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DOES GARBAGE IN THE DIET IMPROVE REPRODUCTIVE OUTPUT OF GLAUCOUS GULLS?

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Abstract. Anthropogenic subsidies are used by a variety of predators in areas developed for human use or residence. If subsidies promote population growth, these predators can have a negative effect on local prey species. The Glaucous Gull (*Larus hyperboreus*) is an abundant predator in northern Alaska that is believed to benefit from garbage as a supplemental food source, but this supposition has never been tested. In summer 2008 and 2009, we recorded the Glaucous Gull's diet and reproduction at 10 breeding colonies in northern Alaska. Colonies were in industrial, residential, and undeveloped areas and ranged from 5 to 75 km from the nearest landfill. By colony, garbage occurred in zero to 85% of pellets and food remains produced during the chick-rearing period, and the average number of chicks fledged per pair ranged from zero to 2.9. Random-forest analysis indicated that percent occurrence of garbage in the diet was the second most important factor (after number of eggs per pair) explaining variance in fledging rate. There was a significant positive correlation between percent occurrence of garbage in the diet and fledging rate in each year. If this correlation reflects a causal relationship, it suggests that human development that increases gulls' access to garbage could result in increased local gull populations. Such an increase could affect the gulls' natural prey species, including at least 14 species of shorebirds and waterfowl of conservation concern.

Key words: anthropogenic food subsidies, breeding biology, Glaucous Gull, human development, Larus hyperboreus.

¿La Inclusión de Basura en la Dieta Aumenta la Producción Reproductiva de *Larus hyperboreus*?

Resumen. Los subsidios antropogénicos son usados por una variedad de depredadores en áreas desarrolladas para uso o residencia humana. Si los subsidios promueven el crecimiento poblacional, estos depredadores pueden tener un efecto negativo sobre las poblaciones locales de presas. La gaviota *Larus hyperboreus* es un depredador abundante en el norte de Alaska que aparentemente se beneficia de la basura al usarla como suplemento alimenticio, pero esta suposición nunca ha sido probado. En el verano de 2008 y 2009, registramos la dieta y la reproducción de esta gaviota en 10 colonias reproductivas en el norte de Alaska. Las colonias estuvieron en áreas industriales, residenciales y en áreas no desarrolladas con distancias hacia el vertedero de basura más próximo que variaron entre 5 a 75 km. Por colonia, la basura apareció en cero a 85% de los pellets y de los restos de alimento producidos durante el periodo de cría de los polluelos, y el nümero promedio de polluelos que eclosionaron por pareja varió entre cero a 2.9. El análisis *random forest* indicó que la ocurrencia porcentual de la basura en la dieta fue el segundo factor más importante (después del nümero de huevos por pareja) en explicar la varianza de la tasa de emplumamiento. Hubo una correlación positiva y significativa entre el porcentaje de ocurrencia de basura en la dieta y la tasa de emplumamiento en cada año. Si esta correlación refleja una relación causal, sugiere que el desarrollo humano que aumenta la basura accesible para las gaviotas puede resultar en aumentos locales de sus poblaciones. Ese aumento puede afectar a las especies que son presas naturales de las gaviotas, incluyendo por lo menos a unas 14 especies de aves costeras y acuáticas que presentan un estado de conservación preocupante.

INTRODUCTION

Human-subsidized predators are those that benefit from associating with commercial or residential land development, often through access to anthropogenic foods or artificial breeding sites (NAS 2003, Gompper and Vanak 2008). In some cases, this benefit can allow the predator's population numbers and/or densities to increase (Garrott et al. 1993, Steenhof et al. 1993, Contesse et al. 2004). If predators using anthropogenic foods also feed on natural prey, the predator's population growth could have negative consequences such as reduced populations or even extinction of prey species

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(Holt 1984, Garrott et al. 1993). Anthropogenic effects on predators are therefore of great interest to conservation efforts in areas that are or will be developed by humans.

One group of human-subsidized predators consists of gulls of the genus *Larus*, whose populations grew worldwide during the 20th century (Kadlec and Drury 1968, Fordham and Cormack 1970, Harris 1970, Conover 1983, Meathrel et al. 1991, Yorio et al. 1998). Most of these populations grew annually at rates of 3–10%, resulting in each population doubling every 8 to 24 years. A major cause of this trend was a general increase in availability of anthropogenic foods, particularly household garbage and fisheries discards, which may have improved gull survival or reproductive success (Fordham and Cormack 1970, Conover 1983, Chapdelaine and Rail 1997, Duhem et al. 2008), but the causes of these trends have been debated (e.g., Pierotti and Annett 2001). Other factors could include reduced human persecution and use of gulls following the Migratory Bird Treaty Act of 1918, reduction in predation on gull eggs by predators that avoid developed areas or are hunted by humans, or creation of additional habitat through human activities (Drury 1973, Conover 1983, Blokpoel and Spaans 1991). Regardless of the cause of these historic trends in growth of gull populations, it seems likely that future development for human use will similarly cause gull populations to grow in some areas.

