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BIAS ASSOCIATED WITH DIET SAMPLES IN AUDOUIN'S GULLS[1]

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Abstract. We analyzed five different types of food samples from Audouin's Gull (*Larus audouinii*), collected during the breeding seasons of 1994 and 1995 at its two main breeding colonies, the Ebro Delta and the Chafarinas Islands. These food samples included spontaneous regurgitates, dry boli containing partially digested food, food remains, pellets, and prey identified during direct observations of chick provisioning. We compared estimates of biomass, levels of taxonomic determination allowed by each kind of food sample, and the associated potential biases to assess which sampling method provides the best estimate of diet in gulls. Regurgitates allowed identification of most prey to species level and reliable biomass estimates, but their collection was time-consuming and invasive. Dry boli provided almost the same information as regurgitates at order level and were easy to collect. However, both underestimated soft-bodied prey and prey with large, hard parts. Food remains provided an estimate of diet composition that was highly biased towards prey with large distinctive hard parts. However, food remains were a good complement to dry boli, enhancing biomass estimates for food items that had a good relationship of weight and linear measurements of prey hard parts. Direct observation allowed identification of prey only to upper taxonomic categories, and is useful when only a broad categorization of prey types is required. Pellets showed important biases towards fish with robust otoliths, and inaccurate conversion to biomass, but they can be useful for monitoring variations in the consumption of certain prey items. Several factors such as time spent collecting, sample availability, disturbance to animals, and the status of the species studied need to be considered when deciding on a method of diet assessment sampling.

Key words: Audouin's Gull, Larus audouinii, *diet assessment, food samples comparison, pellets, regurgitates, direct observation, food remains, otoliths.*

INTRODUCTION

The assessment of feeding habits in birds usually involves the collection of food samples either before, during, or after ingestion. Data collected before ingestion can be obtained only through observation at the feeding area (Pierce and Boyle 1991), but this is usually not possible for gulls. Species such as gulls can regurgitate partly digested or undigested food to either females (courtship feedings) or nestlings, and this provides a potentially important source of information. Additionally, different kinds of remains containing undigested materials are commonly found on the ground of breeding colonies.

Whether digested or undigested, none of these food samples is unbiased (Hartley 1948, Hyslop 1980, Duffy and Jackson 1986). Sources of bias depend on the date of collection (Oro et al. 1995), digestibility of prey (Jackson and Ryan 1986, Jackson et al. 1987, Brugger 1992), the selective retention of harder prey parts (Jackson and Ryan 1986, Jobling and Breiby 1986), or the presence of different parts of the same prey in more than one food sample (Spaans 1971, Brugger 1993).

Additional sources of bias also may come from methods employed by researchers during analysis of the samples, including skills in identifying prey items (Gaston and Noble 1985), bias towards items showing conspicuous characters (Spaans 1971), grouping procedures (Cooper et al. 1990), and the quantitative analyses undertaken (Sherry 1990).

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Because actual diet usually remains unknown, an assessment of the absolute biases linked to each type of food sample usually is impossible. However, the comparative evaluation of biases associated with different diet samples can allow a more accurate assessment of the actual diet. We analyzed five different types of food sample in Audouin's Gull (*Larus audouinii*) in order to determine which factors improved the assessment of diet. We compared potential biases, estimates of biomass, and levels of taxonomic determination among the five dietary sampling methods.

METHODS

This study was performed during the 1993 and 1994 breeding seasons at the two main breeding sites for the Audouin's Gull: the Ebro Delta (NE Spain: 40°37′N, 0°21′E), and the Chafarinas Islands (Melilla, Spain: 35°11′N, 2°26′W), representing about 60% and 24% of the world's breeding pairs, respectively.

