustic biomass during our surveys.

We collected Pigeon Guillemot delivery rate data in July and August during 1996–1999 at six guillemot colonies in Kachemak Bay. We observed breeding Pigeon Guillemots from anchored boats (using binoculars) or from blinds (using telescopes) during all-day watches (06:00–22:00 AST). We watched two to five nests during each watch, and typically could not identify individual mates, so we use the nest as our sample unit (n = 64 nests). We recorded the time of each delivery, and identified each meal to the lowest possible taxonomic level. A subset of nests were accessible so that we could determine brood size and chick age, and we observed these more than once in a year so that we could calculate seasonal variability in delivery rate (n = 22). The mean range of dates for nests watched more than once was 13.5 ± 5.6 [SD] days.

STATISTICAL ANALYSES

Among-day variability in abundance for schooling and nonschooling prey was defined as the coefficient of variability (CV) in abundance among replicates at individual hydroacoustic and scuba transects, respectively. Seasonal variability for both prey types was defined as CV among bimonthly sampling periods at individual beach seine sites, and grand means of annual values from individual sites were used in analysis. Km-scale variability was defined as the annual mean CV among sites. For analysis of seasonal and km-scale variability we used individual taxa nested within prey type (schooling or nonschooling) as our sample unit. We treated CV values for the 11 stations as subsamples of seasonal-scale variability for each prey species by including site as an independent factor in a general linear model (GLM; Zar 1999). For analysis of km-scale variability we treated annual mean values of CV among seine stations as subsamples by including year as a factor. We also compared abundance between prey groups by comparing catch per unit effort in GLM with site, species(prey type), and prey type as factors. Catch per unit effort data were log (x + 1) transformed for this analysis to meet assumptions of homoscedasticity.

We calculated hour-scale variability in delivery rate (meals hr^{-1}) as SD in delivery rate among hours within individual watches for individual nests. To avoid pseudoreplication we used average SD values when individual nests were watched more than once in a year. Seasonal-scale variability was calculated as SD in delivery rate among days for nests that were watched more than once in a year. Delivery rates are affected by changes in nestling demand (brood size and chick age; Drent 1965). We controlled for variability in brood size by calculating per capita delivery rates (meals chick^{-1} hr^{-1}). We controlled for variability in chick age in GLM by including SD in chick age among individual provisioning watches, as well as the mean proportion of schooling prey in the diet, as independent variables, and SD in delivery rate as the dependent variable. We used partial r^2 values in order to assess the contribution to variability in delivery rates due to each of these independent factors. Proportional data were arcsine transformed to meet assumptions of normality, and type-III sums of squares were used for all GLM analysis (SAS Institute 2000). We set $\alpha = 0.05$. Means are presented ± SE, and seine CV values are least-squares means from GLM.

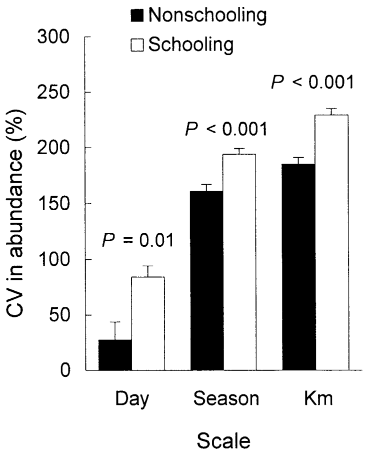

FIGURE 1. Spatiotemporal variability of schooling and nonschooling prey of Pigeon Guillemots in Kachemak Bay, Alaska. Variability is expressed as mean + SE of the coefficient of variation. Day-scale data are from scuba (nonschooling fishes and hermit crabs; n = 7 total replicates of 3 transects) and hydroacoustic transects (schooling fishes; n = 18 total replicates of 6 transects). Seasonal and km-scale data are from beach seines (n = 231 total sets at 11 locations).

RESULTS

Beach seine catches were dominated by three schooling Pigeon Guillemot prey taxa (sand lance, Pacific herring, and Pacific cod) and three nonschooling prey taxa (great sculpin [*Myoxocephalus polyacanthocephalus*], rock sole [*Lepidopsetta bilineatus*], and *Lumpenus* pricklebacks). Together these taxa made up 96% of the 232 224 fish caught in seines. *Lumpenus* pricklebacks, sculpins, and hermit crabs made up 94% of the 573 prey items observed on scuba transects. Among-day CV of schooling prey on hydroacoustic surveys (84 ± 10%) was 211% greater than that of nonschooling prey on scuba transects (27 ± 16%; t_4 = 3.1, P = 0.01; Fig. 1). Seasonal CV of beach seine catch per unit effort (Fig. 1) was 20% greater for schooling prey (194 ± 5%) than for nonschooling prey (161 ± 6%; $F_{15,48}$ = 3.8, $P < 0.001$, Table 1). Km-scale CV in beach seine catch (Fig. 1) was 24% greater for schooling prey (229 ± 6%) than for nonschooling prey (185 ± 6%; $F_{8,15}$ = 17.3, $P < 0.001$, Table 1). Mean catch per unit effort was also 40 times greater for schooling fishes (317 ± 206 fish set^{-1}) than for nonschooling fishes (8 ± 5 fish set^{-1}; $F_{15,50}$ = 6.9, P < 0.001, Table 1).