Although gulls exploit garbage, the effects of this supplemental food on survival and reproduction are not well established. Garbage in the diet may entail a tradeoff between energy and nutrient content, as it can be high in energy and protein (Pierotti and Annett 1987) but may not provide levels of specific nutrients, such as calcium, optimal for breeding gulls or their chicks (Pierotti and Annett 2001). Several studies have found that the reproductive output of gulls that consumed more garbage is lower than that of gulls with a more natural diet (Ward 1973, Pierotti and Annett 1991, Annett and Pierotti 1999). Other studies, however, found the opposite relationship (Spaans 1971, Hunt 1972, Pons and Migot 1995). Variation among studies could be due to differences in the particular types of garbage available or the local abundance or quality of natural foods. Foraging costs associated with particular prey can also influence breeding success (Pierotti and Annett 1991), and these may also vary with local conditions for the same food type. Therefore, it is not clear how human development will affect local gull populations in any given area.

One area that is particularly susceptible to future development and associated impacts is the arctic coastal plain of Alaska. This area is currently sparsely populated but targeted for further exploration for energy production. Widespread oil exploration on the plain began in the 1950s; development for production began in the 1970s, with several additional areas developed since then (NAS 2003). Further development is expected as additional areas of the National Petroleum Reserve–Alaska are leased and explored for production.

The effect that development may have on wildlife of the arctic coastal plain is of concern because this region supports many tundra-nesting birds, including 40 species of waterfowl and shorebirds (Poole 2007). Twenty-one of these have declined or are listed as species of moderate to high conservation concern (Goudie et al. 1994, Brown et al. 2001, Dickson and Gilchrist 2001, USFWS 2005), and two are listed as threatened under the U.S. Endangered Species Act. Alaska Natives in the region hunt some of these birds for subsistence. Factors influencing population trends in these species could therefore affect both conservation efforts and human residents. Several predators on the arctic coastal plain, including the red (*Vulpes vulpes*) and arctic (*V. lagopus*) foxes, polar (*Ursus maritimus*) and brown (*U. arctos*) bears, Common Raven (*Corvus corax*), and Glaucous Gull (*Larus hyperboreus*), use and may benefit from garbage available in developed areas (NAS 2003). These predators have the potential to affect populations of prey species of concern. To address this concern, garbage management in this region has been improved substantially during the past two decades, with both oilfields and residential areas working to limit scavengers' access to garbage, such as by covering or incinerating waste.

The Glaucous Gull is the most abundant human-subsidized predator on the arctic coastal plain (Liebezeit et al. 2009). Although it exploits anthropogenic food sources such as garbage dumps and landfills readily (Ingolfsson 1976, Day 1998) and is believed to benefit from them, this benefit has not been quantified. We quantified the Glaucous Gull's diet and examined factors that could affect its reproductive output at several colonies on Alaska's arctic coastal plain. We were specifically interested in the potential effect of garbage in the diet on fledging rate; we also examined other variables that could confound the effect of garbage in the diet on reproductive output. If garbage improves the gull's reproductive output in this region, garbage management may be an effective tool for limiting its population growth in response to development.

METHODS

In summer 2008 and 2009, we monitored the Glaucous Gull's diet and reproduction at eight breeding colonies in four regions across the arctic coastal plain of Alaska: three near Barrow (residential), one at Simpson (undeveloped), three at Alpine Oilfield/Nuiqsut (industrial/residential), and one at Deadhorse (adjacent to the Prudhoe Bay oilfields; industrial). In 2009 we also monitored two additional colonies, one at Simpson and one at Deadhorse (Fig. 1). The four regions varied with respect to availability of garbage to foraging gulls. At Simpson garbage was not present, at Barrow and Alpine/Nuiqsut it was incinerated, and at Deadhorse/Prudhoe Bay it was disposed of in a landfill. We visited each colony twice per summer, once in June when the gulls were incubating their eggs (pre-hatch) and once in late July or early August just before the chicks began fledging (chick-rearing).

