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CORRECTION FACTORS FOR DIGESTION RATES FOR PREY TAKEN BY SNOW BUNTINGS (*PLECTROPHENAX NIVALIS*)

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A major bias in studies of stomach contents of birds results from differences in digestion rates of various kinds of prey, such that proportions of some food items are underestimated or overestimated (Hartley 1948, Dillery 1965, Goss-Custard 1969, Swanson and Bartonek 1970). To account for such differences, some investigators have applied correction factors in their assessments of diet composition. Goss-Custard (1969) adjusted values of two dietary items (a soft crustacean, *Corophium volutator*, and a shelled gastropod, *Hydrobia ulvae*) found in stomachs of the Redshank (*Tringa totanus*) according to their relative occurrence in stomach versus esophagus. The method appears useful for the most abundant prey items; however, its applicability to uncommon or rare items is weak unless very large samples of birds are taken. Mook and Marshall (1965) attempted to find differences in digestion rates of spruce budworm (*Choristoneura fumiferana*) larvae and pupae fed to Olive-backed Thrushes (*Catharus ustulatus*) by sacrificing birds at specified time intervals after they had been fed known food items. Swanson and Bartonek (1970), studying the Blue-winged Teal (*Anas discors*), concluded that the solution to the problem of differential digestion of stomach contents is simply to use only esophageal samples taken from actively feeding birds. Because of the large esophageal capacity of ducks, this seems reasonable for that group. However, for small passerine birds, whose stomachs hold relatively few items and whose esophagi are often empty, investigation of correction factors by Mook and Marshall's method is made necessary to arrive at an adequate sample size. Existing data on this problem are good for ducks (Swanson and Bartonek 1970), but otherwise they are meager in both variety of avian species studied and types of prey represented in their diets.

In this paper we attempt to develop correction factors for different prey items in the diet of the Snow Bunting (*Plectrophenax nivalis*), using the technique of Mook and Marshall (1965). The primary motive for this study was to obtain correction factors that could be used in dietary studies already completed for the Lapland Longspur (*Calcarius lapponicus*). Buntings were chosen to avoid conflict with ongoing studies of local longspurs and because the diets of these closely related emberizine finches are so similar. Both species are primarily granivorous on wintering grounds, but take both seeds and invertebrates during the breeding and molting seasons. Reviews of longspur and bunting diets are given by Williamson (1968) and Parmelee (1968), respectively. Because the diet of the finches studied is relatively catholic, we hope that the results will have significance also for studies of stomach contents of fringillids in general.

METHODS

This study was carried out at the Naval Arctic Research Laboratory, Barrow, Alaska, during June and July 1973. Twenty male buntings were trapped, using four-celled Glenhaven sparrow traps baited with commercial bird seed. The birds were immediately brought into the laboratory and force-fed known numbers and sizes of prey items collected near the laboratory (fig. 1). General background on the invertebrate fauna of the Barrow area is given by MacLean and Pitelka (1971) and on the seed-producing flora by Wiggins and Thomas (1962).

Types of prey used were selected on the basis of availability and known occurrence in the diet of the bunting. Except for tests involving millet seeds where pure samples of a single item were used, each bird was fed a variety of items. Prey items in the stomachs of experimental birds not part of the force-fed meal were ignored. Force-feeding proceeds easily and does not lead to bias in results since intact bodies of larvae and other invertebrates are regularly to be found in both esophagus and stomach of these finches. After force-feeding, the birds were confined to a darkened chamber and sacrificed after selected five-minute intervals. The stomachs were removed immediately and analyzed for contents. An item was recorded as "present" when remains allowed a count of the original number of individuals ingested (e.g., by wings, head capsules, or tarsi); an item was recorded as "trace" when remains revealed occurrence but not number of individuals ingested (e.g., fragments of elytra).

In this study we did not use a standard combination of food items; that is, we thereby assumed that the diet composition does not influence the digestion rate. This may be dubious, but because stomachs of each experimental bird, when force-fed, already contained some seeds and occasionally invertebrates consumed before experimentation, we consider that the experimental diets were exposed to the usual variability of stomach contents.