We detected a weak, significant relationship between the proportion of schooling prey in the diet and hour-scale variability in meal delivery rates (linear regression, n = 64 nests, r^2 = 0.07, P = 0.01; Fig. 2a). Variability in delivery rate was also higher at the seasonal scale (Fig. 2b) when schooling prey dominated

TABLE 1. Comparisons of variability and abundance between Pigeon Guillemot prey types (schooling and nonschooling), and the effect of the proportion of schooling prey on seasonal variability in meal delivery rates at Pigeon Guillemot nests: GLM results. Seine catch is measured as catch per unit effort (number of fish set^{-1}).

Response variable	df	MS	*F*	*P*
Seasonal CV in seine catch				
Site	10	1706	1.8	0.09
Species (Prey type)	4	4799	5.0	<0.01
Prey type	1	16 627	17.4	<0.001
Error	48	958		
Km-scale CV in seine catch				
Year	3	1918	4.4	0.02
Species (Prey type)	4	10 679	24.5	<0.001
Prey type	1	11 870	27.3	<0.001
Error	15	436		
Mean seine catch				
Site	10	1.0	2.7	0.01
Species (Prey type)	4	3.7	10.0	<0.001
Prey type	1	13.2	35.7	<0.001
Error	50	0.4		
Seasonal SD in delivery rate				
SD in chick age	1	0.03	2.1	0.16
Proportion schooling prey in diet	1	0.06	4.6	0.05
Error	19	0.01		

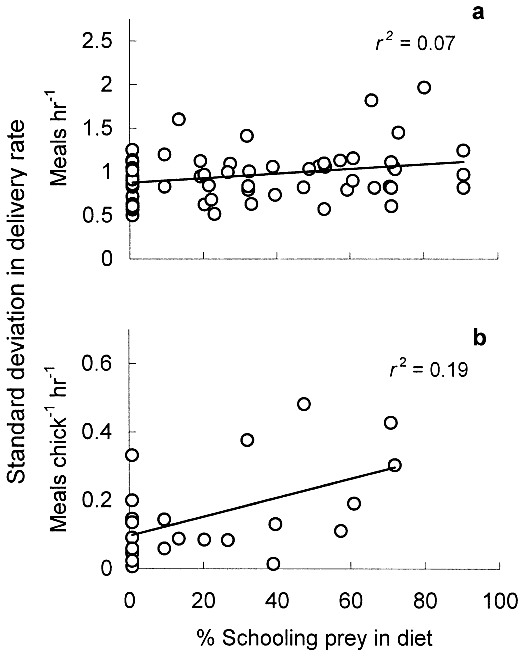

FIGURE 2. Variability in Pigeon Guillemot meal delivery rates in relation to the proportion of schooling prey in the diet at the scale of (a) hours and (b) season. Each dot represents a single nest-year. Twenty dots lie on the *y*-axis in the top panel, nine in the bottom panel. Percentages of schooling prey were arcsine transformed prior to analysis.

the diet (n = 22 nests, $F_{2,19}$ = 4.8, P = 0.02, partial r^2 [SD in chick age] = 0.10, partial r^2 [proportion of schooling prey in diet] = 0.19; Table 1).

DISCUSSION

Our results support the prediction of the quality–variability trade-off hypothesis that nonschooling prey are less variable than schooling prey at multiple spatial and temporal scales. Many species of auks, cormorants, and penguins prey on both nonschooling (mostly demersal) and schooling (mostly pelagic) prey, so this result may have broad implications for many pursuit-diving seabirds (Tremblay and Cherel 2000). Differences between the two prey types were most striking at the seasonal and km scales, as intensive beach seine sampling provided high statistical power for these comparisons. Although sampling effort was limited for both scuba and hydroacoustic surveys, we were also able to detect a large difference between prey types in day-scale variability.

Our results also support the prediction that provisioning with schooling prey will result in increased variability in meal delivery rates. However, diet composition accounted for only 7% of variability in delivery rates at the hour scale, and 19% at the seasonal scale (when nestling demand was controlled for). The proportion of schooling prey in the diet explained 21% of variability among individual nests in mean energy provisioning rates (kJ hr^{-1}), even when nestling demand was not taken into account (Litzow et al. 2002). Diets of lipid-rich schooling prey also increased chick growth rates and reproductive success, and chick survival and reproductive success were less variable for parents that provisioned with schooling prey (Golet et al. 2000, Litzow et al. 2002). The increases in variability in delivery rate that we observed in the current study seem inadequate to explain selection of nonschooling prey, given the known advantages of schooling prey. If variability in prey abundance only weakly affects variability in delivery rates, and has no apparent negative effects on reproductive success, why are nonschooling fishes typically the dominant items in *Cepphus* chick diets?