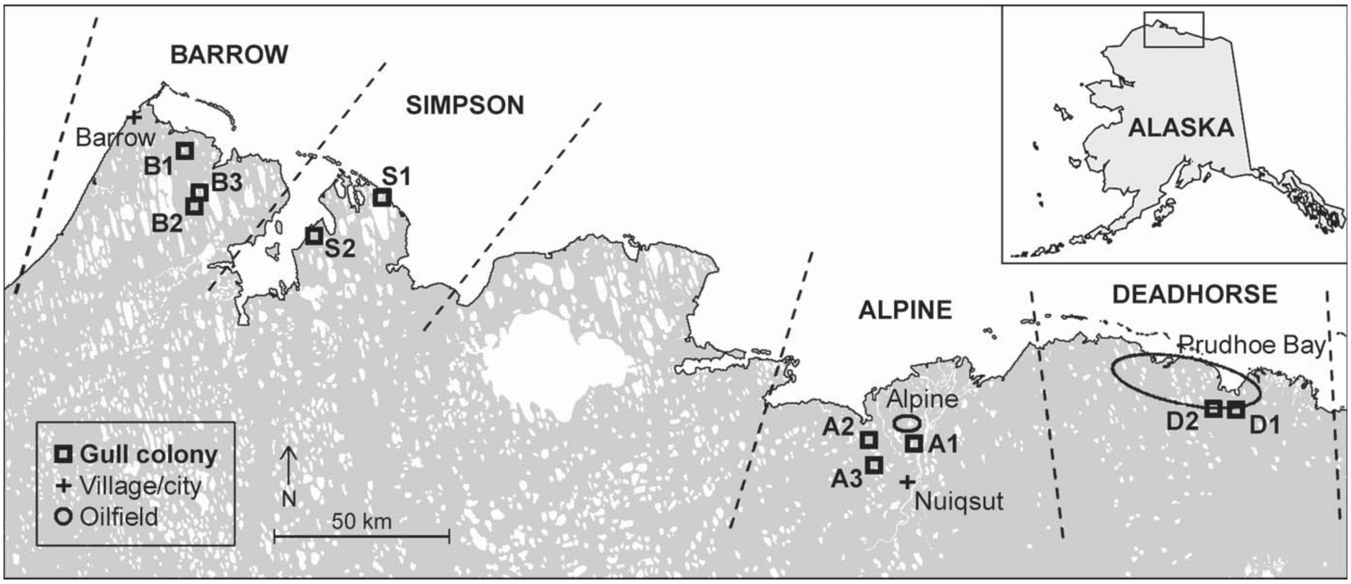

FIGURE 1. Glaucous Gull colonies monitored for diet and reproduction. S2 and D2 were monitored in 2009 only; the others were monitored in 2008 and 2009. Dashed lines divide study regions; villages, cities, and oilfields within each region are shown. Inset shows location of study area in northern Alaska.

DIET ASSESSMENT

We collected regurgitated pellets and food remains from the area around each nest during each visit to a colony. These diet samples are known to be biased toward foods with large or abundant indigestible parts (Duffy and Jackson 1986), but stable-isotope analysis of feathers for diet inference (Hobson and Clark 1992a, b) indicates that pellets and food remains portray the amount of garbage in the gulls' diet at these colonies accurately (Weiser 2010). We collected only fresh diet samples with no evidence of weathering (sun bleaching or epiphyte growth) to ensure that our samples reflected diet during the targeted year and reproductive period. We dissected the pellets and identified all prey items in the samples (pellets and food remains) to the lowest possible taxonomic level. We scored each sample for the presence or absence of each prey class (taxonomic class or garbage) to calculate the percent occurrence of each class in diet samples from each reproductive period at each colony in each year. We expressed the diet's composition as the proportion of occurrences represented by each prey class.

PRE-HATCH DATA

We counted freshly built nests with or without eggs during our first visits to a colony (pre-hatch). We assumed that the fresh empty nests represented potentially breeding pairs that maintained a nest at the colony but either did not lay eggs that year (ELW, pers. obs.) or laid eggs and lost them to predation before our visit to the colony. We counted the eggs at each colony, including any remnants of depredated eggs. We also measured the length and width of each viable egg and calculated egg volume, following Hoyt (1979).

Following a float chart developed for the Glaucous Gull in this area (ELW, unpubl. data), we floated at least two eggs from each nest to age them ±2 days. This method of egg aging has been validated for terns and shorebirds (Hays and LeCroy 1971, Liebezeit et al. 2007) and has been used for gulls (Schreiber 1970, Dinsmore et al. 2002). To calculate dates of laying and expected fledging, we assumed a 28-day incubation period and a 42- to 48-day nestling period (Uspenski 1958) for each floated egg, then timed our second visit to each colony to occur just before fledging.

