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TECHNIQUE-DEPENDENT BIASES IN DETERMINATION OF DIET COMPOSITION: AN EXAMPLE WITH RING-BILLED GULLS[1]

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Abstract. We compared the diet of Ring-billed Gulls during the nestling period using two simultaneous sampling methods: pellets regurgitated by adults and direct observations of chick provisioning. We also compared the dietary composition of courtship feeds and adult spontaneous regurgitations to that of chick provisions and found no difference between the diets of adults and chicks. The two sampling methods suggested strikingly different diets at the same colony location. Pellets were predominantly composed of plant material, birds and scavenged human refuse (67% of individual items identified), while insects (19%) and fish (11%) made up the rest of the identifiable food remains. In contrast, most Ring-billed Gull chicks were fed either earthworms (50%) or whole fish (44%). Our observations of chick diet lacked insects possibly because we did not record feeding data during the evening (due to logistical limitations). Pellet contents were biased by the over-representation of indigestible hard parts of some food types (e.g., plant, human refuse) and lack of hard parts of others (e.g., earthworms). Such technique-dependent biases led to a non-random sample of food remains from gulls that fed on garbage and in farm fields, representing approximately seven percent of the population. Given the importance of diet studies, there is a need for more systematic, controlled studies to calibrate sampling techniques to actual animal diets.

Key words: Ring-billed Gulls; Larus delawarensis; *diet; pellets; chick provisioning; Lake Erie.*

INTRODUCTION

Dietary studies are an important contribution to the understanding of animal population dynamics, ecology and evolution. They also provide practical information that facilitates conservation and management, an assessment of the economic impact on humans, and indication of routes of contaminant uptake and environmental change (Furness and Nettleship 1991; Kushlan 1992, 1993; Furness and Greenwood 1994; Hoffman et al., in press). Numerous sampling techniques have been used to determine the diets of birds (reviews by Hartley 1948, Duffy and Jackson 1986) including analyses of: (1) feces and pellets (Vermeer 1970, Ainley et al. 1981, Pierotti and Annett 1987, Ewins et al. 1994), (2) stomach contents (Spaans 1971, Croxall and Prince 1980, Welham 1987), (3) spontaneous (Vermeer 1970, Smith and Carlile 1993) and forced (Haymes and Blokpoel 1978, Prince 1980) regurgitations by adults and young, and (4) observations of parental provisioning to young (Kirkham and Morris 1979, Burness et al. 1994, Chudzik et al. 1994).

Although each of these dietary parameters are produced at different stages of the digestive process and each represents only a subset of the total dietary inputs, relatively few studies have critically compared the data sets yielded by these different approaches even though major biases might result (see Swanson and Bartonek 1970, Duffy and Laurenson 1983, Jackson et al. 1987, Johnstone et al. 1990, Brugger 1993). For example, pellets represent a processed output of undigested material that may sample several days of feeding. Observations of chick provisioning sample only the instantaneous inputs that are delivered to the young. Therefore, pellets may be biased by the over-representation of indigestible hard parts of some food types while chick provisions may be biased towards highly nutritional foods and temporally abundant foods.

Since 1920, Ring-billed Gull (*Larus delawar-*

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ensis) populations have increased dramatically throughout North America (Ryder 1993). Ring-billed Gulls are opportunists that consume a variety of foods including fish, small mammals and birds, eggs, human refuse and plants (Vermeer 1970, Jarvis and Southern 1976, Blokpoel and Haymes 1979, Welham 1987, Ryder 1993) and often take advantage of locally (e.g., earthworms, Kirkham and Morris 1979; cherries, Blokpoel and Struger 1988) or diurnally abundant foods (e.g., insects; Meuller and Berger 1965, Chudzik et al. 1994).

