USE OF ANTHROPOGENIC FOODS BY GLAUCOUS GULLS (*LARUS HYPERBOREUS*) IN NORTHERN ALASKA

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March 30, 2010
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A
THESIS

Presented to the Faculty
of the University of Alaska Fairbanks

in Partial Fulfillment of the Requirements
for the Degree of

MASTER OF SCIENCE

By

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Fairbanks, Alaska

May 2010

ABSTRACT

Glaucous Gulls are abundant predators in northern Alaska and prey upon several bird species of conservation concern. To assess the benefit gulls may receive from scavenging garbage, I studied diet and reproduction at eight to ten breeding colonies in northern Alaska in 2008-2009. Garbage occurrence in diet was positively correlated with fledging rate; thus any development that increased available garbage could potentially subsidize gull populations through enhanced reproductive success. Garbage could also increase gull populations by enhancing subadult survival. Subadult gulls around the city of Barrow consumed much more garbage than breeding adults, which apparently switch to a mostly natural diet. If garbage enhances subadult survival, more gulls may survive to adulthood, which could impact prey species. When Barrow switched to incinerating garbage instead of disposing it in a landfill, garbage in subadult gull diet decreased.

Using stable isotope analysis of gull chick feathers, I found that the diet samples (pellets and food remains) I used in these analyses overestimated gull use of birds and underestimated use of fishes, but usually accurately portrayed relative importance of garbage. Biases in these samples should be considered when assessing the potential impact of gulls on their prey.

TABLE OF CONTENTS

Page

LIST OF FIGURES

LIST OF TABLES

ACKNOWLEDGMENTS

The work presented here was funded by the North Slope Borough Department of Wildlife Management (with a grant from NPR-A Impact Mitigation Program, Alaska Department of Commerce, Community, and Economic Development), the U.S. Bureau of Land Management (Arctic Field Office), and a University of Alaska Foundation Angus Gavin Migratory Bird Research Grant. ConocoPhillips Alaska, Inc. provided in-kind support. Robert Suydam, Dolores Vinas, and Ambrose Leavitt (North Slope Borough), Debbie Nigro (BLM), and Caryn Rea and Amie Benedict (ConocoPhillips) provided logistical and administrative support and assistance.

Robert Suydam initiated this project and secured the initial funding. My advisor, Abby Powell, was instrumental in the design and implementation of this study. My other committee members, Alan Springer and Christine Hunter, provided support and comments that improved this thesis.

I thank Ruby Baxter and Erin McDonald for field assistance; Ron Barry, Arny Blanchard, and Jonathan Moore for advice on statistics and analyses; Tim Howe and Norma Haubenstock of the Alaska Stable Isotope Facility for sample analysis; and the staff of the UAF Department of Biology and Wildlife, the Institute of Arctic Biology, and the Alaska Cooperative Fish and Wildlife Research Unit for academic, logistical, and research support.

My advisor, Abby Powell, is a co-author on the three manuscripts presented here as thesis chapters. For each, she assisted with planning the field work; I implemented data collection, performed analyses, created figures and tables, and drafted the manuscript. Abby gave valuable feedback on figures and tables and many suggestions for improving the written sections. Her input was instrumental in finalizing and polishing the manuscripts.

The work presented here was conducted under approval #07-46 of the Institutional Animal Care and Use Committee of the University of Alaska Fairbanks.

INTRODUCTION

Human-subsidized predators are those that benefit from associating with human development, often through access to anthropogenic foods or artificial breeding sites (Gompper and Vanak 2008). This benefit can allow predator populations or densities to increase (Steenhof et al. 1993; NAS 2003; Contesse et al. 2004). This artificial increase in predator populations could have negative consequences for prey species, such as reduced populations or even extinction (Holt 1984; Garrott et al. 1993), if those predators continue to feed on natural prey. Anthropogenic subsidies of predators are therefore of great interest to conservation efforts in developed or developing areas.

One group of human-subsidized predators is *Larus* gulls, which experienced worldwide population growth during the twentieth century (Kadlec and Drury 1968; Fordham and Cormack 1970; Harris 1970; Conover 1983; Yorio et al. 1998). A likely cause of this trend was a general increase in availability of anthropogenic foods, including household garbage and fisheries discards, which may have improved gull survival and/or reproductive success (Fordham and Cormack 1970; Conover 1983; Chapdelaine and Rail 1997). This historic trend suggests that future development will similarly support gull population growth unless gull access to anthropogenic subsidies is limited.

Although it is likely that anthropogenic subsidies can cause gull population increases, the effects of garbage on gull survival and reproduction are not well established. In general, increased food availability would be expected to increase survival and reproduction. However, garbage may present a tradeoff between energy and nutrient content, as it can be high in energy and protein (Pierotti and Annett 1987) but may not provide optimal levels of specific nutrients, such as calcium, that are necessary for growth and reproduction (Pierotti and Annett 2001). Gulls that consume more garbage may have lower (Ward 1973; Pierotti and Annett 1991; Annett and Pierotti 1999) or higher (Spaans 1971; Hunt 1972; Pons and Migot 1995) reproductive output than gulls with a more natural diet. The effect of garbage on subadult or adult gull survival has not been demonstrated. Therefore, it is not clear how garbage availability 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 (ACP) of Alaska, USA. Widespread oil exploration began on the ACP in the 1950s; development for production began in the 1970s and has continued over the past several decades (NAS 2003). Further development is expected as additional areas of the National Petroleum Reserve – Alaska are leased and explored for production. The potential effects of development on ACP wildlife are of great concern because this region supports many species of conservation concern. Of the 40 species of waterfowl and shorebirds that breed in the area (Poole 2007), 21 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 waterfowl species for subsistence, so factors influencing population trends in these species could have implications for human residents as well as conservation efforts.

The most abundant human-subsidized predator on the ACP is the Glaucous Gull (*Larus hyperboreus*; Liebezeit et al. 2009). Although Glaucous Gulls readily exploit anthropogenic food sources such as garbage dumps and landfills (Day 1998) and are believed to benefit from them, their use of garbage and the potential benefit have never been quantified. If anthropogenic foods allow gull populations to increase and impact species of concern, it will be important to prevent gull access to anthropogenic foods from becoming more widespread with future development.

The first step in determining the benefit gulls may receive from garbage is to describe their diet and quantify the garbage component. I monitored diet and reproductive output at several Glaucous Gull colonies in northern Alaska. I tested for effects of diet (particularly occurrence of garbage in diet) and colony characteristics on reproductive success at these colonies in two years. I also monitored diets of adult and subadult Glaucous Gulls before and after a change in garbage management at Barrow, Alaska, to determine whether the change was successful in reducing the amount of garbage used by gulls.

For my gull diet analyses, I collected and analyzed regurgitated pellets and food remains. These contain indigestible parts of food items, including remnants of paper, plastic, and other anthropogenic items that indicate the presence of garbage in recent diet. This and similar conventional methods of diet assessment are widely used (e.g. Barry and Barry 1990; Real 1996; Kristan et al. 2004), but diet data resulting from these samples are typically biased toward foods with indigestible parts (Duffy and Jackson 1986; Gonzáles-Solís et al. 1997). In contrast to conventional diet samples, stable isotope ratios of a consumer's tissues represent all foods consumed and absorbed by that animal (Hobson and Wassenaar 1999). Carbon and nitrogen stable isotope ratios in organisms vary predictably among different food webs and trophic levels (Peterson and Fry 1987; Post 2002), so the contribution of each prey type to a consumer's diet can be inferred by testing the stable isotope ratios of a tissue from that consumer (Bearhop et al. 1999). I used stable isotope analysis of gull chick feathers to evaluate biases in diet data obtained from conventional sources.

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CHAPTER 1:

Does Garbage in Diet Improve Glaucous Gull Reproductive Output?[1]

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 impact on local prey species. Glaucous Gulls (*Larus hyperboreus*) are abundant predators in northern Alaska that are believed to benefit from garbage as a supplemental food source, but neither this benefit nor the effect on local prey populations has been quantified. In summer 2008 and 2009, we recorded Glaucous Gull 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. Among colonies, 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 between zero and 2.9. Random forest analysis indicated that percent occurrence of garbage in 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 diet and fledging rate in each year. If this correlation reflects a causal relationship, this suggests that human development that would increase gull access to garbage could result in increased local gull populations. This would have implications for the gulls' natural prey species, including at least 14 species of shorebirds and waterfowl of conservation concern.

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[1] Weiser, E. and A. Powell. 2010. Does garbage in diet improve Glaucous Gull reproductive output? Prepared for submission to *Condor*.

INTRODUCTION

Human-subsidized predators are those that benefit from associating with human settlements, often through access to anthropogenic foods or artificial breeding sites (NAS 2003; Gompper and Vanak 2008). This benefit can allow predator population numbers and/or densities to increase (Garrott et al. 1993; Steenhof et al. 1993; Contesse et al. 2004). This artificial increase in predator populations could have negative consequences for prey species, such as reduced populations or even extinction (Holt 1984; Garrott et al. 1993), if those predators continue to feed on natural prey. Anthropogenic subsidies of predators are therefore of great interest to conservation efforts in developed or developing areas.

One group of human-subsidized predators is *Larus* gulls, which experienced worldwide population growth during the twentieth 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 exhibited annual growth rates of 3-10%, resulting in each population doubling every eight to 24 years. A major cause of this trend was likely 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 that may influence population growth include reduction of 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 of gull population growth, it seems likely that future development for human use will similarly cause gull population growth in some areas.

Although gulls are known to utilize garbage, the effects of this supplemental food on survival and reproduction are not well established. Garbage in diet may present a tradeoff between energy and nutrient content, as it can be high in energy and protein

(Pierotti and Annett 1987) but may not provide optimal levels of specific nutrients, such as calcium, for breeding gulls or their chicks (Pierotti and Annett 2001). Specific amino acids are more limiting than energy or crude protein for gull egg production (Bolton et al. 1992), and it is not clear whether garbage alone would provide those nutrients in sufficient quantity for gull reproduction. Several studies found that gulls that consumed more garbage had lower reproductive output than gulls with a more natural diet (Ward 1973; Pierotti and Annett 1991; Annett and Pierotti 1999). However, other studies 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 (ACP) of Alaska, USA. This area is currently sparsely populated, but targeted for further exploration for energy production. Widespread oil exploration began on the ACP 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 ACP wildlife is of concern because this region supports many tundra-nesting birds, including 40 species of waterfowl and shorebirds (Poole 2007). Twenty-one of these species 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 ACP, including red (*Vulpes vulpes*) and arctic (*V. lagopus*) foxes, polar (*Ursus maritimus*) and brown (*U.*

arctos) bears, Common Ravens (*Corvus corax*), and Glaucous Gulls (*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 improved substantially during the past two decades, with both oilfields and residential areas working to limit scavenger access to garbage, e.g. by covering or incinerating waste.

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

METHODS

Study Sites

In summer 2008 and 2009, we monitored diet and reproduction at eight Glaucous Gull breeding colonies in four regions across the ACP of Alaska: three colonies 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 (Figure 1.1). The four regions varied with respect to availability of garbage to foraging gulls. Garbage was not present at Simpson; garbage at Barrow and Alpine/Nuiqsut was incinerated, and Deadhorse/Prudhoe Bay garbage 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).

Diet Assessment

We collected regurgitated pellets and food remains from the area around each nest during each colony visit. We collected only fresh items 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 pooled by colony for each reproductive period) 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. We expressed gull diet composition as the proportion of occurrences represented by each prey class.

Reproductive Data

We counted the freshly-built nests with or without eggs present during our first colony visits (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 depredation 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).

