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ASPECTS OF THE FEEDING BEHAVIOUR AND
FOOD HABITS OF CERTAIN FISH-EATING
BIRDS IN THE GREAT LAKES

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Abstract

This paper discussed techniques that can be used in the study of the food habits of fish-eating birds, and their relative merit. The available information on the food habits of Herring Gull, Ring-billed Gull, Common Tern, Caspian Tern, Great Blue Heron, and Black-crowned Night Heron in the Great Lakes region is summarized.

Résumé

Nous présentons et évaluons les techniques qu'on peut employer pour étudier les habitudes alimentaires des oiseaux piscivores et résumons ce que nous savons des habitudes alimentaires du Goéland argenté, du Goéland à bec cerclé, de la Sterne commune, de la Sterne caspienne, du Grand Héron et du Bihoreau à couronne noire, de la région des Grands lacs.

Introduction

As the largest freshwater lake system in the world, the Great Lakes represent an immense potential for the study of aquatic ecosystems, including the study of fish and their predators, such as piscivorous birds. Most of the feeding information on this type of bird is derived from studies conducted in marine environments. Hence, their feeding activities in a freshwater regime are not well known.

It has been suggested that a bird's breeding success is dependent upon its food resources (Lack 1954). This alone would give good reason to study this aspect of a bird's biology. Additionally, there is also the question of how co-existing species are able to partition resources and how the availability of these resources affects population stability.

At this time when food studies are becoming more important in understanding the whole biology of fish-eating birds, it is important that methods of study be standardized and information already produced on this subject assembled. This paper will discuss techniques that can be used in the study of the food habits of certain fish-eating birds and will subsequently summarize such habits for certain species in the Great Lakes (Herring and Ring-billed Gulls, Caspian and Common Terns, Great Blue and Black-crowned Night Herons).

Methods of Studying Food Habits

In studying the food habits of any bird, examination of actual food items remains the most important of any of the available methods, and as Hartley (1948) points out, no large-scale food study should be carried out without such an examination. However, for many birds, this examination would entail procuring stomach contents and if the particular bird population is small, decimation would possibly occur before sufficient samples were collected. It is fortunate in the case of the gulls, terns, and herons in question here that their feeding habits eliminate the need to sacrifice individuals for this end. Instead, the natural feeding habits of these piscivorous birds have been studied primarily with the use of four major techniques:

- (1) analysis of regurgitated boli of recently eaten food;
- (2) analysis of regurgitated pellets of indigestible material;
- (3) analysis of faecal material; and
- (4) direct observations of feeding activity.

Analysis of regurgitated boli

It is the habit of many gulls, terns, and herons to regurgitate recently-eaten food which is still held in the gullet (fright response). While adults display this behaviour (i.e.,

Ring-billed Gull adults regurgitating when cannon-netted (Jarvis and Southern 1976)), it is especially marked in the young of the species. Kirkpatrick (1940) used this method of collection to study the food of young Great Blue Herons (Ardea herodias) while Jenni (1969) used it with nestlings of the Snowy Egret (Leucophoyx thula), Cattle Egret (Bubulcus ibis), Little Blue Heron (Florida caerulea) and Louisiana Heron (Hydranassa tricolor). The advantage of this method is that samples can be taken systematically and repeatedly from the same individuals so that a small sample size of broods need not be a disadvantage. Unless identification and measurements are done immediately in the field, some measures must be taken for the preservation of the masses of food (boli). For long-term preservation, freezing is recommended. Alternatively, the bolus may be fixed in 10% formalin for one to several days and then transferred to and stored in 30% isopropanol. Insects may be stored directly in alcohol.

Regurgitation techniques vary and include the use of emetics, collars (made of pipe cleaners or metal rings and secured around the young bird's neck, preventing swallowing) and ordinary handling. Young herons appear to regurgitate as soon as disturbed (a disturbance sufficient to evoke regurgitation may be made even from the base of their nest tree) but gull and tern chicks often require handling to produce a regurgitation response. In this case, the proventriculus may be gently probed and palpated to discern the bolus and then the chick held upside down to promote regurgitation. Occasionally, the

gullet may have to be probed with a finger to encourage regurgitation. Tweezers may also be useful in this operation.

Once the bolus is secured, various information should be recorded:

- (1) identification of each food category;
- (2) number of food items comprising each food category;
- (3) volume by water displacement - of the whole bolus and of each food category; and
- (4) various food item dimensions (i.e., length of fish).

The bolus may be covered in mucus so it may be necessary for this to be washed off before measurements are made. There is some discrepancy in the literature as to whether weight is a valuable measurement to make and this will be discussed in greater detail under "Assessment and presentation of diet". However, wet and dry weights may also be measured ... for the entire bolus and individual categories.