Studies of Ring-billed Gull diets have shown apparently large regional differences in the types and frequencies of food consumed (Ryder 1993). In Ontario, chicks were fed predominantly fish, insects, and earthworms (Haymes and Blokpoel 1978, Kirkham and Morris 1979), whereas in Alberta, adult pellets (and a few spontaneous regurgitations) comprised mostly insects, birds, rodents, plants, and human refuse (Vermeer 1970). While these differences were suggested to reflect food availability to gulls in various habitats (Haymes and Blokpoel 1978), they could also have been an artifact of the different dietary sampling techniques or reflected dietary differences between the two age groups under study.

In 1994, we compared the diet of Ring-billed Gulls during the nestling period using two simultaneous sampling methods: pellets regurgitated by adults, and direct observations of chick provisioning. We asked the following question: Was there a difference between the inferred diets determined by the two sampling methods? We also compared the dietary composition of courtship feeds and adult spontaneous regurgitations to that of chick provisions in order to determine whether or not adult and chick diets differed during our study. Jehl and Mahoney (1983) and Welham (1987) compared the stomach contents of adult California (*L. californicus*) and Ring-billed Gulls, respectively, to spontaneous regurgitations by chicks and found no major differences between the diets of adults and chicks. Vermeer (1970) also found that regurgitants from Ring-billed Gull adults and young contained the same types, and similar frequencies, of foods.

STUDY AREA AND METHODS

The study site was an artificial breakwall located 0.5 km off the north shore of Lake Erie and 1 km west of the Welland Ship Canal near Port Colborne, Ontario (42°53′ N, 79°16′ W). Approximately 2,500 pairs of Ring-billed Gulls nest on a limestone rockpile adjacent to the west arm of the breakwall (Blokpoel and Tessier 1991), locally known as the Port Colborne lighthouse colony.

On 17 April 1994, prior to egg-laying, a 10 × 10 m study plot was marked and an observation blind was erected 2 m from one edge of the plot that allowed maximum visibility of nests. From egg-laying through hatching, the study plot was entered daily to mark new nests, number eggs, record egg laying and hatching dates, and color band each chick. The colony was not entered during periods of rain. The survival of chicks from study broods was recorded from the blind.

PELLET COLLECTION AND ANALYSIS

On 10 June 1994, coinciding with the chick rearing period, 35 fresh pellets (moist and intact) were collected from the immediate vicinity of active Ring-billed Gull nests (one per nest). Each pellet was individually wrapped in aluminum foil, labelled and then frozen at −20°C, and analyzed three months later.

Once thawed, the pellet contents were teased apart under a zoom binocular microscope (5–100× magnification). Food remains were identified to the lowest taxonomic level possible, using a reference collection of fish parts, assorted invertebrates, birds and mammals. Individual food items were grouped into seven categories: (1) vegetation (plant stems, leaves, small seeds, cereals, sweetcorn), (2) insects (mainly beetle and dipteran exoskeletons), (3) birds (white and brown feathers, intact bones), (4) fish (smelt otoliths, Centrarchid scales and vertebrae; freshwater drum *Aplodinotus grunniens* and perch *Perca* spp.), (5) mammals (mainly rodent bones, teeth, skull, hairs), (6) garbage (human refuse, including cut bones of birds and mammals and a wide range of anthropogenic items), and (7) earthworms (*Lumbricus* spp.). Fish remains were identified to species or genera mainly by scales or otoliths, with the aid of published guides (Lagler 1947, Scott and Crossman 1973), and unpublished material provided by Dr. J. Casselman (Ontario Ministry of Natural Resources). We did not attempt to identify insect species. Plant material and garbage items were identified by our familiarity with the types of items available in the area.

Wherever possible, we also scored the minimum number of individual food items in each pellet. For fish, this was done by pairing otoliths or matching scales of greatly differing sizes. The minimum numbers of individual mammals and birds were estimated by segregating hair/feather and bone types. The minimum number of individual insects was scored by pairing elytra, wings, or heads. Plant remains were scored as a single item per pellet unless more than one type of seed, stem or leaf could be distinguished. The occurrence of garbage in a pellet was scored as only one item. The percentage frequency of occurrence of a food type was the proportion of pellets in the sample that contained a given type of item. Both methods of expressing pellet composition were subject to biases, but percent occurrence has been regarded to be the least biased method for estimating diet (Annett and Pierotti 1989, Ewins et al. 1994).