We floated at least two eggs from each nest to age them ± 2 days following a float chart developed for Glaucous Gulls in this area (ELW unpubl. data). 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). We assumed a 28-day incubation period and a 42-48-day nestling period (Uspenski 1958) to calculate lay date and expected fledge date for each floated egg, and then timed our second colony visits to occur just before fledging at each colony.

During our second visits each summer (chick-rearing), we recorded the number of chicks present at each colony 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 individual 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. Gull chick survival 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 this was a good estimate of reproductive output at each colony.

Statistical Analyses

To examine the potential relationship between garbage in diet and fledging rate, we addressed several potential explanatory variables that could confound the effect of diet on reproductive output. These included percent occurrence of the other major dietary components in diet during each period, location characteristics, and relevant reproductive parameters (Table 1.1). We began our analyses by assessing the relevance of each of these potential explanatory variables to fledging rate using random forest analysis [package randomForest in program R (Liaw and Wiener 2002)]. Random forest is a classification and 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), does not overfit the data, and has high predictive accuracy compared to other commonly used methods. 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 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 1.1) and then iteratively removed as many of the least important variables as possible without causing a decrease in model 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).

We further investigated the relationship of each of the top four continuous variables from the final model with fledging rate using linear regression for each year, 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 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

Each colony contained between seven and 23 breeding pairs in each year (Table 1.2). Breeding adults typically forage within 30 km of and not beyond 70 km from their colonies (D. Troy, Troy Ecological Research Associates, unpubl.). Our colonies ranged from 5 to 75 km from permanent human settlements (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 1.3). Glaucous Gull diet was composed mainly of mammals, birds, fish, and garbage (Figure 1.2). Gulls at Deadhorse consumed much more garbage (46-85% occurrence in diet samples) than gulls elsewhere (0-25% occurrence). Use of garbage was indicated by the presence of indigestible anthropogenic items (e.g. plastic, paper, chicken bones) in food samples. Birds (mostly shorebirds and waterfowl) occurred in up to 100% of diet samples. We identified 30 species of birds in gull diet, including 15 that are declining and/or of moderate to high conservation concern (Table 1.4).

Ten of the 17 tested variables (Table 1.1) contributed to the explained variance in fledging rate and were retained in the random forest model. The final model explained 51% of variance in annual fledging rate. Number of eggs per pair was the most important factor explaining fledging rate, followed by percent occurrence of garbage in chick-rearing diet (Table 1.1). 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 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 when there were three eggs per pair, with a moderate positive effect of two eggs per pair (Figure 1.3a). The positive effect of garbage on fledging rate increased sharply as occurrence of garbage in diet approached 20%; the effect then leveled off until garbage occurrence in diet reached 60%, above which the positive influence on fledging rate was slightly stronger (Figure 1.3b).

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 fledging rate and percent occurrence of garbage in diet during the chick-rearing period (2008: $r^2 = 0.91$, $P < 0.001$; 2009: $r^2 = 0.77$, $P < 0.001$; Figure 1.4).

The third most important variable in the random forest model was colony (Table 1.1). Gulls at each colony tended to have similar fledging rates (Table 1.2) and consumed similar amounts of garbage between years (Figure 1.2); there was a significant effect of colony on percent occurrence of garbage in diet (*P* = 0.049) but not on fledging rate (*P* = 0.071). The fourth most important variable in the model, distance to coast, was not related to fledging rate (*P* > 0.17). The fifth most important continuous variable, distance to landfill, was not significantly related to fledging rate (*P* > 0.19) or to 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 Glaucous Gull breeding colonies 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 the diets at colonies in Deadhorse as in the diets at colonies in other regions. This could be due to differences in garbage disposal methods among regions; more food waste would be available at the large Prudhoe Bay landfill, where garbage is only lightly covered with earth, than at the smaller Barrow or Alpine landfills, where putrescible waste (including food waste) is incinerated prior to disposal.

As expected, the number of eggs per pair was positively related to Glaucous Gull fledging rate. The number of eggs at a colony would necessarily constrain 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 colony visits (the first being when we counted eggs, the second when we counted chicks). Percent occurrence of garbage in diet during the chick-rearing period ranked as the second most important factor explaining variance in fledging rate, and showed an even closer positive relationship to fledging rate than did the number of eggs per pair.

Our analyses indicate that the link between garbage in diet and fledging rate is direct, rather than an artifact of another variable such as proximity to development that could affect both diet and reproductive success. Gulls nesting near developed areas could experience higher rates of anthropogenic disturbance and different rates of predation than gulls in undeveloped areas, either of which could influence fledging rate. We found no relationship between proximity to development (measured here as distance to nearest landfill) and gull fledging rate, but a link between the two could be masked if proximity to development has different effects depending on local circumstances. For example, densities of predators such as arctic fox are higher in oilfields than in undeveloped areas (NAS 2003), but arctic foxes are removed from the area surrounding Barrow throughout the breeding season to improve reproductive output of Spectacled Eiders. Similarly, brown bears commonly occur on the Prudhoe Bay and Alpine oilfields, but are rarely sighted around Barrow, possibly due to local hunting pressure around the city (ELW pers. obs.). However, we found fledging rate to be generally higher at Deadhorse than at Barrow, contrary to expectations based on the influence of development on potential nest predators. Proximity to human development therefore seems unlikely to be an underlying factor influencing both diet and reproductive output.

The benefit to chick survival of a diet high in garbage could be direct or indirect. Chicks that are fed garbage may benefit directly from the abundance or nutrient content of the food source through faster growth, larger body size, or better condition. Chicks would benefit indirectly if garbage improves the parents' body condition (Auman et al. 2008) and therefore their ability to care for their chicks (Tveraa et al. 1998). Aside from nutritional or caloric benefits, it is possible that the predictability and ease of obtaining garbage improves fledging rate by allowing parents to spend more time at their nest and with their chicks. Nest attendance is positively related to breeding success in gulls (Bukacińska et al. 1996); higher nest attendance would enable the parents to better defend their eggs and chicks from predation or conspecific attacks and to spend more time incubating eggs and brooding young chicks. More garbage in diet could indirectly improve gull chick survival in this way.

Despite the close relationship between garbage in diet and productivity, 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 predator populations. Such information would likely improve the model. Additionally, we did not monitor colonies immediately following hatching, which is when gull chick mortality is most likely to occur (Vermeer 1963; Reid 1987). Information on weather, disturbance, or other factors that could contribute to chick mortality during that period would likely account for a larger amount of variance in fledging rate.

Regardless of unknown factors that may contribute to fledging rate, our results suggest that more garbage in diet may allow Glaucous Gull chicks higher survival to fledging than a more natural diet. The benefit of a human-subsidized nestling diet may also improve juvenile and subadult survival 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 have an impact on 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 would 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. Garbage management practices in current and future developed areas could be implemented to address this issue.

ACKNOWLEDGMENTS

This study was funded by the North Slope Borough Department of Wildlife Management (with a grant from NPR-A Impact Mitigation Program, Alaska Department of Commerce, Community, and Economic Development), the U.S. Bureau of Land Management Arctic Field Office, and a University of Alaska Foundation Angus Gavin Migratory Bird

Research Grant. ConocoPhillips Alaska, Inc. provided additional support. We thank Ruby Baxter and Erin McDonald for field assistance, and Robert Suydam, Debbie Nigro, and Amie Benedict for logistical support. Arny Blanchard advised on statistical analysis. Alan Springer and Christine Hunter provided comments that improved the manuscript. This study was conducted under approval #07-46 of the Institutional Animal Care and Use Committee of the University of Alaska Fairbanks. Any use of trade, product, or firm names in this publication is for descriptive purposes only and does not imply endorsement by the U.S. Government.

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FIGURES

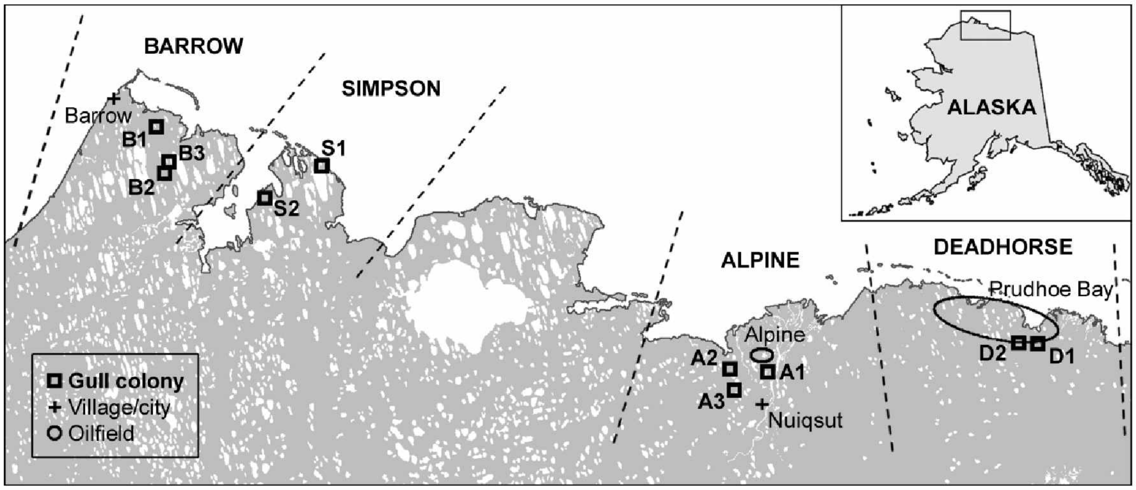

Figure 1.1. Glaucous Gull colonies monitored for diet and reproduction. S2 and D2 were monitored in 2009 only; the others were monitored in 2008 and 2009. Dashed lines divide study regions; villages, cities, and oilfields are shown within each region. Inset shows location of study area in northern Alaska.

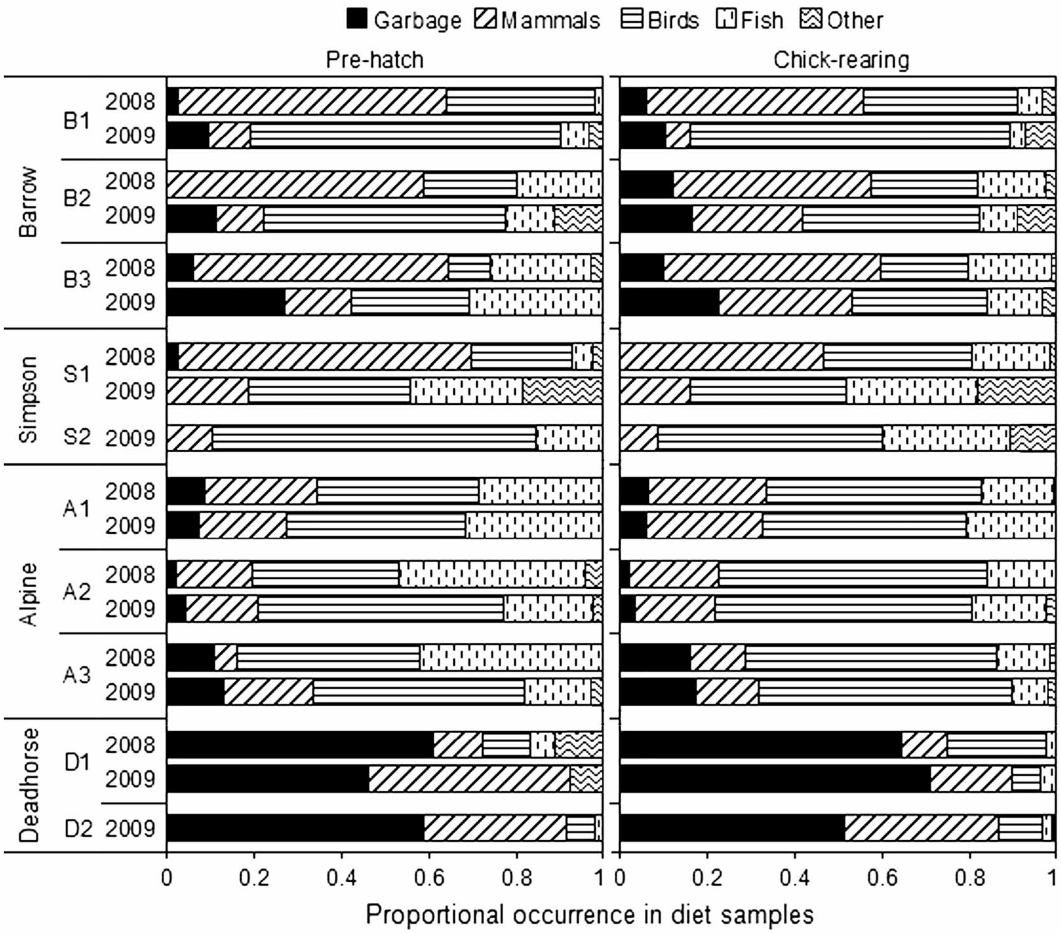

Figure 1.2. Diet of Glaucous Gulls during pre-hatch and chick-rearing periods. Contribution of each prey class is expressed as the proportion of occurrences in diet samples represented by that prey class. “Other” includes bivalves, gastropods, crustaceans, insects, berries, and unidentified prey.