Analysis of regurgitated pellets

Pellets of the indigestible remains of food items are regularly disgorged by gulls, terns and herons. These may be found at the nesting or roosting sites, or near feeding grounds. While pellets have long been used by ornithologists as an index of diet and have at times been shown to reflect the diet with some degree of quantitative accuracy, there are other cases (Hibbert-Ware 1940)

where it has been shown that the pellets are highly unrepresentative of the diet as a whole. Since soft-bodied food items do not show up in a pellet, conclusions based on this analysis are limited to what is present in the pellet and one cannot consider what does not appear. That is, it cannot be said that a food item was not eaten if it was not found in the pellet. Hence, this method of study is valuable, but must be employed in conjunction with other methods.

Since the species of birds concerned are partially piscivorous, pellets can be used to identify the fish being eaten. Fish may be represented by vertebrae, otoliths, small bones, scales, etc. Scales and otoliths are particularly useful in identification. Generally, fewer than 10 fish species will be taken by a bird and if these are known to the investigator, specimens of the various bony parts and scales can be mounted as a standard for comparison with pellet material. Refer to Frost (1925, 1926) for information on otoliths and Allan (1977) and Lagler (1947) for information on fish scales.

Insects may be represented by elytra, wing parts, whole exoskeletons, etc., and may be identified using a similar standard. Birds may be identified by feathers, bills and feet and mammals by fur and teeth.

Analysis of faecal material

Some finely divided indigestible parts may come through in the faeces and if these can be identified, then faecal analysis is an appropriate method of food study, but is even less informative

about the whole diet than are pellets. It can be used only as giving supportive evidence for information derived from another method. For example, when Ring-billed Gulls feed in fields and take earthworms, the faeces is usually muddy brown instead of white/grey/yellow since so much soil is taken as well. The observation of muddy faeces is thus indicative of field-feeding, but cannot be used quantitatively.

Direct observation

While sometimes underestimated in the literature, direct observation of the feeding activity of these birds will provide invaluable information, both quantitative and qualitative, regarding food habits. Field observations of feeding are judged by the normal standards of the reputation of the observer and the repetition of the record. Resulting information can pertain to the individual bird and may give insight into both daily and seasonal trends.

If the bird is in the breeding season, it is possible to make accurate observations of the birds as they bring food to their young. Alternatively, observations may be made at the feeding sites. Observations may include:

- (1) time spent by adults in actual feeding (search, pursuit and handling times);
- (2) time spent by adults in foraging flights;
- (3) food items taken by adults;
- (4) courtship feeding;

(5) food fed to chicks; and

(6) frequency of chick feedings.

It is sometimes possible, in identification of prey items, to make reasonable estimates of prey size (i.e., length of fish) which can be used in determining the weight or volume of that item, using various indices of allometric growth for the prey concerned.

In addition to these direct observations, the investigator may wish to carry out a study of the available prey items. This may entail determination of density figures and accessibility values for these items (i.e., by netting insects, seining fish, live-trapping small mammals). Later, when information is available on what is actually eaten (quantitatively), this prey availability can be correlated with intake values to determine if prey are taken in proportion to the numbers available, or whether they are taken in a more selective or opportunistic manner.

In establishing the food habits of a species, it is necessary to use at least 2, and better 3, of the above methods, including regurgitation, where possible. The method of direct observation will give valuable information on how often the birds feed and how often they feed their chicks. It will also give clues as to the location of feeding sites. Faecal and pellet examination will further define the feeding picture, but regurgitation analysis will enable one to make conclusions about the food habits based upon a quantitative investigation.

There is considerable evidence that birds will feed differently throughout both the day and the season. Therefore, an effort should be made to accommodate these variations. This can be done by sampling at set intervals of the day (i.e., early morning, mid-morning, early afternoon, late afternoon/evening) and different periods of the season (i.e., pre-breeding, incubation, brooding, etc.). In addition to this, certain manipulations of the natural feeding situation may be made. For example, one could answer the question of whether the species feeds selectively on ("prefers") one food item, by exposing this and other food items and making direct observations as to which is taken in the largest quantity (this can be done by knowing the weight before and measuring it again after a set interval). If direct observation is not desirable, the foodstuffs can be dyed with methylene blue and other prominent colours, and it can be observed if the colours show up in the breeding site in the faeces.

This type of manipulation is also very convenient if one wants to establish where a species can feed most effectively. By placing dyed foodstuffs in various habitats (i.e., terrestrial: open fields, woodland; island: shoreline, turf; water: open water, shallows), it can be observed where the bird can most effectively exploit the opportunity.

Assessment and presentation of diet

There are a number of ways to assess and present dietary information. Three methods which are widely used by many investigators and well discussed by Hartley (1948) are numerical, gravimetric and volumetric. A summary of Hartley's discussion follows.