FLEDGING DATA

Each summer, we recorded the number of chicks at each colony during our second visits, just before chicks began fledging. Gull chicks moved off their nest islands into the water and often grouped together when we approached the colony, making it impossible to assign chicks to particular nests. We therefore calculated fledging rate as the average number of chicks fledged per pair for each colony by dividing the number of live chicks present just before fledging by the number of nests (including fresh empty nests) present in June. Survival of gull chicks can be >90% after day 31 (Vermeer 1963, Reid 1987), and chicks at each colony averaged 27–34 days of age during our visits, so we are confident that technique yielded a good estimate of reproductive output at each colony.

STATISTICAL ANALYSES

To examine the potential relationship between garbage in the diet and fledging rate, we addressed several potential explanatory variables that could confound the effect of diet on

TABLE 1. Importance, given as the percent decrease in the model's accuracy when the variable is excluded, of each variable tested in the random-forest model for explaining variance in fledging rate at Glaucous Gull colonies in northern Alaska. Variables with no importance listed did not improve the model's performance and were not included in the final model.

Variable	Percent increase in model's mean squared error when excluded
Number of eggs per pair	41
Occurrence of garbage in chick-rearing diet (%)	40
Colony	27
Distance to coast (km)	20
Distance to landfill (km)	11
Region	10
Occurrence of fish in pre-hatch diet (%)	8
Occurrence of fish in chick-rearing diet (%)	6
Average egg volume	5
Peak nest-initiation date	1
Year	
Number of breeding pairs	
Occurrence of garbage in pre-hatch diet (%)	
Occurrence of mammals in pre-hatch diet (%)	
Occurrence of mammals in chick-rearing diet (%)	
Occurrence of birds in pre-hatch diet (%)	
Occurrence of birds in chick-rearing diet (%)	

reproductive output. These included percent occurrence of the other major components in the diet during each period, location characteristics, and relevant measures of reproduction (Table 1). Percent occurrences of major food types in the diet are correlated, so a higher percentage of garbage could correspond to a lower percentage of another dietary component, with either potentially affecting reproductive output. Proximity to developed areas (indicated by distance to nearest landfill) could influence densities of predators and therefore predation rates on eggs or chicks, as well as diet. Similarly, proximity to the ocean, potentially a major food source for gulls, influences weather, which could affect reproductive output. Variables such as year, region, and colony potentially incorporate spatial and temporal sources of variation not otherwise included in the model. Characteristics such as egg volume, peak nest-initiation date, colony size, and number of eggs per pair can all affect fledging rate and, if correlated with diet, could make the relationship between diet and fledging rate indirect.

We began our analyses by assessing the relevance of each of these potential explanatory variables to fledging rate by using random-forest analysis (package randomForest in program R; Liaw and Wiener 2002). Random forest is a regression-tree algorithm that develops a model to predict to a continuous target variable (Prasad et al. 2006, Cutler et al. 2007). The algorithm is capable of handling a large number of predictor variables (both categorical and continuous, including correlated variables) that may or may not be related to the response variable, it does not overfit the data, and, in comparison to other commonly used methods, it has high predictive accuracy. Predictor variables used in the model are not assumed to have a causal relationship with the response variables. Random forest randomly splits the data into a training set and an out-of-bag test set; for the training set, it randomly selects n predictor variables to use at each node as it grows each tree, until all variables have been used. It then tests the predictions for the out-of-bag dataset to evaluate the fit of the tree. It repeats this for m trees, then averages the trees to assess the importance of each predictor variable. The user specifies the number of variables (n) to try at each node in the tree and the number of trees (m) to grow.

We used random forest to determine which of our predictor variables were most important in explaining variation in annual fledging rate at each colony. We tuned the model to determine the number of variables to try at each node and increased the number of trees grown until successive runs of the model gave similar results (Liaw and Wiener 2002). We initially included all potential explanatory variables (Table 1), then iteratively removed as many of the least important variables as possible without causing a decrease in the model's performance. We used partial-dependence plots from the model to explore associations between the most important predictor variables and fledging rate (Cutler et al. 2007).