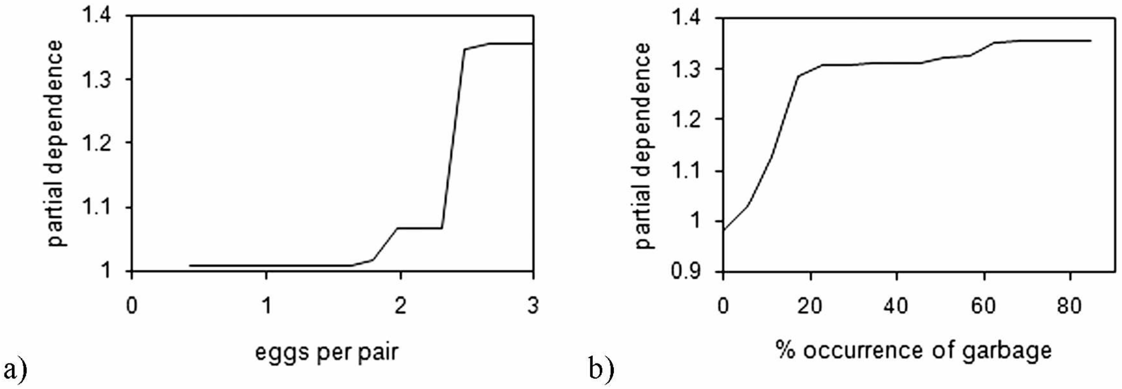

Figure 1.3. Partial dependence of fledging rate on two explanatory variables: a) number of eggs per pair and b) percent occurrence of garbage in diet samples from the chick-rearing period based on the random forest model.

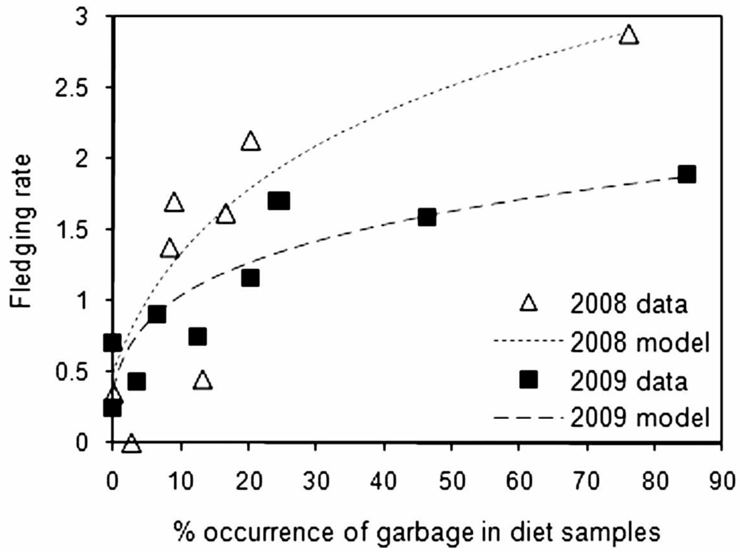

Figure 1.4. Relationship between garbage in diet and fledging rate. Equations for the nonlinear relationship are back-transformed and shown in relation to the original data. Linear regression models included an exponent transformation on fledging rate (2008; $r^2 = 0.89$, $P < 0.001$) or natural log transformations on both variables (2009; $r^2 = 0.77$, $P < 0.001$).

TABLES

Table 1.1. Variable importance from the random forest model for fledging rate. Variables with no importance listed did not improve model performance and were not included in the final model.

Variable	% increase in model MSE when excluded
Number of eggs per pair	41.28
Garbage occurrence in chick-rearing diet (%)	39.96
Colony	26.98
Distance to coast (km)	19.74
Region	10.17
Distance to landfill (km)	10.94
Fish occurrence in pre-hatch diet (%)	7.92
Fish occurrence in chick-rearing diet (%)	5.85
Average egg volume	4.59
Peak nest initiation date	1.47
Year	
Number of breeding pairs	
Garbage occurrence in pre-hatch diet (%)	
Mammal occurrence in pre-hatch diet (%)	
Mammal occurrence in chick-rearing diet (%)	
Bird occurrence in pre-hatch diet (%)	
Bird occurrence in chick-rearing diet (%)	

Table 1.2. Reproductive parameters of Glaucous Gull colonies, 2008 and 2009.

		2008				2009			
Region	Colony	# Pairs	Eggs per pair	Avg clutch[1]	Fledging rate	# Pairs	Eggs per pair	Avg clutch[1]	Fledging rate
Barrow	B1	13	2.0	2.9	1.4	8	1.9	2.5	0.8
	B2	21	1.9	2.8	1.6	12	2.1	2.3	1.2
	B3	20	1.9	2.8	0.5	14	2.6	2.8	1.6
Simpson	S1	17	2.2	2.5	0.4	12	2.1	2.8	0.3
	S2					17	0.9	1.9	0.7
Alpine	A1	23	2.8	2.9	1.7	22	2.1	2.6	0.9
	A2	9	1.6	2.0	0.0	7	0.4	3.0	0.4
	A3	8	2.8	2.8	2.1	7	3.0	3.0	1.7
Deadhorse	D1	8	2.9	2.6	2.9	9	3.0	3.0	1.9
	D2					15	2.9	2.9	1.6

[1] Average clutch for nests with eggs (not including empty nests).

Table 1.3. Numbers of samples (pellets and food remains) from each colony. Samples were collected during pre-hatch and chick-rearing periods at Glaucous Gull colonies in northern Alaska, 2008-2009.

		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

Table 1.4. Bird species and age classes identified in Glaucous Gull diet samples. Many bird remnants could not be identified to species, so the list is likely not comprehensive. Adult waterfowl and loons were likely scavenged by gulls rather than actively depredated. Status indicates the conservation and population status (where known); an asterisk indicates a declining population. Population trends are for subspecies or regions that include Alaska's ACP rather than on a national, continental, or species scale. Sources: a) Larned et al. (2009), b) USFWS (2005), c) Dickson and Gilchrist (2001), d) Suydam et al. (2000), e) Brown et al. (2001), f) USFWS (2008).

Species	Egg	Chick	Adult	Status	Source
Greater White-fronted Goose (*Anser albifrons*)	X	X	X	stable	*b*
Snow Goose (*Chen caerulescens*)			X	stable	*b*
Brant (*Branta bernicla*)	X		X	*	*b*
Cackling/Canada Goose (*B. hutchinsii/canadensis*)		X		stable	*b*
Tundra Swan (*Cygnus columbianus*)	X	X		stable	*b*
Northern Pintail (*Anas acuta*)			X	*	*a*
Greater Scaup (*Athya marila*)			X	*	*b*
King Eider (*Somateria spectabilis*)			X	previous declines	*d*
Long-tailed Duck (*Clangula hyemalis*)			X	*	*c*
Duck spp.	X	X			
Willow Ptarmigan (*Lagopus lagopus*)	X	X	X		
Pacific Loon (*Gavia pacifica*)	X	X	X		*a*
Black-bellied Plover (*Pluvialis squatarola*)			X	Moderate concern *	*e*
American Golden-Plover (*Pluvialis dominica*)		X	X	High concern *	*e*
Whimbrel (*Numenius phaeopus hudsonicus*)		X		Highly imperiled *	*e*
Bar-tailed Godwit (*Limosa lapponica*)		X	X	High concern	*e*
Semipalmated Sandpiper (*Calidris pusilla*)		X	X	Moderate concern *	*e*
Pectoral Sandpiper (*Calidris melanotus*)		X	X	Low concern	*e*
Dunlin (*Calidris alpina articola*)		X	X	Highly imperiled *	*e*
Stilt Sandpiper (*Calidris himantopus*)			X	Moderate concern *	*e*
Long-billed Dowitcher (*Limnodromus scolopaceus*)		X	X	Low concern	*e*
Red-necked Phalarope (*Phalaropus lobaus*)		X	X	Moderate concern *	*e*
Red Phalarope (*Phalaropus fulicarius*)		X	X	Moderate concern *	*e*
Shorebird spp.	X	X	X		
Glaucous Gull		X			*a*
Arctic Tern (*Sterna paradisaea*)		X	X	Species of concern	*f*
Varied Thrush (*Ixoreus naevius*)			X		
Eastern Yellow Wagtail (*Motacilla tschutschensis*)			X		
Lapland Longspur (*Calcarius lapponicus*)		X	X		
Sparrow spp.			X		
Redpoll (*Acanthis*) spp.			X		

CHAPTER 2:

Change in Waste Management Reduces Garbage in Diet of Subadult Glaucous Gulls[1]

ABSTRACT

Human-subsidized predators can negatively impact populations of local prey species. This is of particular concern where prey species are declining, as is the case on Alaska's Arctic Coastal Plain. Populations of Glaucous Gulls (*Larus hyperboreus*), the most abundant human-subsidized predator in the area, may increase with further human development, particularly if more garbage becomes available. Methods to limit that effect will be of interest to future developers. We studied use of garbage by Glaucous Gulls in Barrow, Alaska, when garbage was disposed in a landfill (2007) and when it was incinerated (2008). Garbage was significantly less prevalent in regurgitated pellets and food remains from subadult gulls (< 4 yrs) when garbage was incinerated than under traditional management (28 vs. 43% occurrence in diet samples). However, garbage remained an important part of subadult diet. In contrast, garbage was present in only a minor portion of the diet samples from breeding adults (7-13%) and did not change significantly after incineration was implemented. Glaucous Gulls around Barrow apparently use anthropogenic foods primarily as subadults. If garbage enhances survival of subadults, more gulls may reach adulthood and the local or regional population could increase. Breeding adult gulls have a mostly natural diet, including several species of conservation concern that could be detrimentally affected by gull population growth. Incinerating garbage was an effective means of reducing the benefit gulls derive from human development and would similarly restrict access to garbage by other human-subsidized predators, reducing the indirect impact of human development on prey species of concern.

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[1] Weiser, E. and A. Powell. 2010. Change in waste management reduces garbage in diet of subadult Glaucous Gulls. Prepared for submission to *Waterbirds*.