Numerical methods

There are primarily three numerical methods. The enumeration of occurrences or frequencies is a statement of the number of birds in which each type of food or organism was found. This statement may be the actual number or the percent. The enumeration of the food is a statement of the number of each food item found. The third numerical method is a combination of the first two.

Numerical assessment realizes a problem when certain foods are involved which cannot be counted, i.e., carrion, sap, garbage, fish offal, etc. Such enumeration does not give the size of the food items, although this may be derived from general knowledge. Occurrence values may be misleading in that rarely taken items may be deemed more important than they really are. With all these objections in mind, it remains that such assessment gives valuable information and is especially suited to the study of seasonal changes in diet. Furthermore, it is the advantage of not taking into account the state of digestion of the food items.

Gravimetric methods

Accurate assessment of the weight of food may be difficult due to the various hygroscopic qualities of the different food items. Even if dry weight is measured, it is not certain that the ratio of wet to dry weights is uniform for all food types or that the nutritive values of foods bear a constant relation to their dry weights. Consequently, the value of this measurement is held in question.

Volumetric methods

Volumetric measures may be made directly or by water displacement. In some cases, it may be more advantageous to simply enumerate and calculate an approximate volume of each food item using a standard size (or sizes) for that item. While this may sacrifice a certain degree of accuracy, it saves considerable time and may well give all the information the investigator seeks. Though this method has the advantage that it can be used to assess any food item, it loses meaning if other indications of size are not given, i.e., 100 cc of alewife could mean one very large alewife or several small ones. This loss of information may be crucial to the determination of resource partitioning by size between fish-eating species. Hence, concomitant enumeration is important as well.

If there is some question as to the varying digestion rates of the different food items, a correcting factor may be used. The development of this experimental method (Hess and Rainwater 1939) allows the original amount of each food item to be determined using

the amount remaining and the digestion rate. Another common method is coding for the frequency of each food item using categories such as 'very common', 'common', 'frequent', 'rare', or 'very rare' (Swynnerton and Worthington 1940). These word descriptions are then assigned numbers (i.e., very common - 5, very rare - 1) which are added for each food item and scaled down to a percent basis. While these results give more information than merely presence or absence of a food item, they cannot be readily compared with data obtained through other methods.

In deciding which methods of collection and assessment to use, it should be considered that information is important only insofar as it promotes further understanding and can be compared with that already known. Hence, one should choose a method or methods which gives the most quantitative picture possible and in such a way as to facilitate comparison with that information already produced on the subject. A comparison of the various methods of assessment has been given by Hartley (1948) for the foods of the cormorant and shag.

Hérons

Not a great deal of information has been assembled on the feeding habits of the Great Blue Heron (Ardea herodias) and Black-crowned Night Heron (Nycticorax nycticorax) and Ludwig (personal communication) states that to his knowledge, no work at all has been

done on this aspect of their ecology on the Great Lakes. Food items for both of these species are given in Table 1. While fish are taken in the greatest numbers by both herons, a great complement of other prey also appears. The Great Blue is a proficient insectivore. The appearance of aquatic insects in their stomachs could be the result of the accidental intake of these invertebrates while fishing. However, it is possible that insects are taken purposefully, as perhaps supported by the fact that herons make attempts to catch flies and other flying insects, and grasshoppers and dragonflies during times of seasonal abundance. In taking these food items when they peak in numbers, herons show themselves to be opportunistic feeders. That is, they can take advantage of certain spatio-temporally abundant food resources and can then move on to other foodstuffs as they become available. This would offer an explanation for the particular feeding behaviour that they demonstrate, in that fish are taken in abundance during those seasonal intervals when it is economical to do so. This means that heron feeding activity will be closely tied to the population fluctuations of their prey, especially as dictated by their breeding seasons. In this way, herons can make the best use of their particular morphological features which adapt them for wading postures to maximize fish intake. They can also take advantage of terrestrial feeding opportunities, such as outbreaks of insects in fields, to meet dietary needs. While the heron body structure does not seem quite as fitted to on-land activity as that in water, it is energetically sound for them to avail themselves of this seasonal food item.

As is typical of the Ardeidae, young are fed at first with an almost wholly digested fish "soup". This liquified food is passed directly from the parent's bill to that of the juvenile. Within a few days, soft regurgitated food replaces the soup as nourishment, and this is then replaced by whole fresh prey when the young are large enough to manipulate and digest these items. Because of this feeding system, it is difficult to obtain distinct regurgitant samples from the young during their earliest days. At this time, the prey is so thoroughly minced and dissolved that identification of specific food items is largely impossible. However, as prey is brought more and more in its entirety, the regurgitation technique becomes one of the better methods of studying the food habits of the heron at this stage of development. The juvenile heron's habit of regurgitation upon disturbance facilitates the use of this technique.