RESULTS

Results are summarized in figure 1. Different food items fed buntings remained distinguishable in the stomach for variable times. The small seeds of a native biennial crucifer, *Cochlearia officinalis*, could be recognized over 150 min after ingestion, and large commercial millet seeds remained in the stomach well
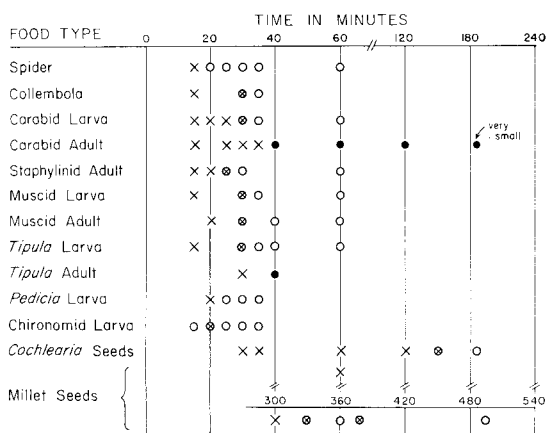
FIGURE 1. Summary of food types and their disappearance rates. Symbols denote results as follows: X alone, all individuals of particular prey type still recognizable; X circled, only some individuals recognizable; solid circle, only trace recognizable; and open circle, no trace.

TABLE 1. Disappearance times and correction factors for prey items of the Snow Bunting.

Food type	Disappearance time (in min)	Correction factors	
		Cochlearia seeds	Carabid beetles
Small (Cochlearia) seeds	150	1	—
Carabid adults	38	3.9	1
Tipula adults	35	4.3	1.1
Collembola	30	5.0	1.3
Carabid larvae	30	5.0	1.3
Muscid larvae	30	5.0	1.3
Muscid adults	30	5.0	1.3
Tipula larvae	30	5.0	1.3
Staphylinid adults	25	6.0	1.5
Pedicia larvae	23	6.5	1.6
Chironomid larvae	20	7.5	1.9
Spiders	18	8.3	2.1

over 300 min; but all invertebrate material became uncountable, or even unrecognizable, after 40 min. Numbers of carabid beetles were usually determined by head parts, which remained recognizable up to 35 min. Though elytra remained qualitatively recognizable for over 180 min, they began to fragment relatively quickly, while head parts were still countable; they could not be used to estimate numbers of individuals ingested. Spiders disappeared after 20 min. A detailed summary of results with individual birds and their food intake is obtainable from the authors upon request.

As figure 1 shows, for each food type there was a regular pattern in time span taken by the digestive breakdown. It is encouraging that the only conflicting result among the arthropods is that shown by chironomid larvae. Three larvae after 15 min were not present in the gut; however, after 20 min, one of two larvae was detected in another bird. We believe the discrepancy in this case results simply from the size of larvae used: the one undigested larva was large (8 mm), whereas the other larvae were small (5 mm gone after 15 min, 6 mm after 20 min). Swanson and Bartonek (1970) also found a relative consistency in digestion rates.

To arrive at correction factors for the various prey types, we use "disappearance time," which is defined here as the time period at the close of which a particular kind of item is barely detectable, with some individuals of a given lot or sample still being recognizable, others not (table 1). Correction factors are derived by dividing the disappearance times of seeds or beetles by the disappearance time of other food items. Thus, for spiders actually present in the gut to be comparable in dietary representation with the number of seeds, spiders should be multiplied by a factor of 8.3. Similarly, to correct the number of spiders in relation to number of beetles, spiders should be multiplied by a factor of 2.1.

A complication may result if size variability of a particular item is strong. Thus, small larvae may pass into the stomach quickly, larger larvae of the same kind may proceed down the esophagus slowly and even appear to be temporarily wedged. This was

witnessed in a few of the experimental birds sacrificed after short digestion intervals.