INTRODUCTION

Human-subsidized predators are those that benefit from associating with human settlements, often through access to anthropogenic foods or artificial breeding sites (Gompper and Vanak 2008). This benefit can allow predator population numbers and/or densities to increase (Steenhof *et al.* 1993; NAS 2003; Contesse *et al.* 2004). This artificial increase in predator populations could have negative consequences for prey species, such as reduced populations or even extinction (Holt 1984; Garrott *et al.* 1993), if those predators continue to feed on natural prey. Anthropogenic subsidies of predators are therefore of great interest to conservation efforts in developed or developing areas. One group of human-subsidized predators is *Larus* gulls, which experienced worldwide population growth during the twentieth century (Kadlec and Drury 1968; Fordham and Cormack 1970; Harris 1970; Conover 1983; Yorio *et al.* 1998). Most of these populations exhibited annual growth rates of 3-10%, resulting in each population doubling every eight to 24 years. A major cause of this trend was likely 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). These historic trends suggest that future development will similarly cause gull population growth unless gull access to anthropogenic subsidies is limited.

One area that is particularly susceptible to future development and associated impacts is the Arctic Coastal Plain (ACP) of Alaska, USA. This area is currently sparsely populated, but targeted for further exploration for energy production. Widespread oil exploration began on the ACP 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 ACP wildlife 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 ACP, including red (*Vulpes vulpes*) and arctic (*Vulpes lagopus*) foxes, polar (*Ursus maritimus*) and brown (*Ursus arctos*) bears, Common Ravens (*Corvus corax*), and Glaucous Gulls (*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 improved substantially during the past two decades, with both oilfields and residential areas working to limit scavenger access to garbage, e.g. by covering or incinerating waste.

Glaucous Gulls are the most abundant human-subsidized predator on the ACP (Liebezeit *et al.* 2009). Although Glaucous Gulls readily exploit anthropogenic food sources such as garbage dumps and landfills (Ingolfsson 1976; Day 1998) and are believed to benefit from them, their use of garbage and the potential benefit have not been quantified. Food availability appears to be a limiting factor for Glaucous Gull abundance (Ingolfsson 1976; Strang 1976), so supplemental foods have the potential to cause population growth. Unfortunately, historical data on Glaucous Gull populations on the ACP are scarce, so it is not clear whether populations have increased in response to past development (Noel *et al.* 2006). However, observations suggest that Glaucous Gull densities have increased in developed areas of western and northern Alaska (Springer 1987; USFWS 2003). Moreover, recent aerial surveys have revealed a clear pattern of gull distribution along the northern Alaska coastline, with higher concentrations of Glaucous Gulls near human settlements and oilfields than in surrounding undeveloped areas (Noel *et al.* 2006). The cause of this pattern is not clear, but one possibility is that anthropogenic foods support or attract higher densities of gulls than undeveloped areas.

If artificially enhanced populations of Glaucous Gulls are detrimentally impacting prey species populations, it will be important to prevent this from becoming more widespread with future development. Waste management strategies can limit the benefit predators and scavengers receive from human subsidies (Curtis *et al.* 1995; Kurosawa *et al.* 2003), but their effects are not often quantified. If effective, such strategies may be of interest to future developers on the ACP.

We used regurgitated pellets and food remains to quantify the use of anthropogenic and natural food items by a population of Glaucous Gulls on the ACP. During our study, garbage management in the area switched from dumping putrescible waste in a traditional landfill to incinerating it. We tested for a reduction of garbage in gull diet corresponding to the change in garbage management. We also compared the diets of loafing (mostly subadult) and breeding (adult) gulls to determine whether the benefit derived from anthropogenic foods changed with age and/or breeding status. The effect of garbage incineration on gull diet will be relevant to developers and managers in areas where current or future gull population growth would be detrimental to local wildlife or human residents.

METHODS

Study Area

This study was conducted in Barrow, Alaska (USA), a city on the ACP with a population of about 4000. Barrow is not accessible by road, and the nearest major city (Fairbanks, Alaska) is 500 miles to the south. The remote nature of the city makes it highly impractical to ship waste to major processing or recycling facilities, so garbage and other waste are dealt with locally. Until mid July 2007, household garbage was disposed in the landfill north of town; after that point, garbage was incinerated and the ashes disposed in a new landfill southeast of town (Figure 2.1). Fresh garbage continued to be available in open dumpsters at the old landfill throughout the summer of 2007 as the city switched over to the new system. When describing gull diet under different management regimes, we therefore considered 2007 to represent the traditional landfill whereas 2008 represented the new strategy of incinerating garbage. In both years, garbage was available in open dumpsters around the city prior to being disposed.

Diet Assessment

We characterized Glaucous Gull diet at nine to ten loafing sites around Barrow, Alaska (Figure 2.1) in 2007 and 2008. In an effort to sample the entire population of gulls loafing around Barrow, we collected samples at all sites where gulls were observed loafing in each year, even when sites differed between years. We sampled eight sites used by gulls in both years, one in 2007 only, and two in 2008 only. All sites were within 20 km of both landfills and the city. This distance is well within typical daily foraging range of Glaucous Gulls in northern Alaska, which is up to 70 km (Declan Troy, Troy Ecological Research Associates, unpubl. data).

Once a week between 7 July and 17 August 2007 and 2008, we counted the gulls present at each loafing site. We assigned each gull to one of two age classes: subadult (< 4 yrs old) and adult (≥ 4 yrs old) based on plumage (Gilchrist 2001). We also collected regurgitated pellets and food remains at each site. These samples consist of indigestible parts of prey and are abundant in gull loafing and breeding areas (Gonzáles-Solís *et al.* 1997). We did not collect items with evidence of weathering, such as sun-bleaching, epiphyte growth, or tannin stains, to ensure the samples were produced in the current year. Diet data from these samples are biased against highly digestible prey (Duffy and Jackson 1986), but these samples are appropriate for monitoring variation in consumption of foods with indigestible parts, including garbage (Gonzáles-Solís *et al.* 1997).

We also collected samples at a Glaucous Gull breeding colony outside of Barrow (Figure 2.1). This colony was also within 20 km of the city and landfills, so we assumed that breeding and loafing gulls had equal access to garbage. We collected diet samples from the colony once during the second week of August each year. We did not collect weathered items, so these samples were produced in July and early August of each year, the same period covered by samples from the loafing sites. Adult Glaucous Gulls regurgitate prey to feed their chicks (Gilchrist 2001), so all of our diet samples represented prey captured by breeding adults. In each year, we recorded the number of breeding pairs (based on the number of current-year nests) and counted the chicks present at the colony just prior to fledging.

Data Analysis

We dissected the pellets and visually examined food remains to identify the foods present in each sample. We identified prey to the lowest possible taxonomic level, but many could not be consistently identified below class, so we grouped prey at class level for diet analysis and considered garbage to be an additional food class. For each group of gulls (breeding or loafing) in each year, we recorded the number of samples (pellets and food remains) in which each food class occurred.

We used pairwise chi-square tests to test for differences in frequency of occurrence of each prey class in diet samples between years for each group of gulls, and between loafing and breeding gulls within each year. We did not conduct chi-square tests where expected values were less than five for at least one cell. Where we conducted multiple tests of significance, we used a Bonferroni correction of $\alpha = 0.05$ / (number of comparisons) for our significance level for each individual test.

RESULTS

At the loafing sites, we collected 193 diet samples in 2007 and 248 in 2008. Loafing group size averaged 25 gulls (SD = 29) in 2007 and 23 (SD = 24) in 2008, with no apparent change with the new garbage management. Eighty-seven percent of the gulls at loafing sites were subadults (89% in 2007, 86% in 2008); thus samples from loafing sites were chiefly representative of subadult gull diet. In each year, the most prevalent component of loafing diet was garbage, followed by crustaceans, birds (43-48% waterfowl), and mammals (67-92% brown lemmings, *Lemmus trimucronatus*); bivalves, gastropods, insects, and unidentified prey were minor components (Table 2.1). Garbage was present in a substantial portion of diet samples in both years, but was significantly less prevalent when the city incinerated its garbage (28% in 2008 versus 43% in 2007; $\chi^2_1 = 10.5$, $P = 0.001$). There were no significant changes in occurrences of other prey classes ($\alpha = 0.008$; $P > 0.038$) between years.

At the breeding colony, we collected 46 samples in 2007 and 402 in 2008. Sample size was much lower in 2007 because we initially planned that year to be a pilot season for a study of breeding gull diet; we collected diet samples from a smaller portion of the colony in that year than in 2008, but collection was not biased by diet sample type or content. There were ten breeding pairs with eleven chicks at the colony in 2007, and 13 pairs with 18 chicks in 2008. In each year, the most common dietary component was mammals (94-100% brown lemmings), followed by birds (34-67% shorebirds), garbage, and fish; crustaceans, bivalves, and unidentified prey were minor components (Table 2.1). Garbage was present in only a small portion (13% in 2007, 7% in 2008) of diet samples from the breeding colony, with no significant change between years ($P > 0.25$). The only prey class to change significantly in occurrence between years was mammals, with a higher occurrence in 2008 than in 2007 ($\chi^2_1 = 14.9$, $P < 0.001$).

In each year, breeding adult gulls ate significantly less garbage, fewer crustaceans, and more mammals and birds than loafing gulls (Table 2.1). We identified eight shorebird species in gull diet, including one highly imperiled species, one species of high concern, and four species of moderate concern, all of which are experiencing population declines (Table 2.2).

DISCUSSION

Garbage was an important food for loafing (subadult) Glaucous Gulls, making up 23% of diet even when garbage was incinerated in 2008. In contrast, breeding adult gulls consumed a diet composed mainly of natural prey, especially lemmings and shorebirds.

Glaucous Gulls and other birds that experience deferred sexual maturity use their time as nonbreeding subadults to develop foraging skills (Ashmole 1963). Subadult gulls forage less efficiently than adults on both natural and anthropogenic foods (Searcy 1978; Skórka and Wójcik 2008), with progressive improvement with age (MacLean 1986). Subadult Glaucous Gulls may therefore prefer garbage as a food source because it is predictably available in time and space and more easily obtained than natural prey such as lemmings and shorebirds. Unlike breeding adult gulls, subadults around Barrow did not increase their consumption of mammals (mostly brown lemmings) in 2008 even though it was a year with very high local lemming abundance (Rick Lanctot, USFWS, unpubl. data). Subadults may not yet have the hunting skills to take advantage of even unusually abundant lemmings and may derive a substantial benefit from easily obtained anthropogenic foods. As subadult gulls are not reproducing or growing (Gilchrist 2001), caloric content of food may be more important to them than nutritional value; garbage would thus be an appropriate food source (Pierotti and Annett 2001). A similar pattern has been found in bald eagles (*Haliaeetus leucocephalus*), where subadults are more likely than adults to specialize in feeding on garbage even when higher-quality natural prey are available (Elliott *et al.* 2006). Garbage can enhance gull body condition (Auman *et al.* 2008) and proximity to anthropogenic food sources can improve survival of American crows (*Corvus brachyrynchos*; Marzluff and Neatherlin 2006), so it is likely that garbage can improve survival to adulthood for immature birds.

In contrast, garbage may not contain sufficient levels of nutrients necessary for gull reproduction (Bolton *et al.* 1992; Pierotti and Annett 2001; Ludynia *et al.* 2005), so breeding gulls may need to rely more heavily on natural prey. Reproductive output can be reduced for gulls that feed on garbage (Ward 1973; Pierotti and Annett 1991; Annett and Pierotti 1999), though other studies have found the opposite or no effect (Hunt 1972; Pons and Migot 1995). If breeding gulls select food items based on their nutritional needs, they may avoid using garbage when possible, even where it is readily available.