The Great Blue Heron is the largest and most widespread of the heron family in North America. This information itself should shed some light upon this bird's ecology, including feeding, and one might hypothesize that the success of this heron is due to its ability to accommodate to a variety of ecological conditions. Such accommodation falls, of course, in the realm of a number of activities including breeding behaviour, but certain feeding behaviours of this species may make it more versatile than others. For instance, while the Great Blue feeds largely during the day, it is also known to feed at night (Bent 1926). Clearly, such an ability opens up new resource possibilities. Furthermore, the rather considerable tarsal length of this bird allows for two major feeding techniques to be used:

still-hunting and stalking (Bent 1926). These feeding techniques have been broken down, described and supplemented by Kushlan's (1976a) integrative analysis of the feeding behaviour of all North American herons. This analysis sheds considerable light on the possible distinctions in the feeding habits of the Great Blue and Black-crowned Night Herons, and these distinctions will be drawn later in this discussion.

One very interesting aspect of the Black-crowned Night Heron's feeding habit is its scavenging behaviour. Gross (1923) made observations that whiting and other dead fish were picked off the beaches and Wetmore (1920) recorded seeing this heron scavenging for dead Axolotls* which they found floating on the water. Given the name of this bird, it is not surprising that a good deal, though not all, of its feeding is carried out at night. The Night Heron becomes proportionately less nocturnal during the time it is brooding as it requires the daylight hours to produce enough food for nourishment of the young.

From this information, the question then arises whether Great Blues and Night Herons can co-exist and if they do, by what mechanisms, especially with regard to feeding techniques. Do they in fact take the same prey and if this is so, what determines the allotment to each? If food resources are sufficient to support any number of these herons, then it would appear that co-existence, or

* Neotenic larvae of Ambystoma tigrinum

its lack, is determined by other ecological factors, such as nest site availability. Other questions manifest themselves too. Do these two species use the same feeding techniques in the same proportions? Do they feed in different locations according to their morphological features? The whole ecological picture is at all times incomplete, especially for animals for which so little is known quantitatively about their food habits. However, the following, though of necessity highly speculative, is an attempt to integrate what is known of these species in general to create a possible foundation for their interaction on the Great Lakes.

It has been suggested by a number of workers that sociality in birds and other vertebrates is a strategy which has evolved to optimize the exploitation of food resources (Fisher 1954; Crook 1965, 1970; Lack 1968; Emlen 1971; Murton 1971a, b; Ward 1965, 1972; Zahavi 1971a, b; Ward and Zahavi 1973; Schaller 1972; Vermeer 1973). This hypothesis has interesting implications for those birds that nest colonially (Lack 1968; Fisher 1954; Crook 1965; Horn 1968; Emlen 1971), and in particular, for the Great Blue and Night Herons.

In conjunction with work done with Brewer's Blackbirds, Horn (1968) has created a model which related colonial nesting to food availability. He has shown that somehow, feeding is done more efficiently because of group membership. In the case of herons, feeding is not done in groups, per se, but a bird who is foraging with little success can follow a member which is more successful to the site that affords this success. Birds forage most successfully when they forage together in this way. That this model holds

significance for herons has been shown by Krebs (1974). Although other authors have concluded that colonial nesting in herons is not an adaptation for exploiting food resources (Lack 1968, Jenni 1969), Krebs' work with Great Blue Herons demonstrated that the colony may be an "information centre" pointing to productive feeding sites, and that flocking birds tend to go where the conditions are good and do better by virtue of this alone.

It is evident then that the colonial nesting habit of the Great Blue Heron facilitates its exploitation of food resources that are unpredictable, both spatially and temporally. This is not to say that colonial nesting evolved for this purpose alone, for the Great Blue Heron can also be a solitary nester and feeder, or a colonial nester and a solitary feeder. This can be understood within the framework outlined by Brown (1964), since herons can afford to be solitary and territorial when food resources are widely scattered and/or easily defensible, but tend to flock when food occurs in large, indefensible, unpredictable "clumps". Even within a flock, however, individual spacing distance is maintained and while Goss-Custard (1970) attributes this distance to a compromise between flocking for safety and spacing for the prevention of intra-specific interference, Krebs (1974) purports that this distance is better recognized as a compromise between a need for spacing to prevent disturbance of prey and a need for flocking in order that highly productive feeding sites be more easily located.