Using linear regression for each year, we further investigated the relationship of each of the top four continuous variables from the final model with fledging rate, transforming the data as necessary because our sample sizes (8 or 10 colonies in each year) were insufficient for a good fit with nonlinear regression. We also examined the relationship of the top categorical variable from the model with fledging rate and with percent occurrence of garbage in the chick-rearing diet for colonies studied in both years with Kruskal–Wallis nonparametric one-way analyses of variance. We used a 5% significance level in all tests. All analyses were performed in program R, version 2.9.2 (R Development Core Team 2009).

RESULTS

Colony size and measures of reproduction varied among colonies and between years (Table 2). Breeding adults typically forage within 30 km of their colonies and not beyond 70 km (D. Troy, unpubl. data). Our colonies ranged in distance from 5 to 75 km from developed areas (the only major sources of garbage in the region) and thus represented a range of availability of garbage to gulls.

We collected between five and 403 diet samples (pellets and food remains) at each colony during each reproductive period (Table 3). The samples consisted mainly of mammals, birds, fish, and garbage (Fig. 2). Use of garbage was indicated by the presence of indigestible anthropogenic items (e.g., plastic, paper, chicken bones) in food samples. At Deadhorse, gulls consumed much more garbage (46–85% occurrence in

TABLE 2. Measures of reproduction at Glaucous Gull colonies in northern Alaska, 2008 and 2009.

		Number of pairs		Eggs per pair		Average clutch[a]		Fledging rate	
Region	Colony	2008	2009	2008	2009	2008	2009	2008	2009
Barrow	B1	13	8	2.0	1.9	2.9	2.5	1.4	0.8
	B2	21	12	1.9	2.1	2.8	2.3	1.6	1.2
	B3	20	14	1.9	2.6	2.8	2.8	0.5	1.6
Simpson	S1	17	12	2.2	2.1	2.5	2.8	0.4	0.3
	S2		17		0.9		1.9		0.7
Alpine	A1	23	22	2.8	2.1	2.9	2.6	1.7	0.9
	A2	9	7	1.6	0.4	2.0	3.0	0.0	0.4
	A3	8	7	2.8	3.0	2.8	3.0	2.1	1.7
Deadhorse	D1	8	9	2.9	3.0	2.6	3.0	2.9	1.9
	D2		15		2.9		2.9		1.6

[a]Average clutch for nests with eggs (empty nests excluded).

diet samples) than did those elsewhere (0–25% occurrence). Birds (mostly shorebirds and waterfowl) occurred in up to 100% of diet samples. We identified 30 species of birds in the gull's diet, including 15 that are declining and/or of moderate to high conservation concern (Suydam et al. 2000, Brown et al. 2001, Dickson and Gilchrist 2001, USFWS 2005, 2008, Larned et al. 2009).

Ten of 17 potential explanatory variables (Table 1) contributed to the explained variance in fledging rate (number of chicks fledged per pair) and were retained in the random-forest model. The final model tried three variables at each split, grew 10 000 trees, and explained 51% of the variance in annual fledging rate. Number of eggs per pair was the most important factor explaining fledging rate, followed closely by percent occurrence of garbage in the chick-rearing diet (Table 1). When we excluded number of eggs per pair from the model, explained variance dropped to 40%. When we also dropped percent occurrence of garbage in the chick-rearing diet from the model, explained variance dropped to 27%. Partial-dependence plots from the model show that number of eggs per pair had the strongest positive effect on fledging rate with >2.5 eggs per pair, with a moderate positive effect of two eggs per pair (Fig. 3a). The positive effect of garbage on fledging rate increased sharply as occurrence of garbage in diet approached 20%, then leveled off (Fig. 3b).

TABLE 3. Sample sizes of diet items (pellets and food remains) collected during pre-hatch and chick-rearing periods at Glaucous Gull colonies in northern Alaska, 2008 and 2009.

		Number of samples			
		2008		2009	
Region	Colony	Pre-hatch	Chick-rearing	Pre-hatch	Chick-rearing
Barrow	B1	101	302	56	65
	B2	37	211	5	69
	B3	47	213	22	58
Simpson	S1	32	59	24	27
	S2	—	—	34	61
Alpine	A1	28	403	124	200
	A2	35	192	38	116
	A3	14	153	30	126
Deadhorse	D1	14	118	11	59
	D2	—	—	134	97

We found a positive linear relationship between fledging rate and number of eggs per pair in each year (2008: $r^2 = 0.64$, $P = 0.02$; 2009: $r^2 = 0.63$, $P = 0.006$). We also found a positive relationship between log-transformed fledging rate and exponent-transformed (2008) or log-transformed (2009) percent occurrence of garbage in the diet during chick rearing (2008: $r^2 = 0.91$, $P < 0.001$; 2009: $r^2 = 0.77$, $P < 0.001$; Fig. 4).