The discrepancy in diet between subadult and breeding adult gulls indicates the potential for human development to detrimentally affect prey species by subsidizing predators. If anthropogenic foods improve subadult gull survival, they may create a larger population of breeding adults preying on other birds, especially shorebirds. In our study area, the minor amount of garbage in breeding adult diet would not be enough to offset this effect, so predation rates on natural prey would increase. Cases like this can cause local declines or extinctions for prey species (Courchamp *et al.* 2000) and may warrant management efforts to reduce this effect.

Incineration was effective in reducing use of garbage by subadult gulls. However, despite changes in disposal methods, garbage remained an important component of subadult diet, and could still potentially improve the survival of those individuals.

Storage methods may be as important as disposal in regulating garbage availability; open dumpsters offer ready access to garbage for avian scavengers and could explain why garbage was still common in subadult gull diet even after incineration was implemented. Effective garbage control will be a necessary step in limiting the negative indirect effects of future development on wildlife.

ACKNOWLEDGMENTS

This study was funded by the North Slope Borough Department of Wildlife Management (with a grant from NPR-A Impact Mitigation Program, Alaska Department of Commerce, Community, and Economic Development), the U.S. Bureau of Land Management (Arctic Field Office), and a University of Alaska Foundation Angus Gavin Migratory Bird Research Grant. We thank Ruby Baxter for assistance with sample collection and analysis and Robert Suydam and Debbie Nigro for logistical support. Debbie Nigro, Declan Troy, Christine Hunter, and Alan Springer provided comments that improved the manuscript. This study was conducted under approval #07-46 of the Institutional Animal Care and Use Committee of the University of Alaska Fairbanks. Any use of trade, product, or firm names in this publication is for descriptive purposes only and does not imply endorsement by the U.S. Government.

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FIGURES

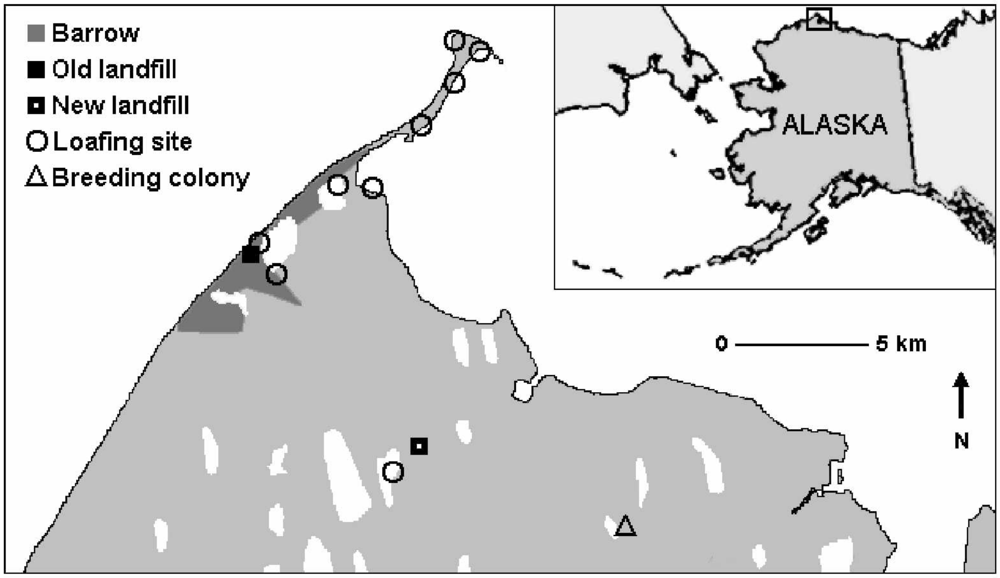

Figure 2.1. Collection sites for Glaucous Gull diet samples in 2007 and 2008. Inset shows location of enlarged map in Alaska.

TABLES

Table 2.1. Diet of loafing and breeding gulls before and after garbage incineration. Diet is given as percent occurrence of each food class in diet samples (pellets and food remains) for loafing (subadult) and breeding (adult) Glaucous Gulls when garbage was (a) disposed in a landfill and (b) incinerated. Chi-square tests were for differences between gull groups in frequency of occurrence of each prey class (df = 1 and α = 0.0125 for each test; asterisks indicate significant differences, all P < 0.001). Bivalves, gastropods, insects (Pterygota), and unidentified items were each present in ≤ 5% of samples from each group in each year and were not tested for differences between groups. Sample sizes given indicate the number of pellets and food remains analyzed for each gull group in each year. Occurrences do not sum to 100 because each diet sample can contain more than one food type.

a) Landfill (2007)

Gull group	Garbage	Mammals	Birds	Fish (Osteichthyes)	Crustaceans (Malacostraca)
Loafing[1]	43	16	33	3	29
Breeding[2]	13	43	59	4	0
χ^2	14.3*	16.6*	10.3*	0.4	-

[1]N = 193; [2]N = 46

b) Incineration (2008)

Gull group	Garbage	Mammals	Birds	Fish (Osteichthyes)	Crustaceans (Malacostraca)
Loafing[1]	29	22	27	5	38
Breeding[2]	7	71	48	6	1
χ^2	55.9*	151.4*	28.7*	0.7	156.2*

[1]N = 248; [2]N = 402

Table 2.2. Shorebird species identified in Glaucous Gull diet around Barrow, Alaska. Conservation status of each is from Brown *et al.* (2001); asterisks indicate species experiencing population declines.

Common name	*Scientific name*	*Conservation status*	
Dunlin	*Calidris alpina articola*	Highly imperiled	*
American Golden-Plover	*Pluvialis dominica*	High concern	*
Stilt Sandpiper	*Calidris himantipus*	Moderate concern	*
Semipalmated Sandpiper	*Calidris pusilla*	Moderate concern	*
Red Phalarope	*Phalaropus fulicaria*	Moderate concern	*
Red-necked Phalarope	*Phalaropus lobatus*	Moderate concern	*
Long-billed Dowitcher	*Limnodromus scolopaceus*	Low concern	
Pectoral Sandpiper	*Calidris melanotos*	Low concern	

CHAPTER 3:

Using Stable Isotope Analysis to Evaluate Biases in Conventional Diet Samples

ABSTRACT

Regurgitated pellets and food remains have been traditionally used in avian diet studies, but these methods are biased toward foods with large or indigestible parts. Stable isotope analysis has been developed over the past two decades as a method for assessing unbiased information on diets of birds and other animals. We analyzed carbon and nitrogen stable isotope ratios of glaucous gull chick feathers from 10 breeding colonies in northern Alaska, and used a Bayesian mixing model to generate a probability distribution for the contribution of each food group to diets. We compared these with probability distributions from conventional diet samples (pellets and food remains) from the same colonies and time period to assess the nature and extent of biases in the conventional data. Conventional analysis almost always overestimated the contributions of bird prey to diets, often underestimated the contributions of fishes, and sometimes over- or underestimated the contributions of small mammals or miscellaneous marine foods. Conventional analysis overestimated the relative importance of garbage in diets at two colonies, but by relatively small amounts. Pellets and food remains therefore may be used to assess the importance of garbage relative to other food sources in diets of gulls and similar birds, but are clearly inappropriate to estimate the potential impact of gulls on bird or fish species. However, conventional samples provide much more species-level information on foods used by gulls than stable isotope analysis, so a combined approach would provide the best information on diet composition.

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[1] Weiser, E. and A. Powell. 2010. Using stable isotope analysis to evaluate biases in conventional diet samples. Prepared for submission to *Journal of Wildlife Management*.

INTRODUCTION

Diet studies are used in a variety of applications to understand wildlife and their relationships to their habitats and communities. For example, diet information can be used to assess predator–prey dynamics (Rieman et al. 1991, Kunkel et al. 1999, Short et al. 1999), evaluate energetic or nutritional requirements (Roby 1991, Ballard et al. 2004), assess the extent of niche overlap and competition between species (DuBowy 1988, Bonesi et al. 2004), or monitor relative trends in prey species abundance (Montevecchi 1993).

Conventional methods of diet assessment, such as analyzing regurgitated pellets and food remains, can be useful in diet studies for many bird species (e.g. Barry and Barry 1990, Real 1996, Kristan et al. 2004). These types of food samples are often abundant and easily collected. However, diet data from such samples are typically biased toward foods with large, identifiable, or abundant indigestible parts (Duffy and Jackson 1986, Gonzáles-Solís et al. 1997). Highly digestible foods are underrepresented or not detected. Most studies do not assess the nature or extent of biases in diet samples, and such assessments are not always possible. If the biases in these samples could be quantified, researchers would have a better idea of what types of studies or species for which these samples are appropriate, and the extent of limitations of the diet information obtained from these sources.

In contrast to conventional diet samples, stable isotope ratios of a consumer's tissues represent all foods consumed and absorbed by that animal (Hobson and Wassenaar 1999). Carbon and nitrogen stable isotope ratios in organisms vary predictably among different food webs, and foods from different habitats or at different trophic levels often have distinct isotopic signatures (Peterson and Fry 1987, Post 2002). For example, foods from a food web based on plants that use a C4 photosynthesis pathway have larger stable carbon isotope ratios than those from a food web based on plants that use a C3 pathway. The relative contribution of each food type to a consumer's diet can be inferred by testing the stable isotope ratios of a tissue from that consumer and correcting for diet–tissue isotopic discrimination (Bearhop et al. 1999).

The tissue chosen for stable isotope analysis depends on the period of interest, as different tissues turn over at different rates and so reflect diet during different time periods (Hobson and Clark 1992a). Feathers are widely used in stable isotope studies of birds; sampling is relatively non-invasive, and stable isotope ratios of feathers are inert after growth and so reflect diet during the period in which they were grown (Bearhop et al. 2002).

When a consumer uses only a few types of isotopically distinct foods, calculating contributions to diet of each food is relatively straightforward (Phillips 2001). However, contributions of larger numbers of foods or of foods with overlapping isotopic signatures can be difficult to determine (Phillips and Gregg 2003). Recently, a Bayesian mixing model (mixSIR) has been developed to deal with these overlapping prey signatures and other sources of uncertainty (Moore and Semmens 2008, Jackson et al. 2009, Semmens et al. 2009). MixSIR incorporates the mean and standard deviation of food signatures and of discrimination factors, which is useful when one value cannot be used with confidence. The model deals with these sources of uncertainty and with overlapping prey signatures by giving a range of potential contributions to diet for each food group. These ranges are often wide when the model incorporates much uncertainty, but can be narrowed by including prior information on diet composition from other sources (e.g. stomach contents). The model also calculates the most likely contribution of each food to consumer diet, but these values are not necessarily accurate and should be interpreted cautiously.

We used mixSIR to evaluate the accuracy of diet information gained from regurgitated pellets and food remains produced by glaucous gulls (*Larus hyperboreus*) in northern Alaska. Glaucous gulls are opportunistic predators that feed on most of the other wildlife in this area (ELW and ANP unpubl.). The extent to which glaucous gulls feed on human food waste is of interest because anthropogenic foods can cause gull populations to increase (Conover 1983, Duhem et al. 2008). If an artificially enlarged gull population feeds extensively on other breeding birds, this could then cause or exacerbate population declines for those birds by reducing their reproductive output

(Guillemette and Brousseau 2001, Finney et al. 2003). This is a particular concern for prey species that are already declining or otherwise of conservation concern. An accurate evaluation of gull use of garbage and birds is therefore of interest in many human-influenced systems.

Garbage and birds both contain indigestible material and so are easily detected in pellets and food remains, but if highly digestible foods are not detected, the importance of garbage and birds in gull diet will be overestimated. Stable isotope analysis could be a useful tool to assess the accuracy of pellets and food remains in reflecting the amount of garbage in diet. Garbage has a distinct isotopic signature in this area because of the strong influence of corn, a C4 plant, in human foods (Jahren and Kraft 2008). Terrestrial C4 plants do not grow naturally in northern Alaska, so any C4 isotopic signature detected would be due to the presence of garbage in gull diet.