DISCUSSION

Data in the literature for different bird species are conflicting with regard to minimal time for digestion of specific types of prey. In this study, soft-bodied items remained in the gut at least 15 min and up to 30 min. Similarly, in one Jackdaw (Corvus monedula), an earthworm, leather jacket, and mealworm were distinguishable after 20 min (Koersveld 1951). On the other hand, Dillery (1965) found that after five minutes, there was no trace of a beetle larva and harvestman fed to a Savannah Sparrow (Passerculus sandwichensis). Also, Turček (1956) reported, in a review of work by Zverov, that mealworms, caterpillars, and earthworms fed to "small insectivorous birds" (presumably passerines) were often unrecognizable in three to five minutes. Swanson and Bartonek (1970) found that after 10 min 100% of the amphipods, 82% of the snails, and 24% of dipterous larvae fed Blue-winged Teal were digested beyond distinction.

Variability in digestion rates within a given species, we believe, is due mainly to the state of the stomach before experimentation. It appears that digestion is more rapid in starved birds. Thus, two spiders fed to a starved bunting were gone from the gut after 10 minutes, whereas they normally remain at least 15 minutes in nonstarved individuals. Additionally, in feeding experiments utilizing starved longspurs, some food items were totally unrecognizable after five minutes. In this study, in contrast to Dillery (1965 and pers. comm.) and apparently also Turček (1956), the buntings had some food in their stomachs just before experimentation. If the experimental teal in Swanson and Bartonek's (1970) work also had ingested grit and "fowl crumble diet" and therefore if their stomachs were full, their digestion rates are high compared to fringillids. At this time, the difference between our results and theirs cannot be further analyzed, but it does suggest the likelihood of differences in digestive physiology between ducks and small passerines.

In other words, to arrive at reasonable correction factors, nonstarved birds should be used, at least in those species in which feeding goes on throughout the day and there is, therefore, usually some fresh food in the gut. Moreover, such birds taken im-

mediately from the field will possess a normal complement of grit in the stomach. Accordingly, we believe that birds used in this study showed normal digestive rates and that the correction factors obtained can be applied confidently in analyses of stomach contents of birds taken in the field and freshly examined.

There are, however, some cautions to be noted. Two basic and necessary assumptions underlying correction factors are that all food items are sampled continuously and randomly. In actuality, however, feeding occurs in bouts and there may be variable selectivity. The seriousness of these assumptions diminishes as the sample of stomachs examined increases. Also, when correction factors are used, we intend that they be applied only to actual stomach content data, with adjustment only for those kinds of items present. We reject the possible implication that, given random take of available food items, one could infer diet composition without specimen clues.

A possible means of testing correction factors resulting from the method used here is to take the most abundant food items and compare results with those obtained by study of the contents of esophagus versus stomach as was done by Goss-Custard (1965). This was not done here because we did not sample buntings on the large scale necessary to perform this test.

Because of the variety of items tested, our work appears to be broader in scope than that of other similar investigations on passerines to date. Nevertheless, it is specific to arctic finches near Barrow, Alaska, and its applicability to other prey items, other avian species, and other habitats should be tested. There is a serious need for dietary analysis pursued with more detailed investigations than ours and carried out on more expendable kinds of birds (e.g., House Sparrows or Starlings). What we have done, along with authors cited above, establishes the importance of applying correction factors in dietary analyses and provides a basis for comparisons by future workers.

SUMMARY

Analyses of stomach contents of birds are complicated by differential rates of digestion and therefore by variable bias according to diet composition. This study was undertaken to develop correction factors for the main prey items ingested by Snow Buntings near Barrow, Alaska, to permit more accurate assessment of diet. Nonstarved buntings were force-fed a variety of food items, they were sacrificed at given time intervals, and their stomach contents were analyzed immediately. It was found that, of the invertebrates used as prey, spiders remained distinguishable the shortest time (18 min) and carabid beetles, the longest time (38 min). Small seeds could be recognized over a much longer time (150 min). Thus, in relation to seeds, correction factors for invertebrates tested ranged from 3.9 to 8.3. Results from similar studies in the literature are compared.

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