FOOD SAMPLES

Five different kinds of sample were collected to assess diet at the colonies: (1) spontaneous regurgitates, (2) dry boli containing partially digested food, (3) food remains, (4) pellets, and (5) prey identified during direct observations of chick provisioning. Spontaneous regurgitates were disgorged discrete food items that showed a variable degree of digestion, and which were produced by gulls disturbed by the researcher (Mudge and Ferns 1982, Furness and Todd 1984, Noordhuis and Spaans 1992). Dry boli contained compacted partially digested food. Food remains were pieces of prey discarded before ingestion by adults or nestlings, or individually ejected, and found scattered all over the nesting areas. Pellets were small boli that contained only indigestible food remains including otoliths, scales, fish back-bones, and feathers, loosely cemented by gastric mucus.

SAMPLING

Since time of the day might affect the types of food eaten (Derby and Lovvorn 1997), regurgitates, boli, food remains, and pellets always were collected in the morning (09:00–12:00), every two or three days during the breeding season (May and June). Direct observations of chick feedings at nest were made from a blind at distances ranging from 3–10 m (n = 30), with the aid of 8x30 binoculars. Observations were restricted to the last 15 days of the nestling stage (late June), encompassing all of the diurnal hours during five days (60 hr of observation). All samples analyzed here belonged to adult or fledgling birds (> 20 days old); diet of fledglings does not differ significantly from that of adult Audouin's Gulls (Pedrocchi et al. 1996). Once collected, regurgitates were immediately frozen, and boli, pellets, and food remains were preserved in 70% ethyl alcohol until analyzed.

DIET ANALYSIS

Prey were identified using taxonomic keys and our own reference collections. Each prey item was identified to the lowest taxonomic level possible for each type of diet sample. Quantification always followed the minimum numbers rule (i.e., by pairing bilateral elements such as otoliths or elytra, matching for different sizes, and scoring a single item per food sample when remains of fur, feathers, garbage or plants are found, unless different types can be distinguished, see Brown and Ewins 1996). Dry weight biomass of prey was assessed using three different methods: (1) obtaining dry weight directly from undigested items, (2) estimating dry weight biomass through linear relationships with lengths of well-preserved pieces of the prey item, or (3) assigning average values for each taxonomic category with regard to the biomass values obtained through methods (1) and (2). We used method (1) when undigested prey items were available; method (2) when, despite digestion, the lengths of prey or suitable pieces were measurable; and method (3) when neither of the previous methods was applicable. Lengths (± 0.1 mm) of small pieces were measured using ocular micrometers, and lengths (± 1.0 mm) of large pieces were measured with calipers. In the field (direct observations), lengths were estimated to the nearest cm relative to bill length.

DATA ANALYSIS

Statistical comparisons among diet composition (counts of the different prey items) obtained for each kind of food sample were performed using G-tests on contingency tables of prey taxonomic categories. Infrequent categories were pooled (Table 1) in order to avoid cells with too low expected frequencies. Thus, we obtained four categories at each locality: clupeiforms, perciforms, unidentified fish, and other prey. When

the G-test resulted in significant differences, the Studentized residuals were examined to assess the influence of each cell in the differences observed (Haberman 1973). To avoid interaction with dietary differences between areas, comparisons among food samples were performed separately for each locality. Independence among observations is a basic assumption for the statistical tests, and this condition is not guaranteed for prey items in a food sample. However, because in macrophagous animals, the prey catching process is essentially item by item (Feisinger et al. 1981) and many factors are involved in each of the several steps of the process (Sih 1993), we assumed that each consumed item can be regarded as independent.

Statistical comparisons between levels of identification for each kind of food sample also were performed using G-test on contingency tables at the taxonomic level. Because in this case several expected frequencies were lower than 1, significances for the G-test were calculated using the exact Monte Carlo inference based on 6,000 random tables (G_{MO}) (Noreen 1989, Manly 1991)