We used mixSIR to predict gull diet based on the stable isotope signatures of gull chick feathers grown at each colony, and compared these results with conventional diet data from regurgitated pellets and food remains collected during the chick-rearing period at the same colonies. This enabled us to describe the extent of biases in the conventional method of diet analysis and assess the accuracy of our estimates of glaucous gull diet composition at these colonies.

METHODS

Study Sites

We monitored glaucous gull diet at 8 sites in northern Alaska: 2 in both 2008 and 2009, one in 2008 only, and 5 in 2009 only (Figure 3.1) for a total of 10 site–year combinations (referred to here as colonies). Glaucous gulls in this area nest in small (5–30 pairs) colonies, generally on small islands in tundra lakes. Our colonies sometimes also contained breeding geese, but never other gull species. A variety of shorebirds, waterfowl, loons, ptarmigan, and a few sparrows nest in this region; lemmings, voles, and freshwater and marine fish are also available as potential prey. Subsistence-hunted whales, seals, caribou, and waterfowl carcasses are available around residential areas to be scavenged. Municipal landfills are present in most residential and industrial areas. The landfill at Prudhoe Bay is the largest; other areas typically incinerate garbage rather than disposing it 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–early August just before the chicks began fledging (chick-rearing). We timed our second visits by floating eggs to estimate age during the June visit (ELW unpubl. data) and assuming a 28-day incubation period and a 42–48-day nestling period (Uspenski 1958). We accessed colonies by helicopter or vehicle, and traveled through colonies on food and small inflatable rafts.

Conventional Diet Analysis

During each colony visit, we collected regurgitated pellets and food remains from the area around each gull nest. We collected only fresh items with no evidence of weathering (sun-bleaching or epiphyte growth) to ensure that our samples reflected diet during the targeted year and reproductive period. Here we use data from only the samples collected during the second (chick-rearing period) colony visits. Collecting all samples from the pre-hatch period ensured that samples from the second visit were representative of the chick-rearing period.

We dissected the pellets and identified all food components in the pellets and food remains to the lowest possible taxonomic level. We grouped foods at the taxonomic level at which they were consistently identifiable in diet samples and so that stable isotope signatures of specific foods were very similar within each food group. We scored each food sample for the presence or absence of each of the seven food groups (garbage, birds, small mammals, caribou, fishes, zooplankton, and other marine). To estimate the relative importance of each food group in diet at each colony, we then randomly subsampled, with replacement, the original dataset from each colony. Each subsample was 2/3rds the size of the original dataset. We calculated the frequency of occurrence of each food group in the subsample as the proportion of subsampled pellets and food remains containing at least one element of that group, then adjusted these values so that diet composition summed to 1.0. This gave the proportional contribution to diet of each food group. We repeated the subsampling procedure 100,000 times to create a probability distribution for the contribution of each food group to diet for each colony. We truncated each of these distributions at the 1st and 99th percentiles to remove outliers, leaving about 98,000 subsampled estimates of diet composition for each colony.

Stable Isotope Analysis

During the chick-rearing period colony visits, we used small inflatable rafts to capture as many gull chicks as possible at each colony. We sampled one mantle feather from each chick for stable isotope analysis. These feathers are grown between 8 and 30 days of age (ELW unpubl. data), so their stable isotope ratios represent diet during that period. All field methods were approved by the Institutional Animal Care and Use Committee of the University of Alaska Fairbanks (07–46).

We stored feather samples in dry envelopes. Prior to analysis, we cleaned the feathers of surface contaminants using 100% ethanol and allowed them to air dry. We submitted 0.2–0.4 mg of material from the distal tip of each feather to the Alaska Stable Isotope Facility for carbon and nitrogen isotope ratio analysis in a continuous-flow system with a Costech Elemental Analyzer (ESC 4010), ThermoFinnigan Conflo III interface, and Delta^{plus} XP Mass Spectrometer. We expressed the isotope ratios in delta notation relative to international standards (Vienna PeeDee Belemnite for carbon, atmospheric air for nitrogen) according to the following equation: $\delta X = ([R_{sample}/R_{standard}] - 1) \times 1000‰$, where X is either ^{13}C or ^{15}N, and R is the ratio of $^{13}C/^{12}C$ or $^{15}N/^{14}N$ for the sample and the standard.

We obtained isotopic signatures of potential foods, including garbage, from the literature and from unpublished databases for northern Alaska and outlying waters (Figure 3.2). We supplemented these values by collecting samples of additional potential prey in 2009, including muscle tissue from crab spp., marine isopods (*Saduria entomon*), and adult shorebirds and passerines found dead. We freeze-dried the tissues and submitted subsamples of 0.2–0.4 mg for analysis by the Alaska Stable Isotope Facility.

We used the same food groups for the isotopic analysis as for the conventional analysis, except that we separated marine and freshwater fish, which have very different stable isotope signatures. The stable isotope signatures of some food groups overlapped, but grouping foods reduced the isotopic redundancy of foods and facilitated comparisons with conventional data.

When combining isotopic values from several specific foods into one group, we used the arithmetic mean of the foods being combined into each group; and calculated the standard deviation according to Equation 1, where V_i = variance of food i, n_i = sample size for food i, and g = number of specific foods combined into that group.

$$\overline{SD} = \sqrt{\frac{\sum_{i=1}^{g} V_i(n_i - 1)}{(\sum_{i=1}^{g} n_i) - g}} \qquad \text{Equation 1}$$

We used the Bayesian stable isotope mixing model mixSIR (Semmens and Moore 2008) to estimate the range of possible contributions of each food group to gull diet at each colony based on the isotopic signatures of chick feathers. In each model, we used the mean and standard deviation of isotope signatures for each food group (Figure 3.2). We used the mean and standard deviation of diet-feather discrimination values from captive studies that fed related, full-grown bird species (ring-billed gulls, *Larus delawarensis*, and great skuas, *Stercorarius skua*) a carnivorous diet (fish or beef; Hobson and Clark 1992b, Bearhop et al. 2002), and corrected for the fact that chicks in this study were growing by reducing the mean value for $\delta^{15}N$ discrimination by 0.55‰ (Sears et al. 2009). The final discrimination values used in the model were therefore 1.5 ± 1.12 for $\delta^{13}C$ and 3.7 ± 1.06 for $\delta^{15}N$.

We evaluated the fit of each model by checking that the number of posterior draws was over 1000, there were no duplicate draws, and the ratio of best posterior density to total posterior density was < 0.01 (Moore and Semmens 2008). If a model did not meet any one of these criteria, we ran it again with more iterations until the criteria were satisfied. For comparison with the conventional analysis, we summed the estimated contributions of marine and freshwater fish to estimate the contribution of total fishes for each colony. We then calculated probability distributions for the contribution of each food group to diet at each colony. As with the conventional probability distributions, we truncated these at the 1st and 99th percentiles to remove outliers and calculated the most likely estimated contribution of each food group at each colony.

Biases in Conventional Data

For each food group at each colony, we compared the probability distributions for contribution to diet from conventional analysis to the distributions from the stable isotope mixing model. In each comparison, we calculated the proportion of the approximately 98,000 conventional subsamples that fell above or below the range of contributions estimated by the stable isotope model. This corresponds to the frequency with which conventional samples would over- or underestimate contributions of the food group to diet at a particular colony, and represents the chance of bias in conventional samples if the stable isotope model estimates are correct. We examined the magnitude of bias in each case by subtracting the most likely stable isotope estimate of contribution from the most likely conventional model estimate. We calculated the mean and standard deviation of these differences across colonies (assuming independence between years) to evaluate general trends in biases present in conventional diet data.

RESULTS

We collected 59–302 pellets and food remains from each glaucous gull colony (Table 3.1). Conventional analysis of these samples showed that diet was highly varied across colonies, with small mammals (rodents), birds, garbage, and fishes comprising the majority of foods consumed (Table 3.2). We identified 40 species in conventional samples, of which only one (caribou) could have been identified by the stable isotope model.

We captured 3–15 chicks, representing 21–83% of those present, at each colony (Table 3.1). The number of chicks captured was limited by conditions such as high winds and large lakes, either of which enabled some chicks to evade capture. Isotopic signatures of chick feathers varied among colonies, especially in $\delta^{15}N$ (Table 1).

Each of our final mixSIR models required between 10×10^5 and 10×10^9 iterations. Each model run resulted in > 1400 posterior draws with no duplicates and a ratio of best posterior density to total posterior density of < 0.01. The models requiring the most iterations took up to 1.5 days to run on a 2008 laptop with 2.4 GHz duo core processor and 2 GB RAM. The range of possible contributions of each food group given by the stable isotope mixing models was sometimes wide and poorly resolved (Table 3.2).

Most food groups had a tendency to be either over- or underestimated by conventional methods (Figure 3.3). Conventional estimates of contributions of each food group always fell outside the modeled ranges from the stable isotope model at 2-7 colonies, and had some chance of being biased at 1-6 others (Table 3.3). The magnitude of bias was largest for birds and fishes, substantial for small mammals and miscellaneous marine foods, and minor for other food groups (Figure 3.4).

DISCUSSION

Glaucous gulls at these colonies consumed a variety of foods, with considerable variation in the relative importance of each food group among colonies. This enabled us to evaluate the accuracy of conventional samples for a range of diets. Conventional samples confirmed the presence of 39 species in gull diets that would not have been identified by stable isotope analysis alone. These were species for which we did not have stable isotope signatures or that shared very similar signatures and could not be reliably distinguished isotopically.

Conventional estimates of diet composition did not always agree with stable isotope estimates, revealing that conventional estimates for each food group were potentially biased at several colonies. Contributions to diet of food groups with abundant indigestible parts were generally overestimated. This effect was most pronounced for bird prey, the relative importance of which was almost always dramatically overestimated by conventional samples. Pellet analysis also overestimates bird occurrence in great skua diet (Votier et al. 2003). Captive skuas produce 4x as many pellets per meal of birds as per meal of fish, probably because of the large amount of indigestible material (feathers) in bird meals (Votier et al. 2001); the same is likely true for wild gulls. Use of only conventional data could therefore lead to erroneous conclusions about the extent to which gulls prey upon other birds. Small mammals (lemmings, voles, and ground squirrels) also contain large amounts of indigestible fur and bones, suggesting that these also have the potential to be overestimated by conventional diet analysis. We found that the importance of small mammals in diets was usually overestimated by conventional samples, but was accurate or underestimated at some colonies. The amount of mammalian prey in skua diets may also be overestimated (Votier et al. 2003), but the mixed results in our study indicate that this trend should be generalized with caution.

Garbage can contain large amounts of indigestible material (e.g. paper, plastic), but we were unsure of the extent to which gulls swallowed indigestible material along with food waste. If gulls selected for edible refuse, garbage occurrence in diet would be underestimated by pellets and food remains; if they instead did not discriminate between digestible and indigestible items, garbage occurrence in diet could be overestimated by conventional samples. However, our stable isotope models for garbage contributions to diets generally agreed with our conventional estimates. Conventional samples always overestimated the amount of garbage in diets at two colonies, but the magnitude of the bias was substantial for only one colony. The two colonies at which conventional samples always underestimated the amount of garbage in diets were far enough from any human settlement that gulls breeding there probably did not have access to garbage, so those apparent cases of underestimation in conventional samples may instead indicate uncertainty in the isotope models. Therefore, for almost all colonies, pellets and food remains provided a fairly accurate representation of the importance of garbage, relative to other food groups, in diets.