Pigeon Guillemots react to variability in prey abundance with prey switching and flexible foraging effort (Litzow et al. 2000, Litzow and Piatt 2003), and these behavioral buffers likely reduce the effect that high variability in schooling prey abundance has on variability in meal delivery rates. However, km-scale patterns of prey utilization and availability in Kachemak Bay suggest that these behavioral adaptations may allow Pigeon Guillemots to buffer against high variability only when schooling prey are available close to the colony. Sand lance comprise 67–73% of chick diets at three colonies that are <0.5 km from an area that supports the highest density of sand lance in Kachemak Bay (Abookire et al. 2000, Litzow et al. 2000). In contrast, diets are 15% and 0% sand lance at two colonies that are 4 km and 10 km, respectively, from the same sand-lance-rich area (Litzow et al. 2000). We hypothesize that *Cepphus* guillemots are able to buffer against high short-term variability in schooling prey abundance only when these prey are available very close to the colony (within $\sim$1 km). Successful foraging on variable schooling prey apparently requires a buffer of discretionary time that can be allocated to foraging when prey availability is low (Litzow and Piatt 2003). Because Pigeon Guillemots make so many foraging trips during peak chick demand (10–15 trips day^{-1} parent^{-1}, Litzow et al., unpubl. data), such discretionary time is likely not available to individuals foraging at maximal ranges.

Finally, schooling prey abundance (mean beach seine catch per unit effort) in this study was more than an order of magnitude greater than that of nonschooling prey. This high abundance may help Pigeon Guillemots to buffer against temporal variability in abundance, and may make schooling prey less susceptible to depletion around the colony (‘‘Ashmole's halo''; Ashmole 1963), as has been demonstrated for the nonschooling prey of Double-crested Cormorants (*Phalacrocorax auritus*; Birt et al. 1987).

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RAPTOR PREDATION ON WINTERING DUNLINS IN RELATION TO THE TIDAL CYCLE

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Abstract. At Boundary Bay, British Columbia, Canada, Peregrine Falcons (*Falco peregrinus*) captured 94 Dunlins (*Calidris alpina*) in 652 hunts. The two main hunting methods were open attacks on flying Dunlins (62%) and stealth attacks on roosting or foraging Dunlins (35%). Peregrines hunted throughout the day, yet the kill rate per observation hour dropped 1–2 hr before high tide and peaked 1–2 hr after high tide. The drop in kill rate coincided with the departure of the mass of Dunlins for over-ocean flights lasting 2–4 hr. The peak in kill rate occurred just after the tide began to ebb and the Dunlins returned to forage in the shore zone. The hypothesis that closeness to shoreline vegetation is dangerous for Dunlins is supported by three converging lines of evidence: (1) the high success rate (44%) of peregrine hunts over the shore zone compared to the rate (11%) over tide flats and ocean; (2) the high kill rate per observation hour at high tide; and (3) the positive correlation of kill rate with the height of the tides. Seven of 13 Dunlins killed by Merlins (*Falco columbarius*) and all five Dunlins killed by Northern Harriers (*Circus cyaneus*) were also captured in the shore zone.

Key words: Calidris alpina, *Dunlin,* Falco peregrinus, *Peregrine Falcon, raptor predation, tidal cycle.*

Depredación de *Calidris alpina* por Rapaces durante el Período Invernal con Relación al Ciclo de la Marea

Resumen. En la Bahía Boundary, Columbia Británica, Canadá, halcones *Falco peregrinus* capturaron 94 ejemplares de *Calidris alpina* en 652 horas. Los dos métodos principales de caza fueron ataques abiertos sobre individuos que estaban volando (62%) y ataques encubiertos sobre individuos que estaban posados o forrajeando (35%). *F. peregrinus* cazó a lo largo del día, pero la tasa de matanza por hora de observación disminuyó 1–2 hr antes de la pleamar y alcanzó un máximo 1–2 hr después de la pleamar. La caída en la tasa de matanza coincidió con la partida en masa de *C. alpina* para realizar vuelos sobre el océano que duraron 2–4 hr. El pico en la tasa de matanza ocurrió justo después de que la marea comenzó a menguar y de que los individuos de *C. alpina* regresaron a forrajear a la zona de playa. La hipótesis de que la cercanía de la vegetación a la línea de playa es peligrosa para *C. alpina* es apoyada por tres líneas convergentes de evidencia: (1) la alta tasa de éxito (44%) de las cacerías de *F. peregrinus* sobre la zona de playa comparada con la tasa (11%) de las cacerías sobre los planos de la marea y el océano; (2) la alta tasa de matanza por hora de observación durante la pleamar; y (3) la correlación positiva de la tasa de matanza con la altura de las mareas. Siete de 13 individuos de *C. alpina* cazados por *F. columbarius* y todos 5 individuos de *C. alpina* cazados por *Circus cyaneus* también fueron atrapados en la zona de playa.

Predation risk has been implicated by many researchers as an important determinant in the feeding behavior of a wide variety of prey species (Lima et al. 1985, Milinski 1986). According to theory, avian prey species balance predation risk with foraging needs. For instance, in a trade-off between relative safety from predators and optimal caloric gain, forest passerines tend to forage close to the protective cover of trees and bushes, whereas open-country birds stay well

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