RESULTS

We analyzed 40 regurgitates (21 at Chafarinas and 19 at the Ebro Delta), 96 dry boli (33 and 63, respectively), 114 food remains (35 and 79, respectively), 36 pellets (15 and 21, respectively), and 70 direct observations (45 and 25, respectively). Fish were the main prey of Audouin's Gull (Table 1), but there were significant differences within each locality between diet compositions inferred from the different diet sampling methods ($G_{12} = 298.2$, $P < 0.001$ in the Ebro Delta; $G_{12} = 139.7$, $P < 0.001$, in the Chafarinas Is.). In both localities we found that regurgitates had significantly lower proportions of unidentified fish, dry boli had significantly higher clupeiforms and lower unidentified fish, food remains had significantly lower clupeiforms and higher other prey, pellets had significantly lower clupeiforms and higher unidentified fish, and direct observation had significantly higher unidentified fish and lower other prey.

There were overall significant differences within each locality between the taxonomic levels of identification allowed by each type of diet sample (Table 1, $G_{MO} = 252.5$, $P < 0.008$, Ebro Delta; $G_{MO} = 114.9$, $P < 0.008$, Chafarinas Is.). However, because these differences may have been due to taxonomic levels below order, and the critical level of identification used was order, data were reanalyzed with only two groups: prey identified to order level vs. prey identified to class level, giving similar results for both areas ($G_4 = 77.8$, $P < 0.001$, Ebro Delta; $G_4 = 60.6$, $P < 0.001$, Chafarinas Is.). Most regurgitates allowed identification to genus or species level, so they also showed the highest percent identification of prey items to order level. Dry boli and food remains were intermediate, whereas pellets and direct observations gave the lowest percent identification as can be noted through the increased proportion of higher taxonomic categories in these two dietary samples (Table 2).

Most prey items (62.8%) from regurgitates allowed direct measurement of prey biomass (method 1) because they were undigested, 11.6% allowed assessment using linear relationships (method 2), and 25.6% allowed only the assignment of average values (method 3). For

TABLE 1. Percent diet composition standardized to taxonomic order level for all types of food samples collected at two Audouin's Gull colonies.

	Regurgitates	Dry boli	Food remains	Pellets	Direct observation
Ebro Delta					
Clupeiformes	34.0	65.3	—	6.5	3.2
Perciformes	19.1	19.4	—	6.5	45.2
Anguilliformes	—	1.0	—	—	—
Gadiformes	—	4.1	—	35.5	—
Passeriformes	—	3.1	1.3	—	—
Other birds	2.1	—	—	—	—
Gnathobdellida	25.5	—	—	—	—
Sepioida	—	2.0	15.2	—	—
Decapoda	12.8	2.0	50.6	9.7	—
Coleoptera	—	—	30.4	3.2	—
Orthoptera	6.4	—	—	—	—
Waste meat	—	—	1.3	—	—
Unidentified fish	—	3.1	1.3	38.7	51.6
Chafarinas Is.					
Clupeiformes	41.9	54.2	2.9	—	17.0
Perciformes	32.6	3.4	—	14.3	15.1
Anguilliformes	2.3	—	—	—	1.9
Atheriniformes	2.3	1.7	—	—	—
Zeiformes	—	1.7	—	3.6	—
Gadiformes	—	1.7	—	17.9	1.9
Passeriformes	—	—	5.7	—	—
Sepioida	2.3	16.9	14.3	3.6	—
Decapoda	—	—	2.9	—	—
Orthoptera	11.6	5.1	—	—	—
Fruits and seeds	—	—	28.6	—	—
Waste meat	2.3	—	11.4	—	—
Unidentified fish	4.7	15.3	34.3	60.7	64.2

TABLE 2. Levels of taxonomic determination (percent of prey items) achieved for every food sample at two Audouin's Gull colonies.