The third most important variable in the random-forest model was colony (Table 1). In the two years of the study, fledging success at each colony, whether relatively high or relatively low, was similar (Table 2), though most colonies were more successful in 2008 than in 2009, and we did not find a significant effect of colony on fledging rate ($P = 0.07$). At each colony, the amount of garbage the gulls consumed in the two years was similar (Fig. 2); the effect of colony on percent occurrence of garbage in the diet was marginally significant ($P = 0.05$). The fourth most important variable in the model, distance to coast, was not correlated with fledging rate ($P > 0.17$). The fifth most important continuous variable, distance to landfill, was not correlated with fledging rate ($P > 0.19$) or percent occurrence of garbage in diet samples ($P > 0.32$).

DISCUSSION

Garbage was one of four major dietary components detected in pellets and food remains from breeding colonies of the Glaucous Gull in northern Alaska. Percent occurrence of garbage in diet samples varied widely among colonies; garbage was absent in diets of gulls at some colonies and made up the majority of diets of gulls at others. Garbage occurred two to three times as frequently in diet samples from colonies in

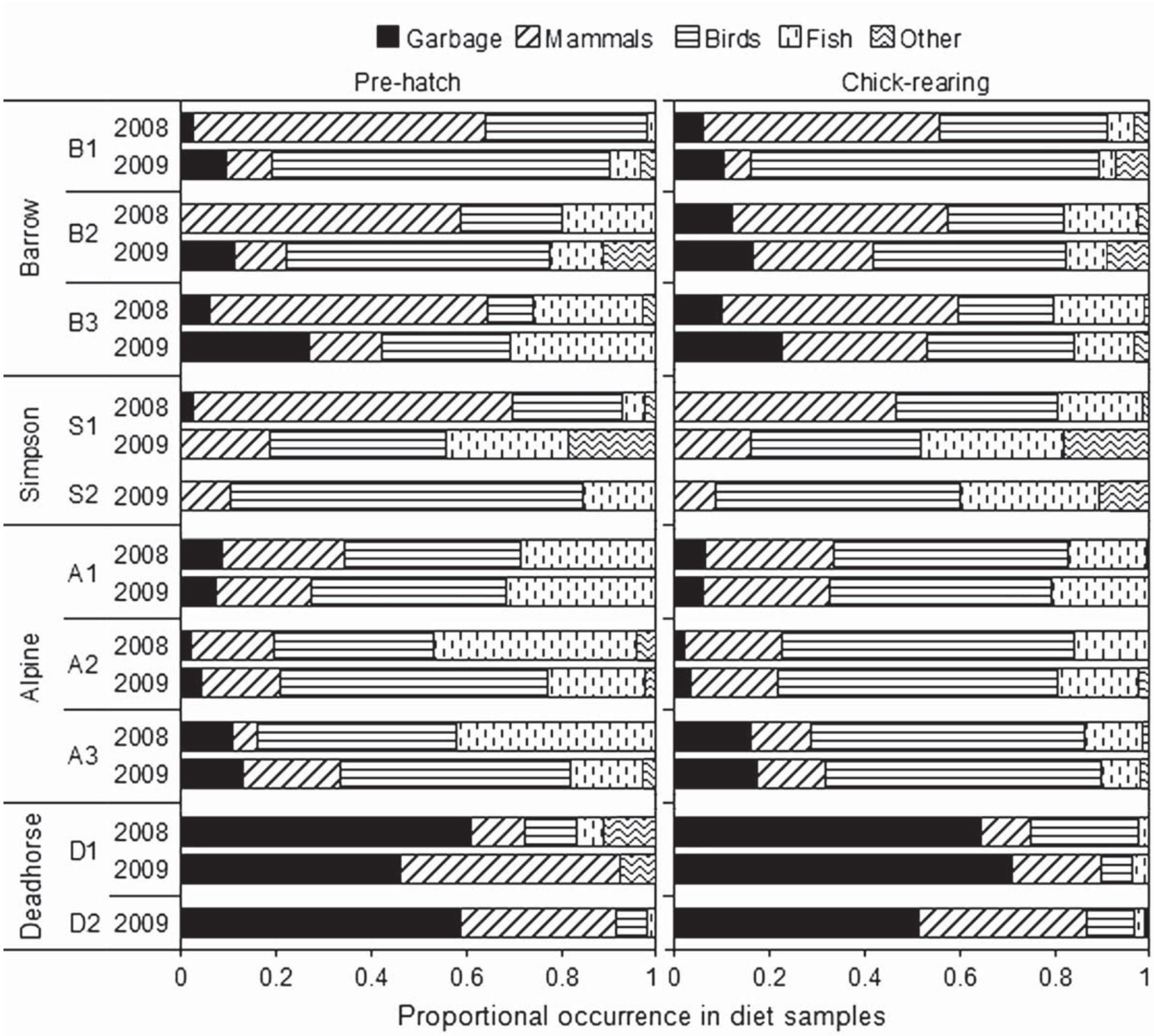

FIGURE 2. Composition of Glaucous Gull diet during pre-hatch and chick-rearing periods in northern Alaska, 2008 and 2009. Contribution of each prey class is expressed as the proportion of occurrences in diet samples represented by that prey class. "Other" includes bivalves, gastropods, crustaceans, insects, berries, and unidentified prey.

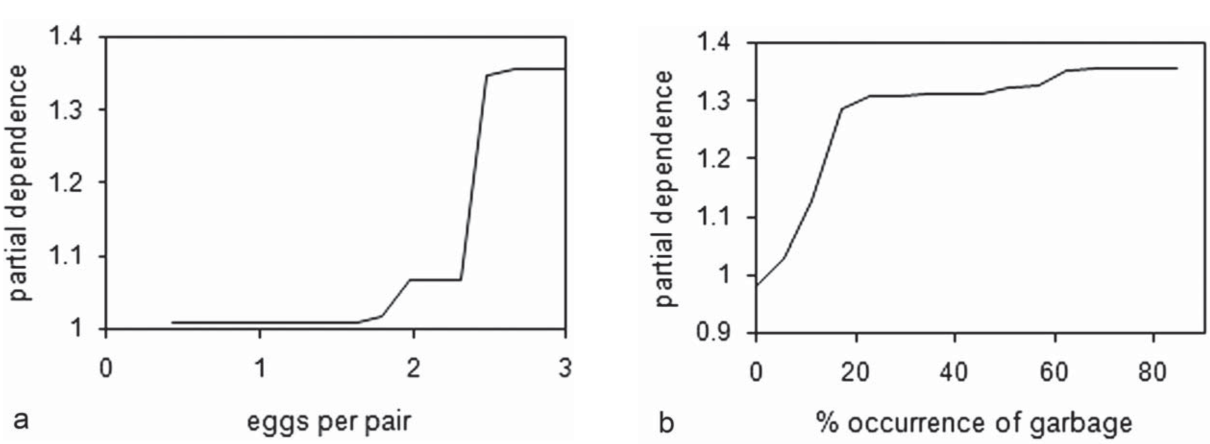

FIGURE 3. Partial dependence of fledging rate on (a) number of eggs per pair and (b) percent occurrence of garbage in diet samples from the chick-rearing period, as based on the random-forest model.

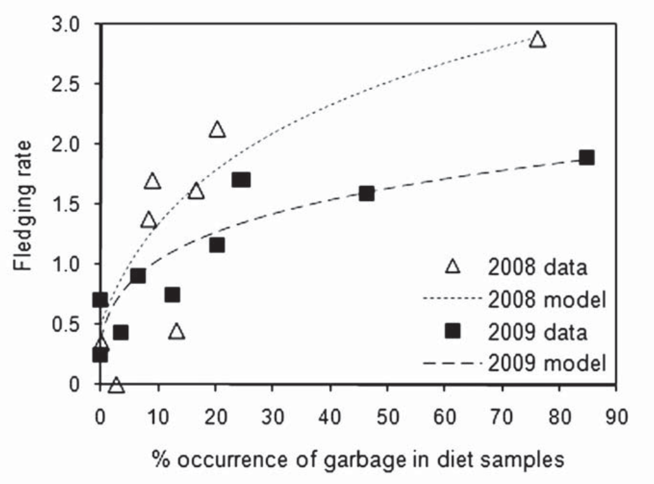

FIGURE 4. Relationship between percent occurrence of garbage in diet samples and average fledging rate for Glaucous Gulls at colonies in northern Alaska in 2008 (dotted line and unfilled triangles) and in 2009 (dashed line and filled squares), back-transformed and shown in relation to the original data. Linear regression models included an exponent transformation on fledging rate (2008; $r^2 = 0.89$, $P < 0.001$) or natural-log transformations on both variables (2009; $r^2 = 0.77$, $P < 0.001$).