CHICK PROVISIONING

From 1 to 7 June, we recorded (from the blind) chick provisioning by each partner of 26 Ring-billed Gull pairs. The criteria for choosing study pairs for detailed observations were: (1) close proximity to the blind (each pair nested within a 5 × 5 m area located at the front of the larger study plot), and (2) partners of each pair were uniquely color banded and of known sex. The number of 'gull-days' of observation was calculated as the number of adults multiplied by the number of days (52 × 7 = 364). Daily observation periods were 3 hr in duration and began between 06:00 and 06:15 EST. For each observed feeding, we recorded the time, the food type, the number of regurgitations, and the band combinations of the feeding parent and all individuals (e.g., chicks, mate, kleptoparasites) that consumed some of the food.

Food items in chick provisions were divided into seven categories (as described above). Note that vegetation was rarely fed to chicks unless it was part of a 'brown liquidy' bolus that contained whole kernels of corn, dirt, small worms and other unidentified invertebrates. However, we grouped parents that fed 'brown liquid' into the vegetation category in order to facilitate a comparison of diet composition between adult pellets and chick provisioning.

ADULT VERSUS CHICK DIETS

Nestling Herring Gulls (*Larus argentatus*) completely digest fish bones, but not bird or mammal bones, whereas adults regurgitate pellets containing indigestible parts of all types of animal foods (Spaans 1971; Annett and Pierotti 1989; PJE, pers. obs.). Since our collections of fresh pellets probably represented regurgitations of indigestible material by adult Ring-billed Gulls (we have not observed chicks regurgitating well-formed pellets), it was possible that any dietary differences that we recorded were a result of comparing the diet of adults to that of chicks.

From 19 April and 5 May 1994 (AM only), we recorded courtship feeding by male Ring-billed Gulls (n = 17) and collected 20 spontaneous regurgitations from adults that were trapped on their clutches between 5–18 May (10:00–13:00 hr). These data were used to determine whether or not adult and chick diets differed during our study.

The contents of each pellet were identified by PJE. Adult spontaneous reguririgtations, courtship feeding and chick provisioning data were collected by KMB. Non-parametric statistics (r × k contingency table, Spearman rank correlation) were used to analyze categorical data. The alpha level of significance was 0.05.

RESULTS

NESTING CHRONOLOGIES

In 1994, the mean (±SD) clutch initiation date in our study plot (10 × 10 m) was 30 April ± 8 days (n = 98, range = 16 April–23 May). The mean clutch initiation date of study pairs (n = 26) was 26 April ± 4 days (range = 16 April–2 May). First chicks hatched in study nests between 16–31 May (mean 24 May ± 3 days, n = 26). On 1 June, the mean age of first hatched chicks in study broods was 9 ± 3 days (n = 26, range = 2–27 days).

DIET BASED ON PELLET ANALYSES

Six different food types (fish, mammal, bird, insect, plant and garbage) were identified in the 35 freshly-produced Ring-billed Gull pellets collected on 10 June (Table 1). Plant material occurred most frequently (80%) in pellets, followed by bird remains, insect exoskeletons, garbage, fish scales and otoliths, and mammal bones. Of the 91 individual food items identified in the 35 pellets (Table 1), plants, birds and garbage accounted for 61 (67%), insects of fish accounted for 17 (19%) and 10 (11%) of the items, respectively. Therefore, the contents of pellets indicated that the diet of adult Ring-billed Gulls during

TABLE 1. The number of Ring-billed Gull pellets that contained each of the seven food types, and the percent frequency of occurrence in the pellet sample ($n = 35$ pellets), at the Port Colborne lighthouse colony, in early June 1994. The minimum number of individual items of each food type, and the percent of the total number ($n = 91$) of individual items, are also shown.