The matter of resource division between the two herons requires consideration. As suggested by Meyerriecks (1959, 1960a

and 1962), differences in food choice or intake may be tied into tarsal length, but for all practical purposes, potential differences in depth of wading are slight and important differences between the two species are likely to be behavioural. In Kushlan's (1976b) study of the predation effects of herons on a seasonally fluctuating pond, it was observed that the Black-crowned Night Heron and other small herons were the first to feed on a pond after the water level had receded enough. The maximum use of the pond's resources appeared to coincide with the invasion of Great Blue Herons. In addition to this difference in the seasonal use by the two species, there was a temporal difference as well, with Night Herons utilizing the pond most heavily at dawn, with Great Blue Herons arriving somewhat later in the morning. Kushlan states that wading birds feeding in the pond were apparently ecologically separated by a combination of size, feeding location and feeding behaviour. He noted that the Great Blues fed by the stand and wait techniques. The Night Herons on the other hand, fed in a manner similar to the smaller herons, though when other herons were present, the Night Heron was represented by a small number. This decrease in the number of Night Herons has been attributed to the maintenance of individual distance. Since this heron overlapped other herons in size, feeding location and behaviour, it was excluded by other herons (Kushlan 1973).

Kushlan (1976a) has re-evaluated the feeding behaviours of North American herons and a summary of the behaviours appropriate to Black-crowned Night Herons and Great Blue Herons is given in Table 2. From this, it can be seen that the Night Heron and the Great

Blue share all of the feeding techniques they use, with the exception that the Night Heron occasionally uses bill-vibrating and the Great Blue uses wing-flicking and standing flycatching.

In summary, it would seem that a combination of the niche parameters of size, feeding location and feeding behaviours is responsible for the ecological segregation of any co-habiting herons, including the Great Blue and Night Herons of the Great Lakes. Kushlan (1976b) suggests that these differences indicate that available food is divided among species in a nonoverlapping manner, though actual food data is not available to point this out. Presumably, size differences account for two ways of apportioning food: the larger the bird, the deeper the water it can frequent; the smaller the bird, the smaller the food items it can take (Krebs (1974) noted that a heron (Great Blue) rarely can handle a fish in excess of 1 1/3 times its own beak length). Lastly, overlapping of behaviours may exclude one heron from the feeding site of others.

Gulls and Terns

The majority of larid populations in central Canada are situated in the Great Lakes region. Here they are primarily represented by the Herring and Ring-billed Gulls (Larus argentatus and L. delawarensis) and the Caspian and Common Terns (Hydroprogne caspia and Sterna hirundo), though other gulls do frequent this area.

In a general evaluation of the feeding techniques of seabirds, Ashmole (1971) suggests that differentiation in behaviour is a factor in the variety of prey taken by different species. Such behaviours are outlined in Table 3.

Ring-billed Gull

The Ring-billed Gull has been studied the most extensively of these four species in the Great Lakes. Nonetheless, only two feeding studies have been carried out with adults of this species. The first study (Ludwig 1966) was conducted on Lakes Huron and Michigan from 1963 to 1965 in conjunction with an investigation of spectacular population increases. Food habits were examined using two methods: stomach contents, and retrieval of dropped or regurgitated items in the colonies. The results of this study are given in Table 4. It was concluded that alewife (Alosa pseudoharengus) was the principle item, comprising from 50-60% of the total net weight of the diet. It was also found that Ringbills consume a large and diverse number of insects, but these represent less than half the total intake by wet weight. The diet also included some other fish species, principally rainbow smelt (Osmerus mordax) and small numbers of crayfish, gull chicks, garbage and unidentified material. This particular study was continued and presented once again (Ludwig 1974), this time with additional information up to 1967, and including Lakes Erie and Ontario. These data are remarkably similar to those generated by the 1966 study (Table 4).

While this information has a qualitative usefulness for the understanding of Ring-billed Gull feeding habits, its importance is limited by a number of factors. First, as Jarvis and Southern (1976) point out, sample sizes have not been included in the analysis and a sample-by-sample analysis was not made. In dealing with pooled data such as this, no individual differences will be brought out, so that if individuals are feeding in different areas and taking different prey items, this will not be detected. Furthermore, in using retrieved fish and regurgitated samples collected from the ground in the colony, another bias is possibly introduced. Fish of one size may be dropped onto the ground more frequently than fish of another size. In this way, one species or one size-class may be over-represented in the sample of retrieved food items. In addition, a seasonal basis for food habits cannot be established from this study. As this particular investigation was designed to shed light upon the question of population dynamics, its approach is general and nonquantified.