Deadhorse as in samples from colonies in other regions. This could be due to differences by region in garbage-disposal methods; more food waste would be available at the large Prudhoe Bay landfill, where garbage was only lightly covered with earth, than at the smaller Barrow or Alpine landfills, where putrescible waste (including food waste) was incinerated prior to disposal.

We identified several variables as potentially explaining variance among colonies in fledging rate. As expected, fledging rate was positively related to the number of eggs per pair. The number of eggs at a colony necessarily constrains the number of chicks produced, but the imperfect relationship between these two variables indicates that some other factor(s) affected fledging rate between our two visits to a colony (the first being when we counted eggs, the second when we counted chicks). Percent occurrence of garbage in the diet during the chick-rearing period ranked as the second most important factor explaining variance in fledging rate, and it showed an even closer positive relationship to fledging rate than did the number of eggs per pair.

If both garbage in the diet and fledging rate were influenced by some other variable(s), our data could suggest a direct link between the two where none exists. For example, gulls nesting near developed areas, which might be expected to consume more garbage than those in undeveloped areas, could experience higher rates of anthropogenic disturbance and different rates of predation than gulls in undeveloped areas, and either of these factors could influence fledging rate. However, we found no relationship between proximity to development (measured as distance to nearest landfill) and the gulls' fledging rate or diet. Proximity to development was therefore unlikely to be an underlying factor explaining the apparent relationship between diet and fledging rate. Our analyses do not suggest any other variable that could be underlying this relationship, though it is possible that some factor we did not measure was responsible for the apparent link between diet and fledging rate.

If the relationship between garbage in the diet and fledging rate was direct and causal, it may be either that diet affected reproductive output or that the number of chicks in a brood affected the foraging strategies of parents. Garbage is a predictable and easily obtained food, so gulls with more chicks may use it to provision their chicks while reducing their foraging time and effort. However, optimal-foraging theory (MacArthur and Pianka 1966) predicts that all individuals should use the most efficient food source available. Thus even gulls with only one chick should use garbage if it reduces their energy expended for chick provisioning. If there was a causal relationship between garbage in the diet and fledging rate, it seems more likely to have been in the other direction, with gulls that consumed more garbage experiencing higher reproductive success.

The benefit to chick survival of a diet high in garbage could be a direct or indirect result of garbage consumption. Garbage can be high in energy and protein (Pierotti and Annett 1987), which could directly benefit chicks through faster growth, larger body size, or better condition. Garbage may also improve the parents' body condition (Auman et al. 2008) and therefore their ability to care for and successfully raise their chicks (Tveraa et al. 1998). Aside from nutritional or caloric benefits, it is possible that the predictability and ease of obtaining garbage allow parents to spend more time at their nest and with their chicks. Reduced foraging time would enable the parents to spend more time defending their eggs and chicks from predation or conspecific attacks, incubating eggs, and brooding young chicks, which could improve breeding success (Bukacińska et al. 1996).

Despite the close relationship between the top two explanatory variables and fledging rate, our model explained only 51% of the variance in fledging rate. The remaining variance may be explained by variables not measured in this study. Glaucous Gull eggs and chicks are subject to avian and mammalian predation (Gilchrist 2001), but we could not detect predation with only two visits to each colony in each year, nor did we have data on local populations of predators. Including such information would likely improve the model. Additionally, we did not monitor colonies during the period immediately following hatching, when mortality of gull chicks is most likely (Vermeer 1963, Reid 1987). Information on weather, disturbance, or other factors that could contribute to chick mortality during that period would likely explain additional variance in fledging rate.

Regardless of unknown factors that may contribute to fledging rate, our results suggest that more garbage in the diet may allow Glaucous Gull chicks higher survival to fledging than a more natural diet. The benefit to nestlings of a human-subsidized diet could also improve survival of juveniles and subadults well beyond the time that chicks are fed by their parents (Webb et al. 2004). Improved productivity and/or survival to breeding age could result in a larger population of breeding gulls than would be present without anthropogenic food sources.

A larger gull population could affect prey species if the surplus production increases colonies with limited access to garbage. About 40% of Glaucous Gulls that reach adulthood return to their natal site to breed (Gaston et al. 2009); some of the remaining individuals from our colonies that rely heavily on garbage probably disperse to areas without anthropogenic food sources, where they must rely on natural prey such as rodents and birds. The availability of garbage may therefore have an indirect negative effect on the populations of prey species even outside of developed areas. In developed areas, current and future, garbage could be managed to address this issue.

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