Food type	Frequency of occurrence of food type		Minimum number of individual items	
	n	Percent	*n*	Percent
Fish[1]	8	23	10[7]	11
Mammal[2]	3	9	3	3
Bird[3]	18	51	18	20
Insects[4]	16	46	17	19
Vegetation[5]	28	80	28	31
Garbage[6]	15	43	15	16
Earthworms	0	0	0	0

[1] Rainbow smelt otoliths, Centrarchid scales and vertebrae; freshwater drum and yellow perch.
[2] Mainly rodent bones, teeth, skull, hairs.
[3] Feathers, intact bones.
[4] Mainly beetle and dipteran exoskeletons.
[5] Plant stems, leaves, small seeds, cereals, sweetcorn.
[6] Human refuse, including cut bones of birds and mammals and a wide range of anthrophogenic items (plastic, paper, aluminium foil etc.)
[7] Remains of 10 fish found.

the mid-nestling period was predominantly plants and scavenged refuse (human and bird).

DIET BASED ON OBSERVATIONS OF CHICK PROVISIONING

During the 364 gull-days of observation, chick provisioning was observed on 250 (69%). We restricted the analyses to the 217 chick provisioning days during which each adult fed one food type to its chicks during an observation period (3 hr). On the other chick provisioning days, two food types were fed by one parent ($n = 17$) or the food item could not be identified ($n = 16$) because either visibility was obstructed or the item was consumed too quickly. Gulls that fed two food types to their offspring, during a single observation period, were occasionally seen stealing food from conspecifics or swallowing food that was regurgitated by their partner.

Four different food types (fish, earthworms, vegetation, garbage) were regurgitated to chicks during the mid-nestling period (Table 2). Adults fed earthworms (range 37 to 69%, average 50%) and fish (25 to 57%, average 44%) most frequently to their chicks. Gulls were observed foraging for earthworms on football fields, park and church lawns shortly after dawn while the ground was wet with dew, and following periods of rain (also see Kirkham and Morris 1979). Whole fish (shiners *Notropis* spp. and rainbow smelt *Osmerus mordax*), that appeared to have been freshly caught, were regurgitated to chicks in boli that were estimated to contain up to 12 fish. The remaining gulls (7%) fed garbage or vegetation (i.e., 'brown liquid') to their chicks. Gulls foraged for invertebrates behind ploughs in farm fields (Conover 1983, pers. obs.) which explains the presence of dirt and corn in the 'brown liquid' bolus. These data suggest that the diet of Ring-billed Gull chicks during the mid-nestling period was primarily earthworms and fish.

There was little daily variation in the frequencies of food types fed to chicks (Table 2). On all sampling days, garbage and vegetation were fed infrequently to chicks. To reduce the limitations of minimum expected values (≥ 5 in 80% of cells, Daniel 1984) in each cell of $r \times k$ contingency tables, we restricted statistical analyses of daily variations in food type to worms and fish. From 1 to 7 June, there was no statistical difference among the frequencies that fish and worms were fed to chicks ($r \times k$ contingency table; $\chi^2 = 8.0$, $df = 6$, $P > 0.05$).

There were also no significant differences between the numbers of males and females that fed earthworms and fish to their chicks (Brown, unpubl. data). However, more males ($n = 8$) than

TABLE 2. The number of adult Ring-billed Gulls per day (and percent) that regurgitated each food type to their chicks from 1 to 7 June 1994 at the Port Colborne lighthouse colony. The number of adults (n) sampled per day is also shown. Note that adults were not observed regurgitating insects, mammal or bird remains to their chicks.