As we expected based on previous studies, conventional samples underestimated the relative importance of highly digestible foods such as caribou (scavenged carcasses), zooplankton, and miscellaneous marine foods (potentially including scavenged whale and seal carcasses). However, based on the stable isotope results, these food types comprise only a minor part of gull diets in this region, so these biases were relatively small. The biases would be more pronounced for birds feeding more heavily upon these food groups. Fishes also seemed to be highly digestible by glaucous gulls, as conventional samples tended to substantially underestimate the importance of fishes in gull diets. Pellets also tend to underestimate the amount of fish in diets of ring-billed gulls, Audouin's gulls (*Larus audouinii*), and great skuas (Brown and Ewins 1996, Gonzáles-Solís et al. 1997, Votier et al. 2003). Our results agree that pellets and food remains are not appropriate samples for assessing the amount of fish in these birds' diets.

The extent of each bias we detected in conventional estimates of diets was dependent on the amount of fully digestible foods in gull diet. The biases we measured cannot be extrapolated to diets that may include larger or smaller proportions of highly digestible foods that are not detected in conventional samples. However, the relative representation of foods with indigestible parts (birds, small mammals, fishes, and garbage) in conventional samples would likely hold across diets that otherwise vary in contributions of digestible foods.

As in most stable isotope studies of animals' diets, our models were based on several assumptions. We assumed that our stable isotope values for potential foods were correct, despite the necessity of using averages of values from related species when we could not obtain values for all individual species. We included stable isotope values from 11 of 21 families identified in our diet samples (90% of the families excluded occurred only rarely in conventional samples), but we have no way to know whether our list of species included all those fed upon by glaucous gulls in our area, or whether the values included encompass the full range of variation in isotopic signatures of each food group. Our models assume that the diet–tissue discrimination values, including the correction for growth, were accurate for wild glaucous gull chicks. These values were the best available relevant to our study species, but we could not evaluate their accuracy. Finally, our comparisons with conventional estimates were based on the assumption that the same diet produced both the pellets and food remains and the stable isotope signature of the chicks' feathers. The conventional samples were produced by both adults and chicks, but our isotopic information came only from chick feathers. We therefore had to assume that adult glaucous gulls consume a diet similar to what they feed their chicks, though it is not known if this is the case for glaucous gulls (Gilchrist 2001). Because we used the best available information in our models, any violation of these assumptions would likely have only a minor effect on our assessments of biases in conventional samples. However, we recognize that while our stable isotope models provide an estimate of diet composition that is closer to the truth than estimates from conventional samples, we cannot be certain that our modeled estimates reflect actual gull diet.

Management Implications

Conventional data provided relatively accurate estimates of the relative importance of some food groups to glaucous gull diet. For example, conventional samples could be a convenient and effective method to monitor the extent to which human-subsidized predators feed on garbage. In contrast, contributions of bird prey to diet were usually overestimated by conventional data, and contributions of fish were often underestimated. In some systems, including our study area, this could have implications for assessing the impact of gulls on bird species of conservation concern. Sources of data besides conventional samples would be necessary for an accurate portrayal of the extent to which gulls may impact bird or fish species of concern.

However, conventional samples allowed identification of foods to species in many cases, whereas this was generally not possible with the stable isotope model. Isotope models cannot accurately distinguish between contributions of food species with similar isotopic signatures, e.g. those with similar diets. Conventional samples are therefore still useful in studies aiming to identify prey species in a predator's diet. Stable isotope models used in conjunction with conventional methods could then provide an assessment of the predator's impact on particular prey groups.

ACKNOWLEDGMENTS

We thank the North Slope Borough Department of Wildlife Management (with a grant from NPR-A Impact Mitigation Program, Alaska Department of Commerce, Community, and Economic Development), the U.S. Bureau of Land Management (Arctic Field Office), ConocoPhillips Alaska, Inc., and a University of Alaska Foundation Angus Gavin Migratory Bird Research Grant for providing funding and other support for this study. We thank Ruby Baxter and Erin McDonald for assistance with sample collection and Robert Suydam and Debbie Nigro for logistical support. Jonathan Moore advised on stable isotope analysis methods. Christine Hunter and Alan Springer provided comments that improved the manuscript. Any use of trade, product, or firm names in this publication is for descriptive purposes only and does not imply endorsement by the U.S. Government.

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FIGURES

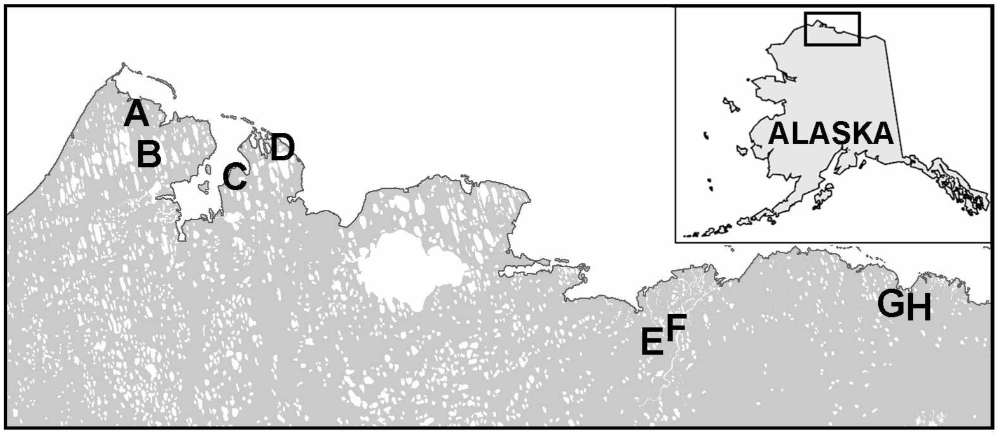

Figure 3.1. Collection sites for conventional diet and stable isotope samples. Colonies A and B were sampled in both years, D in 2008 only, and all others in 2009 only.

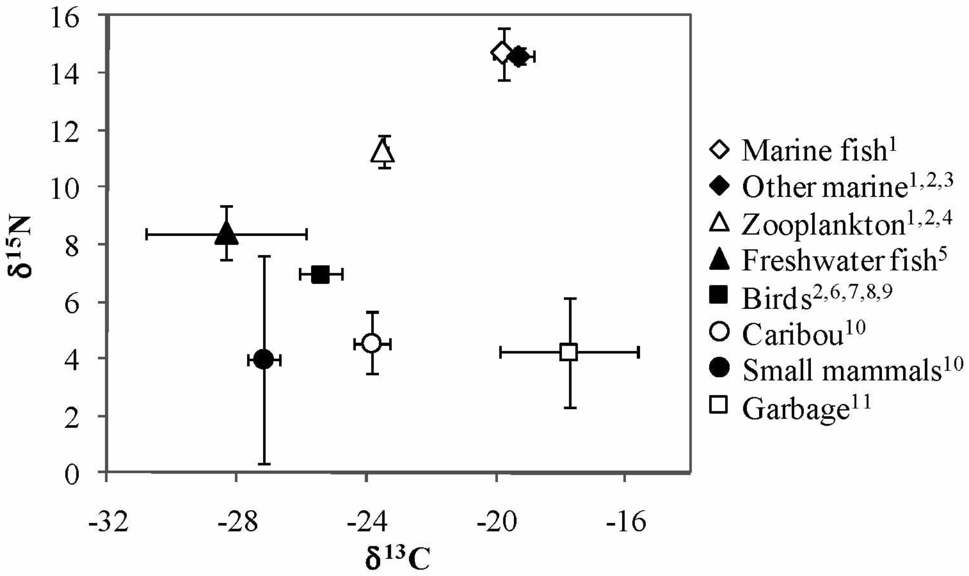

Figure 3.2. Stable isotope signatures (mean ± standard deviation) of food groups. Carbon and nitrogen isotope ratios are given in per mil relative to international standards. Tissues with substantial lipid content (bird eggs, whole fish) were lipid-extracted prior to analysis (Hobson and Clark 1992b) or adjusted by adding 2‰ to $\delta^{13}C$ (Lawson 2006). Bird egg values were estimated from the arithmetic means of separately analyzed lipid-free yolk and albumen fractions. "Small mammals" were mostly microtine rodents and arctic ground squirrels. "Other marine" included marine mammals, isopods (*Saduria entomon)*, and crabs. References: [1]Dehn et al. (2007), [2]this study, [3]Dehn et al. (2006), [4]Iken et al. (2005), [5]Kline et al. (1998), [6]Lawson (2006), [7]S. Oppel, University of Alaska Fairbanks, unpubl. data, [8]Gauthier (2003), [9]Jamieson (2009), [10]Alaska Dept. Fish and Game unpubl. data, [11]Jahren and Kraft (2008).

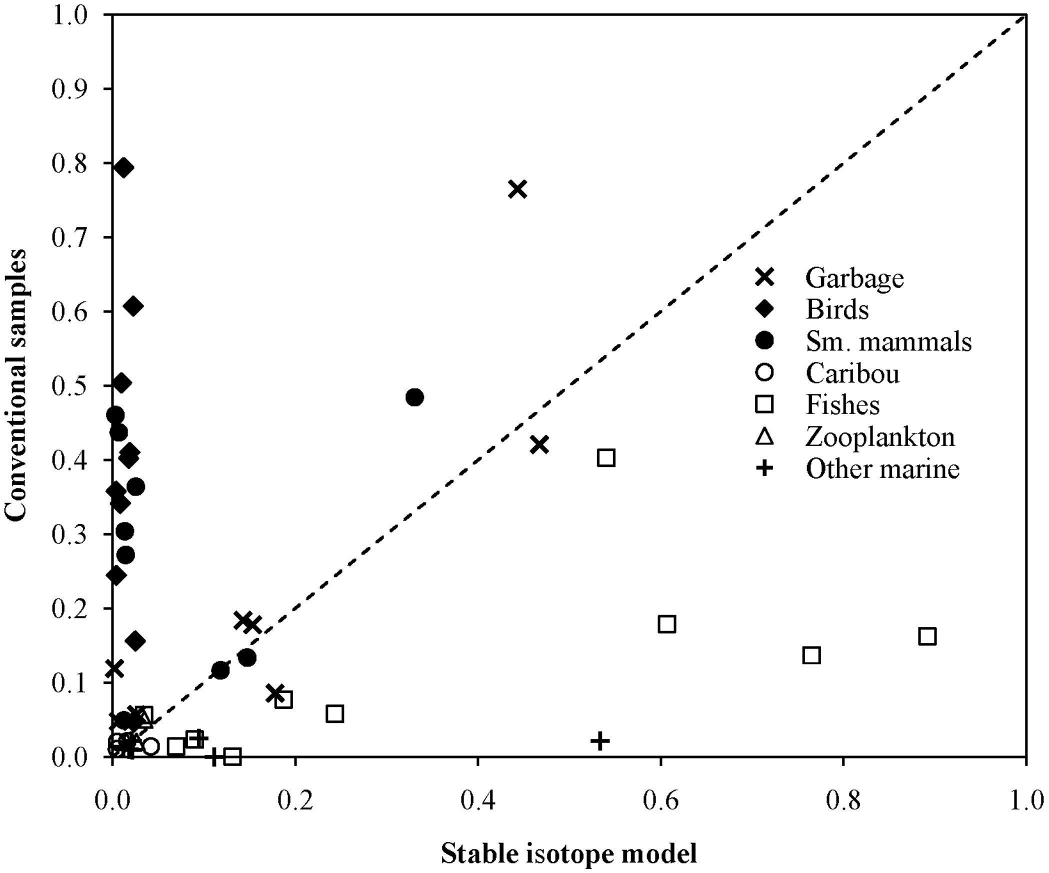

Figure 3.3. Most likely contribution estimated by two methods for each food group. Dashed line shows a 1:1 match between the two methods.