Jarvis and Southern (1976) have since done a more detailed study of Ring-billed Gull food habits in Lake Michigan. More care was taken to establish seasonal and distributional trends in these habits by recording collection dates of the samples and making collections in three discrete colonies. Percentage composition of the diet by frequency of occurrence was calculated for the three major fish species taken: alewife, smelt and stickleback, and these are compared

with Ludwig's results in Table 4. What becomes immediately obvious from this comparison, is that the intake of alewife in this lake drops off appreciably over the interval between the two studies (i.e., between 1967 and 1971), constituting only 20% of the diet, where it once constituted about 71%. This comparison is unfortunately very superficial as it must remain as a comparison of numbers (frequency of occurrence) alone. To be completely valid, the nutritional value of the food items taken in each study should be compared (i.e., caloric value), but since this is rarely done, at least comparable indices such as wet weight or volume should be compared. This is not possible for these data, as Jarvis and Southern (1976) have calculated percent composition by volume and Ludwig (1966) has speculated as the wet weights of the species of fish represented, but reserves actual calculations of wet weight values for publication "later in a complete report on the food items of these species". Though wet weight and volume measurements may not be comparable, Jarvis and Southern (1976) still see the data on food habits as being substantially different from Ludwig's. For example, the data for the Rodgers City colony indicate that insects are taken in the greatest volumes at three times in the breeding season, and earthworms comprise the greatest proportion of the diet by volume of the first month (May) in this colony. However, it may well be that fish comprise the greater proportion of the nutritional intake of the bird, even when fish are represented by lesser volumes than other food items. This is only a possibility, but a valid one since fish

are composed of more digestible material in general per unit of body weight than are insects (due to exoskeletal features).

It remains to be explained why samples in the two studies presented here were different, especially where fish species taken are concerned. Ludwig (1966) suggests that the large proportion of alewives that he found in the diet of Ring-billed Gull is due to the peaking in alewife populations in Lakes Huron and Michigan at this time. It is believed that prior to 1955, when alewife populations were very small, no alewife appeared in the diet of this species (Ludwig, F.E., personal communication to Ludwig 1974). Jarvis and Southern (1976) showed that the frequency of intake of smelt decreased over the season (May, 39% of volume; June, 45%; July, 23%) while alewife consumption increased as the season progressed (May, 4% of volume; June, 15%; July, 37%). Thus, it would appear that the intake of the fish has a seasonal basis, probably founded upon the seasonal movements of the smelt between shallow and deep water (Lackey 1970) and the spawning and seasonal movement patterns of alewife (Galligan 1962, Norden 1967). The overall smaller proportion represented by alewife in the Jarvis and Southern (1976) study could be attributed to the decline in alewife populations and the increase of other fish numbers. The surprising difference in the food habits recorded in each study is the remarkable increase in the intake of stickleback. Although Jarvis and Southern (1976) do not specify which species of stickleback was being taken, as does Ludwig (1966), it remains that if quantity of intake is calculated on the basis of frequency of

occurrence, the 1976 study shows at least a five-fold increase in the consumption of this fish. Ludwig (1966) includes stickleback as a component in the "other fishes" category, which corporately makes up only 10.7% of the total number of fishes taken. However, in Jarvis' and Southern's study, stickleback make up 50% of the total number of fish taken, and 71% of the total number of fish taken in July alone. McKenzie and Keenleyside (1970) report that stickleback breed in shallow, rocky water at this time in northern Lake Huron.

As one might expect of birds nesting farther from shore as in the case of the Ile aux Galets colony (Southern and Jarvis 1976), fewer insects were taken and more of the diet was made up of fish. In addition to this, this more isolated colony showed a greater diversity in diet, with 13 of the major food categories being recorded for 10% or more of the individual samples, while the mainland colony at Rogers City had only 5 of the food categories present in 10% or more of the individual samples.

Two more factors were noted by Southern and Jarvis which Ludwig failed to take into account. First, Ring-billed Gulls may have a daily variation in their food habits. Secondly, they may be influenced in their prey selection or ability to catch certain prey, by the weather conditions. Thus, insects may be less available in the early morning when temperatures are lower and at this time, fish may be favoured. Also, insects may be less available on overcast or rainy days.

Problems which have arisen with these two studies have been, in part, alleviated by more recent studies done in Lake Ontario by Haymes and Blokpoel (1977) and Allan (1977) and in Lake Huron (Allan 1978). These studies sought to eliminate the bias produced by age of bird, and time of day and season. As for the study of Jarvis and Southern (1976), the investigation of Ring-billed Gull chick diet on Leslie Spit (Haymes and Blokpoel 1977) indicated that insects and earthworms play a major role. This is not always the case for Ring-billed Gull chicks of Gull Island (Allan 1977) for which fish predominate.

In studies of adult gulls (Allan 1977, 1978) on both Lakes Ontario and Huron, it would appear that food may not be the most important factor in the recent population increases of these birds. While it is true that alewife and smelt are important during some parts of the breeding season, the versatility of both Herring and Ring-billed Gulls appears to make them capable of feeding on other food items, and thus not dependent on these fish.