	Regurgitates	Dry boli	Food remains	Pellets	Direct observation
Ebro Delta					
Species	87.2	16.3	94.9	12.9	45.2
Genus	10.6	55.1	2.6	32.3	—
Family	2.1	19.4	1.3	3.2	3.2
Order	—	6.1	—	12.9	—
Class	—	3.1	1.3	38.7	51.6
Chafarinas Is.					
Species	71.4	30.5	38.7	17.9	17.0
Genus	19.0	33.9	6.5	3.6	17.0
Family	2.4	18.6	—	—	—
Order	2.4	1.7	16.1	17.9	1.9
Class	4.8	15.3	38.7	60.7	64.2

dry boli, these percentages were 18.6 and 81.4 for methods 2 and 3, respectively, and were very similar in the case of food remains (11.8%, method 2; 88.2% method 3). In pellets, biomass was assessed using method 3 in all cases. In direct observations, 41.4% was assessed using method 2, and 58.4% using method 3.

DISCUSSION

DIET COMPOSITION

Some soft-bodied animals only were recorded in regurgitates and direct observation (e.g., invertebrates such as leeches, Gnathobdellida). This has been observed previously in other gull diet studies (Fox et al. 1990, Hario 1990, Nogales et al. 1995), and is due to differential digestibilities as shown by *in vitro* studies (Jackson et al. 1987). Moreover, the differential ability to disgorge different prey types may be an important source of bias (Spaans 1971). Dry boli showed greater prey degradation than did regurgitates. However, they allowed good identification to family or genus level. In dry boli, soft-bodied prey were under-represented, but at the order level they provided similar information to that of regurgitates.

Food remains were formed almost exclusively from prey having large hard parts (over 3 cm in length), such as elytra of aquatic beetles (*Hydrous pistaceous*), chelipeds of crustaceans (*Procambarus clarckii*), large cuttlebones, bones from garbage, and olive seeds. About half of the prey could be identified to species, because these parts were highly characteristic and durable (Table 2).

Pellets were formed of highly eroded hard parts of prey, and lacked soft-bodied items (Duffy and Jackson 1986, Brown and Ewins 1996), allowing taxonomic identification only to higher levels. Therefore, pellet analyses over-estimated prey items bearing hard and distinctive elements, such as lateral line scales of some Carangidae (*Trachurus* sp.), scales of zeiforms (*Capros aper*) or fish species having particularly large and hard otoliths (Gadiformes). *In vitro* studies have shown that gastric juices can completely dissolve small otoliths (Jobling and Breiby 1986, review in Pierce and Boyle 1991). This is the case for the sardine (*Sardina pilchardus*) and other clupeiforms, which constitute the main proportion of the diet in the Audouin's Gull (Pedrocchi et al. 1996, Ruiz et al. 1996). Furthermore, otolith occurrence can be the result of secondary consumption, that is the consumption of a prey containing otoliths in its stomach (Blackwell and Sinclair 1995). Therefore, otoliths can be useful in identifying fish species, but not diet composition in gulls.

Diet composition based on direct observation of chick provisioning contained a large number of prey items identified only to upper taxonomic categories (Table 1). In our study, the possibility of identifying a prey item to lower categories depended on the extent of pre-digestion, the size of prey items (because of time spent in manipulation), and the observation distance. Diet composition tended to be biased toward prey with conspicuous color or shape, such as red bandfish *Cepola rubescens,* and prey requiring lengthy manipulation such as anguiliforms (Cézilly and Wallace 1988). In contrast, easily digestible prey such as sardines were underestimated (Table 1). Similar results have been reported previously (Spaans 1971, Fox et al. 1990, Brown and Ewins 1996).

BIOMASS ASSESSMENT

In agreement with Duffy and Jackson (1986), the best method to obtain dry weight biomass of prey was the collection and desiccation of undigested food items. However, this material was found only in regurgitates of recently ingested meals and it was often necessary to rely on indirect methods to obtain biomass data. Prey weight can be obtained through predictive equations based on linear relationships between size

and biomass (Pierce and Boyle 1991, Ridoux 1994) for many different hard parts of prey, which is especially useful for dry boli and food remains.