Sampling date	*n*[1]	Frequencies of each food type regurgitated to chicks (%)			
		Fish[2]	Earthworms	Vegetation[3]	Garbage
1 June	32	8 (25)	22 (69)	0 (0)	2 (6)
2 June	30	17 (57)	13 (43)	0 (0)	0 (0)
3 June	27	15 (56)	10 (37)	1 (4)	1 (4)
4 June	32	12 (38)	16 (50)	2 (6)	2 (6)
5 June	35	16 (46)	17 (48)	1 (3)	1 (3)
6 June	31	14 (45)	16 (52)	1 (3)	0 (0)
7 June	30	13 (43)	14 (47)	3 (10)	0 (0)
Total	217	95 (44)	108 (50)	8 (4)	6 (3)
Mean (± SD)	31 ±2.3	13.6 ±2.8	15.4 ±3.4	1.1 ±1.0	0.8 ±0.8

[1] The number of adults that were observed feeding their chicks at least once on each day. Feeding events during which the food type was not identified ($n = 16$) were excluded.
[2] Primarily rainbow smelt *Osmerus mordax* and shiners *Notropis* spp.
[3] Vegetation was only fed to chicks as part of a 'brown liquidy' bolus that contained dirt, corn, small worms and other unidentified invertebrates.

TABLE 3. A summary of the relative ranks of food types from the four sampling techniques used to estimate the diet of Ring-billed Gulls at the Port Colborne lighthouse colony in 1994. Relative ranks are given in descending order of percent frequency of occurrence.

	Dietary sampling technique (relative ranks)			
Food type	Adult pellets[1]	Chick provi-sioning[1]	Courtship feeding[2]	Spontaneous regurgi-tations[3]
Vegetation	1	3	3	3.5
Birds	2	6	5.5	6
Insects	3	6	5.5	6
Garbage	4	4	5.5	2
Fish	5	2	2	3.5
Mammals	6	6	5.5	6
Earthworms	7	1	1	1

Spearman rank correlations:
Adult pellets *vs* chick provisioning: $r_s = -0.4$, $Z = -0.9$, $n = 7$, $P > 0.1$.
Courtship feeding *vs* chick provisioning: $r_s = 0.9$, $Z = 2.3$, $n = 7$, $P < 0.025$.
Spontaneous regurgitations *vs* chick provisioning: $r_s = 0.9$, $Z = 2.1$, $n = 7$, $P < 0.05$.
Spontaneous regurgitations *vs* courtship feeding: $r_s = 0.7$, $Z = 1.7$, $n = 7$, $0.1 > P > 0.05$.
Other pairwise correlations were not significant: Ps > 0.1.

[1] Collected/recorded during the chick period.
[2] Courtship feeding was recorded during the egg-laying period.
[3] Spontaneous regurgitations were collected from adults during the incubation period.

females ($n = 1$) fed garbage to their chicks ($\chi^2 = 5.4$, df $= 1$, $P < 0.05$). Four of these males also fed another food type during that observation period.

COURTSHIP FEEDING AND SPONTANEOUS REGURGITATIONS

During the egg-laying period, a total of 53 courtship feeds were recorded from 17 male Ring-billed Gulls. Seven males fed fish (11 of 53 feeds, 21%), 13 fed earthworms (35 feeds, 66%) and 3 fed vegetation ("brown liquid"; 7 feeds, 13%) to their mates.

During the incubation period, 20 spontaneous regurgitations were collected from adult gulls. Each spontaneous regurgitation was composed to a single food type; 13 (65%) contained earthworms, five (25%) were composed of human garbage (e.g., pork, chicken, vegetables), one (5%) contained 6 rainbow smelt, and one (5%) contained corn.

COMPARISON OF DIETS

A summary of the relative ranks of food types for each of the four sampling techniques is shown in Table 3. The relative ranks of food types in chick provisions were positively and significantly correlated to those of both courtship feeds and adult spontaneous regurgitations (Spearman rank correlations: $r_s = 0.9$, $Z = 2.3$, $n = 7$, $P < 0.025$; $r_s = 0.9$, $Z = 2.1$, $n = 7$, $P < 0.05$, respectively). A similar correlation between courtship feeds and spontaneous regurgitations approached significance ($r_s = 0.7$, $Z = 1.7$, $n = 7$, $P < 0.1$). Garbage was more common, and fish less common, in spontaneous regurgitations compared to courtship feeds. These results suggest that adult and chick diets did not differ greatly during the course of our study.