Since so little information is available on the diet of Ring-billed Gulls, in the Great Lakes, it is helpful to include here additional information on food habits as given by Vermeer (1970) for populations of this species nesting in Alberta.

Data collected for Beaverhill and Miquelon Lakes show that Ringbills favour plant foods in May, insects in June and garbage in July. However, what is also remarkable is the large number of rodents taken by this bird. There is an especially impressive representation

of these mammals in the diet, in those colonies found towards the south of Alberta. In fact, it appears that gulls take fish in an increasing proportion the further north they breed. Vermeer (1970) has attributed this to the fact that northern Alberta is more heavily forested than the south, and birds will have a more difficult time trying to pick up rodents. Other studies on western colonies of Ring-billed Gulls (Munro 1936, Rothweller 1960) confirm that it is not unusual for gulls to forage in terrestrial habitats as feeding opportunities, like an abundance of rodents, present themselves. It would appear then that western and eastern populations of Ring-billed Gulls behave rather differently where feeding is concerned, and yet the versatility of these species is at all times borne out, and it is evident that this species has an ability to maximize on temporary abundances of certain prey types.

Herring Gull

Bent (1921) calls Herring Gulls "scavengers" and Ludwig (personal communication) suggests that anything that a Herring Gull can eat, it probably will eat, whether the food is dead or alive.

The literature is resplendent with records of Herring Gulls feeding in unusual ways or upon unusual prey. It is well known that they depend largely in some areas upon human waste disposal (Cogswell 1970, Davis 1975) and fishing industry castoffs (Davis 1975), but in addition to this, they have been known to demonstrate robbing

behaviour for food (Bunker 1966), cannibalistic behaviour (Parsons 1971, Moreau 1923, Paynter 1949, Goethe 1956), hawking for insects (Mayr 1948, Sheppard 1945), exploiting local outbreaks of a prey item such as grasshoppers (York 1949, Berthel 1940), cicadas (Forbush 1924) and other insects in fields (Walker 1949, Cruickshank 1938), larvae of lobster (Mills 1957), starfish (Dewar 1937). They have also been known to eat some vegetation such as berries (Harris 1961) and grain and corn (Davis 1956, Rintoul and Baxter 1925) and to take the odd bird (Rodgers 1968) and bat (Cleeves 1969).

What becomes immediately noticeable is the fact that this species is versatile and highly capable of exploiting an opportunity as soon as it avails itself. This is no better recorded than by Vleugal (1951) when he observed that Herring Gulls learned to feed where mine explosions exposed prey items.

A considerable number of food studies have been done on this species (Throne 1940, Harris 1965, Helle 1975) including ones in Montana (Rothweller 1960), Britain (Threlfall 1968b), Newfoundland (Threlfall 1968), the Canadian prairies (Vermeer 1973) and Sweden (Andersson 1970). However, as for the Ring-billed Gull, very little in this line of research has been done on this species in the Great Lakes area. In fact, it appears that Ludwig (1966) has been the only investigator to publish this type of information for this region. This data is given in Table 4. It would appear from this Table that

the Herring Gulls too were taking a large proportion of alewife, comprising about 80% of the diet by wet weight. F.E. Ludwig (in personal communication with Ludwig 1966) suggests that at one time Herring Gulls consumed more insects than they do now, since he observed that chicks regurgitated cicadas, grasshoppers and mayflies instead of fish on a number of occasions. Ludwig (1966) purports that such food habits would have put Herring Gulls into a more directly competitive confrontation with Ring-billed Gulls, and now that they are taking seemingly fewer insects, such competition would be reduced.

Common Tern

The food of the Common Tern has never been studied in detail in the Great Lakes region. However, it seems to be the common consensus of writers who have done studies in other areas that this species feeds largely on fish (Waltz 1976, Lemmetyinen 1976, Hopkins and Wiley 1972, Palmer 1941). Of course, the fish species which are taken in the greatest proportions vary according to the geographic location of the colony. Palmer (1941) provides a good review of the general food habits of this bird.

Perhaps the most comparable food data to that which one might anticipate generating from a Great Lakes study can be found in a study done in another freshwater habitat, Lake Winnipeg (Vermeer 1973). The results from this study indicate that the Common Tern specializes somewhat in insect prey, while the Caspian Tern favours

fish. In addition to this interspecific difference in food habits, there also appears to be a difference in the prey size favoured by each species, with Common Terns taking smaller fish than the Caspians. Presumably, this feeding situation may also be found in the Great Lakes where insects have been found in the pellets of other larids.

Morris and Hunter (1974) suggested that food did not appear to be a limiting factor in the successful breeding of Common Terns in five colonies in the lower Great Lakes, but this evidence is anecdotal.