Several authors have reported relationships allowing reliable predictions of fish weight or length from otolith measurements (Furness and Hislop 1981, Jobling and Breiby 1986, Pierce and Boyle 1991). However, erosion by gastric juices can reduce the size of some otoliths, thus producing an underestimation of fish size or weight (Jobling and Breiby 1986, Harris and Wanless 1993, Zijlstra and Van Eerden 1995). Prey size distributions might be estimated using uneroded otoliths (Härkönen 1986), but for many species it seems impossible to separate eroded from uneroded items with any confidence (Harris and Wanless 1993). Correction factors for size reduction during digestion can be applied, but the resulting estimate is likely to be inaccurate (Pierce and Boyle 1991). For these reasons, pellets allow biomass estimates only through average values.

In direct observation, biomass can be assessed only by reference to prey size or by reference to average biomass values. However, the accuracy of estimation of prey size during direct observation has never been assessed in seabirds, but it appears rather inaccurate in herons, owing to individual variability in bill-length and difficulties in determining reference points, mainly when a prey is longer than the bill (Bayer 1985).

SAMPLING CONSTRAINTS

Regurgitates can be collected easily when nestlings are caught for other purposes such as banding or growth monitoring, taking advantage of the natural response of gulls to regurgitate when handled (e.g., Mudge and Ferns 1982). However, the collection of regurgitates can have detrimental effects. These effects are greater in older chicks due to their increased mobility (Brown and Morris 1995). One way to reduce researcher-induced chick mortality is the construction of wire-fenced enclosures, which restrict the movement of young gulls, or the selection of areas with an abundance of suitable hiding places (see Götmark 1992, Brown and Morris 1994, for reviews).

Because a nestling's ability to disgorge when handled may depend on the type of prey, the nestling's age, the amount of food in the stomach, and the amount of stress generated (Johnstone 1977, Duffy and Jackson 1986, Schramm 1986), the quantity of regurgitates obtained per sampling effort is highly variable. We were successful in obtaining regurgitates in all cases when nestlings were handled after they had recently been fed by adults. However, when nestlings were randomly sampled, the percentages regurgitating were much lower and variable (0.5–20%), as reported in other gull studies (9–16%, Furness and Todd 1984; 45% Hario 1990). Spaans (1971) strongly recommended that only one regurgitate per brood be collected in each sampling effort, because broodmates may be fed by the parent bird with pieces of the same prey item, especially for early young broods.

Dry boli, food remains and pellets are found on the ground, thus they easily can be collected periodically. However, since they can persist for variable periods, depending on their composition or location (Furness and Hislop 1981), existing remains should be removed from the collection area prior to the collection of additional samples for diet analyses. Nevertheless, dry boli can be rather scarce, found only during the incubation and chick rearing periods, and not available for all gull species.

Direct observation is a good method of obtaining large sample sizes in a few days and it can be combined with other kinds of study. This method only allows assessment of chick diet, but in the case of gulls, older chicks (> 20 days old) do not differ significantly from adults in diet (*Larus argentatus,* Nogales et al. 1995; *L. delawarensis,* Brown and Ewins 1996; *L. audouinii,* Pedrocchi et al. 1996).

The selection of a type of food sampling method for dietary analysis should be evaluated according to the objectives of the study, the status of the species involved, and time available to obtain samples. In any case, it is important to discriminate between food samples according to the biases they produce, and to analyze separately the different kinds of food sample, and then use the information provided by each food sample in a complementary way. Ideally, bias and suitability of each type of food sample should be assessed before undertaking any gull diet study. Regurgitates were the best food sample to evaluate Audouin's Gull diet composition, due to the identification level allowed and the reliability of biomass estimates (see also Oro et al. 1997). In our view, food remains constitute

a poor type of food sample for diet assessment, but they are a good complement to dry boli because they contain mainly large, hard parts of prey, which are underestimated in dry boli. Pellets have been widely used to study diet in gulls (Witt et al. 1981, Noordhuis and Spaans 1992, Nogales et al. 1995); however, in our view, this is the least useful of the food samples analyzed here, although it could be useful to monitor variations in the use of certain prey items.

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