The two different dietary sampling methods (adult pellets and observations of chick provisioning) used in early June suggested strikingly different diets at the same time and colony location (Tables 1, 2). Analyses of fresh pellets indicated that adult Ring-billed Gulls fed themselves predominantly plant material, birds and scavenged human refuse (67% of individual items identified), while insects and fish (19% and 11%, respectively) made up the rest of their diet. In contrast, most Ring-billed Gull chicks were fed either earthworms (50%) or whole fish (44%). The correlation between the relative ranks of food types between pellets and chick provisions was not significant ($r_s = -0.4$, $Z = -0.9$, $n = 7$, $P > 0.1$; Table 3). Adult diets, estimated from courtship feeds and spontaneous regurgitations, were also not significantly correlated to the adult diet estimated from pellets ($P > 0.1$).

DISCUSSION

While the regional differences in the diets of Ring-billed Gulls may reflect variation in food availability in different habitats (Vermeer 1970, Haymes and Blokpoel 1978, Ryder 1993), our results suggest that apparent dietary differences (adult pellets vs. chick provisioning) can also reflect biases associated with the various sampling methods used to infer diet. Similar differences likely exist for species across a broad range of taxonomic groups (e.g., Duffy and Jackson 1986, Johnstone et al. 1990, Robinson and Stebbings 1993).

TECHNIQUE-DEPENDENT BIASES

There were four important differences between the two diets that were estimated from adult pellets and chick provisioning: (1) worms were not detected in pellets, (2) fish were under represented in pellets, (3) vegetation was rarely fed to chicks unless it was part of a bolus (brown liquid often contained kernels of corn), and (4) we did not observe insects, mammals or birds being fed to chicks.

The absence of worms and the under representation of fish in pellets was likely the consequence of differential digestion of stomach contents. Ryder (1993) points this out as a possible explanation for the absence of earthworms in Vermeer's (1970) study. Soft-bodied prey items leave no hard parts to be regurgitated while otoliths from smaller fish may be dissolved completely or pass through the digestive tract (Duffy and Laurenson 1983, Furness et al. 1984, Johnstone et al. 1990, Brugger 1992). This explanation was consistent with our observations that Ring-billed Gulls fed predominantly rainbow smelt and shiners to their chicks (except one male that consistently fed larger fish; possibly 5″ bass), while the composition of fish species in pellets included only freshwater drum and perch. In controlled feeding studies, Duffy and Laurenson (1983) and Johnstone et al. (1990) found that bones of smaller fish were often greatly under represented in pellets regurgitated by adult cormorants (*Phalacrocorax* spp.). Similarly, Double-crested Cormorants (*P. auritus*) egested bony pellets when they ate channel catfish (*Ictalurus punctatus*) and bluegill (*Lepomis macrochirus*), but not when they ate thread herring (*Opisthonema oglinum*) and gizzard shad (*Dorosoma cepedianum*, Brugger 1993). The inability of gulls to digest vegetation would explain the frequent occurrence and over representation of vegetation in pellets. In Blue-winged Teal (*Anas discors*), soft-bodied amphipods were digested completely within 20 minutes after ingestion while some hard seeds were retained in the gizzard for more than three days (Swanson and Bartonek 1970). In vitro studies have also revealed that some invertebrates (e.g., Cnidaria) digest in less than 20 minutes and so, could disappear from diet samples (Jackson et al. 1987). Similarly, 38 squid (*Loligo reynaudi*) beaks were retained for seven weeks in the stomach and gizzard of a captive Shy Albatross (*Diomedea cauta*) while none were found in pellets or feces (Furness et al. 1984).

Other potential biases of pellet analyses include the presence of otoliths that result from secondary consumption (i.e., the consumption of a prey fish with otoliths in its stomach; Blackwell and Sinclair, unpubl. data) and that the hard remains of one prey item may be present in several pellets (Brugger 1993; also see Robinson and Stebbings 1993). In our study, 217 (93%) of the chick feedings and all courtship feeds and spontaneous regurgitations consisted of one food type, but pellets consisted of several food types suggesting that they were not produced daily.