The Caspian Tern, being somewhat larger than the Common Tern, is capable of taking larger fish prey (Vermeer 1973). Like other terns, it takes primarily fish and its food habits have been studied in a limited fashion by Ludwig (1965, 1966). As with the data for food that this author produced for Herring and Ring-billed Gulls, these data suffer from incompleteness in that sample sizes and seasonal variations are not given. Nonetheless, it appears that the alewife once again predominates in the diet with American smelt and yellow perch running second and third in proportions in colonies located in Lakes Huron and Erie.

Given that Caspian Terns are capable of rather long distance flights for purposes of foraging (Gill 1976, Soikkeli 1973), it is foreseeable that this species is less restricted by local food shortages and can meet dietary needs by feeding far afield of the nesting site.

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Table 1: Major food items of the Great Blue and Black-crowned Night Herons

Food Item	Great Blue Heron	Black-crowned Night Heron	Reference
Snakes	X		Tufts 1961
Birds ¹	X	X	Audubon 1840, Peters and Burleigh 1951, Winterbottom 1957, Beckett 1964, Kale 1965, Collins 1970, Nickell 1966
Small Mammals ²	X	X	Tufts 1961, Allen and Mangels 1940, Audubon 1840
Amphibians ³	X	X	Wetmore 1920, Tufts 1961
Crustaceans ⁴		X	Bent 1926
Insects ⁵	X	X	Wilson 1832, Wolford and Boag 1971
Fish ⁶	X	X	Bent 1926, Gross 1926

1 - including young egrets, ibises, ducks, terns, gulls, red-winged blackbirds

2 - including voles, shrews, rats

3 - including Ambystoma, Rana, salamanders, tadpoles

4 - including crabs, shrimp

5 - including aquatic insects, flies, moths, butterflies, dragonflies

6 - including horn-pouts, pickerel, suckers, shiners, chubs, black bass, herrings, whiting, cummers

Table 2: Feeding behaviours of the Great Blue and Black-crowned Night Herons

	Black-crowned Night Heron	Great Blue Heron
Stand and Wait	*	*
Bill Vibrating	Kushlan 1973a	
Standing Flycatching		Audubon 1840
Walk Slowly	*	*
Wing-flicking		Meyerriecks 1960, 1962
Hovering	Meyerriecks 1960b	Kushlan 1976
Plunging	Kushlan 1973b	Dickinson 1947
Feet First Diving	Kushlan 1973b	Bent 1926
Swimming Feeding	Kushlan 1973b	Bent 1926

* commonly reported behaviours

Table 3: Techniques of feeding favoured by some fish-eating birds

	Ring-billed and Herring Gulls	Caspian and Common Terns
Piracy	++	+
Dipping	++	++
Pattering ¹	+	
Surface-seizing	++	
Scavenging	++	
Plunging	++	+++
Pursuit-diving ²		
Bottom feeding		

+ minor importance

++ moderate importance

+++ major importance

(after Ashmole 1971)

¹ using feet to agitate water

² wings not in use for propulsion through water

Table 4: Food habits of the Ring-billed Gull
and Herring Gull of the Great Lakes

Fish Species	Number and Percent of Sample					
	Lakes Huron and Michigan		Lakes Erie and Ontario			Lakes Huron and Michigan
	1963 - 1965 ¹		1963 - 1967 ²			1971 ³
	RBG	HG	RBG	RBG	RBG	RBG
Alewife	265 (70)	298 (83)	527 (71.4)	7 (12)	110 (33)	138 (20)
Smelt	69 (18)	35 (10)	147 (20.1)	52 (87)	223 (67)	186 (27)
Yellow perch ⁴	5 (1.3)	10 (3)	5 (0.8)	0	0	0
Stickleback ⁵	0	0	0	0	0	344 (50)
All others ⁶	36 (10.7)	15 (5)	51 (7.7)	1 (1)	0	21 (21)
Total No.	372	358	730	60	333	689 ⁷

¹ Ludwig 1966

² Ludwig 1974

³ Jarvis and Southern 1976

⁴ Perca flavescens

⁵ No species specified

⁶ For Ring-billed Gull includes: gizzard shad (Dorosoma cepedianum), brook stickleback (Culaea inconstans), nine-spine stickleback (Pungitius pungitius), rock bass (Ambloplites rupestris), white sucker (Catostomus commersoni), crayfish; for Herring Gull: sunfish (Lepomis spp.), rock bass, mudpuppy (Necturus spp.), meadow vole (Microtus pennsylvanicus), duckling, Red-winged Blackbird (Agelaius phoeniceus), crayfish.

⁷ This is the total number of fish recorded for a total of 232 samples. As individual frequencies given did not agree with the percent of sample by frequency of occurrence, actual numbers were calculated using this total (689) and the percent values in the right column.