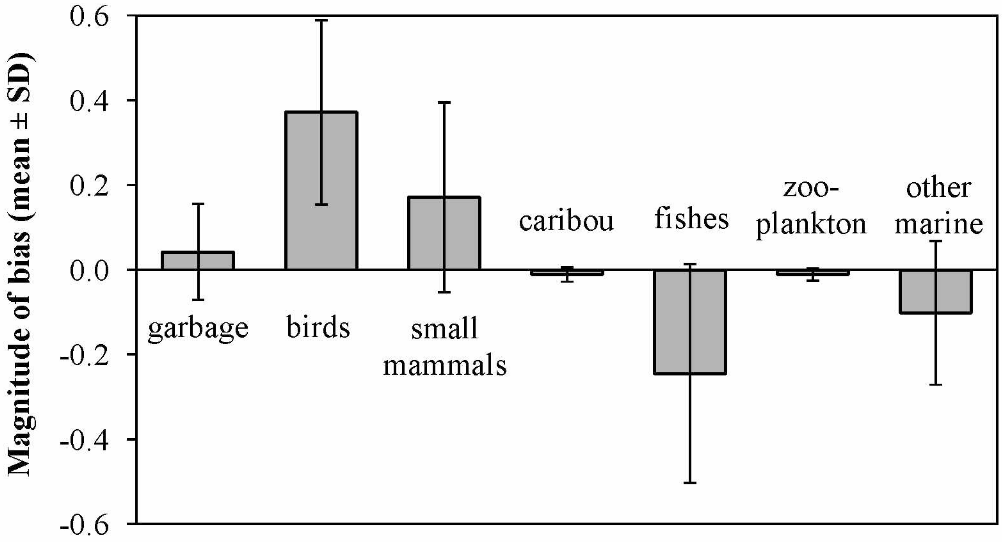

Figure 3.4. Magnitude of bias in conventional samples for each food group. Average bias is given as the mean (± SD) difference between the most likely contribution to diet calculated by conventional methods and the most likely contribution calculated by the stable isotope mixing model, for 10 glaucous gull colonies. The value for garbage does not include differences between methods for the two colonies at which gulls do not have access to garbage during the breeding season.

TABLES

Table 3.1. Sample sizes and stable isotope signatures of feathers at each colony. Stable isotope signatures are given as mean ± SD. Colonies with the same letter but different numbers were the same sites studied in two years (2008 and 2009).

Colony	**Conventional samples**	**Chicks sampled**		**Isotopic signatures**	
		#	**%**	**$\delta^{13}C$**	**$\delta^{15}N$**
A1	302	15	83	–20.6 ± 1.3	13.7 ± 2.1
A2	65	3	50	–21.1 ± 0.5	11.8 ± 1.9
B1	211	14	37	–23.0 ± 1.8	15.3 ± 1.2
B2	69	3	21	–19.9 ± 0.5	13.8 ± 0.6
C	59	5	83	–19.8 ± 0.3	17.4 ± 0.5
D	61	6	50	–20.1 ± 0.8	15.6 ± 0.7
E	126	7	54	–21.8 ± 0.9	12.0 ± 1.0
F	200	10	40	–25.4 ± 2.1	12.4 ± 1.6
G	97	5	21	–19.8 ± 1.0	9.3 ± 1.3
H	59	6	35	–20.4 ± 1.5	9.6 ± 1.5

Table 3.2. Diet estimates from two methods at each colony. Estimates given as range of possible percent contribution to diet of each food group, from a) conventional methods (analysis of pellets and food remains) and b) stable isotope mixing models, for each of 10 glaucous gull colonies in northern Alaska. Colonies with the same letter but different numbers were the same location studied in both years.

a) Conventional estimates

Colony	**Garbage**	**Birds**	**Small Mammals**	**Caribou**	**Fishes**	**Zoo–plankton**	**Other Marine**
A1	4–13	42–59	61–76	0–4	4–12	0–0	1–7
A2	2–25	74–97	0–0	0–9	0–7	0–9	0–9
B1	10–24	24–43	53–72	0–0	14–30	0–0	0–5
B2	9–35	30–63	15–46	0–7	2–22	0–13	0–0
C	0–0	25–61	38–74	0–10	10–41	0–0	0–8
D	0–0	22–59	0–20	0–0	22–59	0–17	0–15
E	13–35	65–87	8–26	0–0	2–15	0–0	0–6
F	2–12	53–73	29–48	0–0	11–26	0–0	0–2
G	69–97	0–20	3–31	0–0	0–13	0–0	0–0
H	32–60	8–29	28–56	0–8	0–8	0–0	0–6

b) Stable isotope estimates

Colony	**Garbage**	**Birds**	**Small Mammals**	**Caribou**	**Fishes**	**Zoo–plankton**	**Other Marine**
A1	0–17	0–7	25–39	0–8	0–67	0–8	0–60
A2	1–38	0–30	1–41	0–48	0–64	0–39	0–37
B1	0–3	0–7	0–6	0–5	38–100	0–13	0–46
B2	1–29	0–27	0–21	0–32	1–71	0–40	1–51
C	0–6	0–13	0–12	0–8	3–93	0–33	1–72
D	0–12	0–24	0–17	0–18	1–86	0–42	1–63
E	0–27	0–50	0–37	0–47	0–69	0–47	0–32
F	0–10	0–16	0–26	0–13	50–100	0–20	0–14
G	30–58	0–34	0–35	0–41	0–44	0–21	0–15
H	31–63	0–30	0–31	0–44	0–38	0–19	0–15

Table 3.3. Proportion of conventional subsamples that gave biased diet estimates. Proportions from each colony that gave overestimates (a) or underestimates (b) for the contribution of each food group to diets are in comparison to ranges of possible contributions estimated by the stable isotope mixing models.

a) Proportion of overestimates

Colony	**Garbage**	**Birds**	**Small Mammals**	**Caribou**	**Fishes**	**Zooplankton**	**Other Marine**
A1	0	1.00	1.00	0	0	0	0
A2	0	1.00	0	0	0	0	0
B1	1.00	1.00	1.00	0	0	0	0
B2	0.02	0.99	0.85	0	0	0	0
C	0	1.00	0.02	0	0	0	0
D	0	1.00	1.00	0	0	0	0
E	0	1.00	0	0	0	0	0
F	0	1.00	0.95	0	0	0	0
G	1.00	0	0	0	0	0	0
H	0	0	0.90	0	0	0	0

b) Proportion of underestimates

Colony	**Garbage**	**Bird**	**Small Mammals**	**Caribou**	**Fishes**	**Zooplankton**	**Other Marine**
A1	0	0	0	0.01	0	0	1.00
A2	0	0	1.00	0.25	0.52	0.26	0.26
B1	0	0	0	1.00	1.00	0.06	1.00
B2	0	0	0	0.51	0	1.00	0.12
C[1]	1.00	0	0.02	1.00	0	0.13	0.06
D[1]	1.00	0	0	0.25	0	0.51	1.00
E	0	0	0	1.00	0	0.26	1.00
F	0	0	0	1.00	1.00	0.51	1.00
G	0	0.02	0	1.00	0.26	1.00	1.00
H	0.02	0	0	0.26	0.26	0.26	1.00

[1] These colonies are outside typical daily foraging range of breeding adult glaucous gulls (~60 km; Declan Troy, Troy Ecological Research Associates, unpubl. data) from any source of garbage. Model estimates of garbage contributions to diet may reflect uncertainties in the models.

CONCLUSION

This study examined the relationship between Glaucous Gulls and human settlements in northern Alaska, specifically with regard to access to and use of garbage. The work presented here addressed the extent to which gulls in this area used garbage, the benefits they may have derived from this food source, and the effectiveness of one measure taken to limit these benefits.

Reproductive output was positively correlated with the amount of garbage in diet at several Glaucous Gull breeding colonies in 2008 and 2009. This suggests that an increase in garbage availability, e.g. with future development, could cause gull populations to increase. Some Glaucous Gulls return to their natal area to breed upon maturity (Gaston et al. 2009), but others disperse to other breeding colonies. In northern Alaska, this could cause artificial gull population growth even in undeveloped areas. These conclusions contrast with some previous studies that have found garbage may have a detrimental effect on gull reproductive output (Ward 1973, Pierotti and Annett 1991, Annett and Pierotti 1999).

Subadult (nonbreeding) gulls consumed much more garbage than adult (breeding) gulls at Barrow in summer 2007 and 2008. This may be because Barrow food waste is an easy, abundant food source for inexperienced young gulls to obtain, but is less convenient or nutritionally insufficient for breeding adults. If this artificial food source enhances subadult survival and if more garbage becomes available, gull populations may increase. Gulls around Barrow apparently switch to a mostly natural diet as breeding adults, so enhanced subadult survival would result in higher predation pressure from adults on prey species. This study provides some of the only evidence available that subadult gulls (of any species) may benefit disproportionately from garbage. Further research in additional areas would be necessary to determine whether this pattern is widespread across the North Slope.

The comparison of conventional and stable isotope diet assessment methods indicated that conventional analysis overestimates the importance of birds and underestimates the importance of fishes in gull diet. The amount of garbage was slightly overestimated at two out of 10 colonies, but in only one case was the difference from isotope estimates substantial; so my conclusions about the amount of garbage in gull diets and its potential effects on gull populations are not substantially biased by my method of diet analysis. The information presented here can therefore be successfully used by managers and developers in planning future development.

Garbage apparently has the potential to increase gull populations through both enhanced reproductive output and improved subadult survival. Given that gulls are feeding on bird species of conservation concern, managers may decide to limit gull access to garbage to avoid indirect negative impacts on wildlife. Incinerating garbage successfully reduced the amount of garbage in gull diet at Barrow and could be used as a strategy in future developed areas. If incinerating garbage presents an environmental concern, other strategies such as completely enclosing the landfill and garbage-processing areas could be considered (Gabrey 1997). Covering garbage with earth and hazing gulls with canons or other deterrents can also be effective (Spaans and Blokpoel 1991), but this has had apparently limited success at the Prudhoe Bay landfill; garbage makes up 50-63% of gull diet in that area. Future research on this subject could focus on assessing methods of garbage control. Given the unusual logistic and environmental constraints on development in northern Alaska, strategies that are effective in other areas may not be feasible there. Further research could determine the most environmentally friendly and cost-effect disposal method to limit scavenger access to garbage.

Additional research on gull survival at different life stages, as influenced by diet, and work to quantify gull impact on prey species of concern would be useful to justify costly methods of garbage control. For example, a study that incorporated bioenergetics, an accurate assessment of species-level prey use by gulls, and an accurate measure of regional gull and prey species populations could be used to determine the population-level impacts of Glaucous Gulls on specific prey species. An assessment of gull prey selection would also be useful in determining the potential impact of gulls on rare species. If gulls select prey in proportion to their availability rather than selecting certain species in preference to others, their impact on rare species may be negligible. If, on the other hand, gulls do hunt for specific species, including species of concern, an individual-level diet analysis could determine the extent of individual specialization. Managers could then assess the effectiveness of removing individual gulls to improve survival or reproductive output of the prey species of interest.

The work presented here adds several elements to existing knowledge about effects of development on human-subsidized predators. I found that Glaucous Gulls, like other scavengers, use garbage where it is available; but the extent to which they use it varies with location and apparent garbage availability. I determined that Glaucous Gulls may benefit from garbage through improved reproductive output and enhanced subadult survival. I identified prey species used by Glaucous Gulls to determine the potential conservation implications of potential future gull population growth, and identified one successful measure that could limit or prevent that growth. Finally, I assessed the biases inherent in conventional samples that are widely used in avian diet studies. This information will be useful to researchers studying a variety of species and systems, especially those examining the effects of development on wildlife.

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