While pellets represent a subset of the foods ingested over several days, observations of chick provisioning include food items consumed during a relatively shorter period of time (06:00–09:00 EST in our study) and so may fail to detect any temporal differences in diet. Our observations of chick diet lacked insects possibly because we did not record feeding data during the evening (due to logistical limitations). At two other Ring-billed Gull colonies in southern Ontario, insects were usually fed to chicks during the evening (Kirkham and Morris 1979, Chudzik et al. 1994). We also did not record mammal or bird remains being regurgitated to chicks, or to partners or spontaneously. At the Port Colborne colony, intra- and interspecific predation of eggs and chicks occurs infrequently, perpetrated by a few individual gulls ('specialists'), usually males (Brown, unpubl. data).

In our study, fish occurred less frequently in spontaneous regurgitations (collected during the incubation period) than in other dietary samples. While this result may reflect nutritional or seasonal differences in diet, we observed that parents had more difficulty regurgitating fish (i.e., more side to side neck movements, head shakes and failed regurgitation attempts) to their chicks than other food types (e.g., worms).

PRACTICAL IMPLICATIONS

The diet inferred from pellet analyses was biased by the over-representation of indigestible hard parts of some food types (Duffy and Jackson 1986), and lack of hard parts in others (e.g., earthworms). Such technique-dependent biases led to a non-random sample of prey remains (i.e., diet) from gulls that fed on garbage and in farm fields (i.e., seven percent of the population). This result was consistent with the observation that few pellets ($n = 7$) were collected from the large study plot that contained 98 active nests. Therefore, we suggest that future studies that use pellets to assess avian diets also count the number of active nests where no pellets are found. This would yield some information regarding the relative proportion of the population sampled.

Pellets are, however, useful for identifying some of the individual food items consumed (Duffy and Laurenson 1983) and for indicating the diet of seabirds away from colony sites during the non-breeding season (Ewins et al. 1994). The calibration of pellet production to diet would increase the reliability and usefulness of these data (Duffy and Jackson 1986). We echo the caution expressed by Johnstone et al. (1990) that "fundamental questions need to be answered before pellets can be used in general dietary studies of seabirds"; how do egested materials, that represent only a subset of the inputs, relate to diet?

While observations of parental provisioning to offspring are an ideal approach to identify and quantify the composition of diet of some species (e.g., Common Terns *Sterna hirundo* carry a single whole fish cross-wise in the bill to their young), this approach is labor intensive and also has its own inherent biases (see Duffy and Jackson 1986). Fish size delivered to offspring by male Common Terns is known to increase with chick age (Wiggins and Morris 1987, Burness et al. 1994) and so, fish fed to chicks may not be representative of those captured by parents. Regurgitating species may not completely empty their crop, and it is often difficult to identify and quantify the prey items.

The lack of daily variation, within our short sampling period, of food types regurgitated to chicks has useful practical implications because it suggests that an assessment of Ring-billed Gull diet could be obtained by recording chick provisioning data during infrequent visits into colonies—a visitation schedule similar to that used for pellet collection. However, several confounding variables should be considered when sampling including time of day, chick age, rain fall, humidity and season (Haymes and Blokpoel 1978, Kirkham and Morris 1979, Chudzik et al. 1994).

In conclusion, we suggest that: (1) researchers use caution when comparing the diets of birds from studies that used different sampling techniques, and (2) future diet studies should incorporate a variety of approaches to collect data such that the inherent biases may be identified, and possibly corrected. Given the importance of diet studies, there is a need for more systematic, controlled studies to calibrate sampling techniques to actual animal diets (e.g., Swanson and Bartonek 1970; Duffy and Laurenson 1983; Jackson et al. 1987; Johnstone et al. 1990; Brugger 1992, 1993).

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