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Quantitative Comparison of Two Methods of Assessing Diet of Nestling Skylarks (Alauda arvensis)

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Studies of the diet of nestlings traditionally have been based on direct or indirect methods, corresponding to diet assessment before ingestion (e.g. observations or collection of prey fed to chicks) or after ingestion (e.g. analysis of crop contents, feces or regurgitants). The actual approach adopted often depends on circumstances, and the welfare of the birds involved is an increasingly sensitive issue to be taken into consideration. We present a comparison of a direct and an indirect method, one potentially much more dangerous to the chicks than the other.

The first method involves the use of neck collars on chicks, which prevent chicks from swallowing the food that they have been fed by their parents, thereby allowing the collection of the food before digestion. It has been applied by several authors (Orians 1966, Jenny 1990, Poulsen 1993) and, clearly, is invasive. The primary limitation of using neck collars is the very short period during which the collars are safe to use. For example, Skylarks (*Alauda arvensis*) younger than four days may be hurt by the physical handling involved when placing the collar around the neck and, after seven days, the chicks risk fledging with collars still attached (Orians 1966, Jenny 1990).

The second method is the much safer and noninvasive one of fecal analysis (i.e. collection and analysis of chick feces), which has been applied to gamebirds (Gray Partridge, Perdix perdix [Green 1984]; Red-legged Partridge, Alectoris rufa [Green 1984]; Ringnecked Pheasant, Phasianus colchicus [Hill 1985]), and small passerines (House Martin, Delichon urbica [Bryant and Westerterp 1981]; Pied Wagtail, Motacilla alba yarrelli; Yellow Wagtail, Motacilla flava flavissima [Davies 1976, 1977], and Skylark, Alauda arvensis [Rjabow 1968, Green 1978, 1980, Jenny 1990, Poulsen 1993]). The most serious problem related to fecal analysis is that of differential digestion, whereby the proportion of certain prey items in the diet is either under- or overestimated according to the particular item's relative digestibility (Hartley 1948, Owen 1975, Ralph et al. 1985). We compare the diet composition of nestling Skylarks assessed from analyses of feces and from food samples obtained by neck collars, collected from the same chicks at similar times.

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Study area and methods.—Our field study was conducted in arable farmland in southern England on the borders of Dorset and Hampshire (51°10'N, 1°40'W) from mid-April until mid-July 1992. The samples were collected from nests in fields of three different areas and in three different habitats, each area containing at least two habitats. Feces were collected from, and neck collars applied to, the same nestlings. Comparable pairs of diet samples were obtained by applying the neck collars at midday visits for no longer than 1 h, then collecting feces 2 to 4 h later. Taking into account the time it took for food to pass through the gut, this ensured that the pairs of samples corresponded approximately to the same time of day.

Neck collars were successfully applied to 32 chicks from 12 nests, of which 4 were in spring barley, 4 were in silage grass, and 4 were in set-aside (arable land taken out of production, covered in naturally regenerated vegetation). The method was based on Orians (1966) and Jenny (1990), and applied to chicks four to seven days old. Collars were made of waterproof cotton yarn (ca. 1 mm in diameter) made into a loop by tying a clove-hitch knot (this particular material was used after preliminary field trials with other more absorbant materials had been unsuccessful). The size of the loop was easily adjusted by pulling on the loose end of the knot. The loop was carefully laid around the neck of the chick, which could still breathe unhindered, but was unable to swallow food. After one to two food deliveries by the parents, or at most after 1 h, the food was carefully removed from the mouth and esophagus of the chick, and the neck collar removed. As compensation for the removed food, one to two mealworms (flour beetle larvae, Tenebrio molitor) from a laboratory culture were fed to the chicks. Flour beetles are easily recognizable in the feces (special slide reference material was prepared to aid in identification), and does not occur in the field. Food collected by neck collars consisted of complete insects that had been given to the nestlings intact, except for large carabids whose elytra often had been removed by the parent.

When handled, the nestlings usually defecated in the hand and most of the feces were obtained by holding a vial immediately under the chick. The feces remained intact and individually separable when kept in preservative (96% ethyl alcohol). They contained arthropod fragments and sometimes insect eggs. Fragments of insect cuticle were well preserved in the feces, and these were identified following Moreby (1987) and using two types of reference collections: (a) a photograph reference collection of characteristic parts of available arthropod food items (from pitfall traps); and (b) a collection of insects (in 70% ethyl alcohol) identified to species or genera. The analyses were carried out under a microscope at 25-40× magnification. Ten randomly selected feces were analyzed using specially made slide preparations for analysis at 100× magnification. For each sample, the number of individuals in each taxonomic group was determined by counting numbers of characteristic parts, dividing by the number of parts per individual, and rounding up (Moreby 1987).

To monitor the behavior of the parents feeding the chicks under study, a video camera was placed at the nest, recording the delivery of food to the chicks. Subsequently, the film was studied to determine what the parents did with the food brought back to the nest.

The statistical comparison of diet composition measured by the two methods was carried out using compositional analysis (Aitchison 1986, Aebischer et al. 1993). This technique was chosen because the proportions of individual prey groups in the diet summed to one (i.e. were linearly dependent); compositional analysis specifically recognizes this problem and overcomes it by log-ratio transformation (see below). Being a multivariate technique, it also provides a single test for the comparison and avoids the need for Bonferroni adjustment of probabilities required by multiple testing. Analysis was based on diet composition estimated for nest-days as follows. Samples from all chicks at each nest were pooled for each day that samples were obtained. The diet composition for each of 32 nest-days was given by the frequency distribution of food items across eight taxonomic groups: Diptera (adults only); Hymenoptera (adults only); Carabidae; other Coleoptera (beetles other than Carabidae); larvae (of Lepidoptera, Hymenoptera and Diptera); Hemiptera; Araneae; and others (all other arthropods). For each group, the frequency was expressed as a proportion of the total number of items in the sample. For each nest-day, the proportions describing diet composition summed to one, so were transformed to seven linearly independent log-ratios by dividing the first seven proportions of each sample by the eighth, and taking logarithms of the resulting ratios to normalize their distribution (Aitchison 1986). Let (c_1, c_2, \ldots, c_7) be the log-ratios for a diet sample obtained by using a neck collar, and (f_1, f_2, \ldots, f_7) be those for the paired fecal sample. Under the null hypothesis of no difference between the two methods, $(c_1, c_2, ..., c_7)$ and $(f_1, f_2, ..., f_7)$ belong to the same multivariate normal distribution so that the log-ratio differences (d_1, d_2, \ldots, d_7) where

$$d_i = f_i - c_i$$
 (i = 1, 2, ..., 7) (1)

belong to a multivariate normal distribution with mean (0, 0, 0, 0, 0, 0, 0). This hypothesis of multivariate zero mean was tested by multivariate analysis of variance (MANOVA; Chatfield and Collins 1980) using SYS-TAT 5 (Wilkinson 1990), and was the multivariate analogue of a paired *t*-test. The pairing removed possible fixed effects of area, habitat, nestling age and nest, the latter in particular being a potential cause of nonindependence among the data.

Results.—No instances were recorded on video of parents eating food intended for chicks when the

	Mean diet tion	t composi- (%)			
	Neck-	Fecal	L	og-ratios ($\bar{x} \pm 1$ SE)	
Diet group	method	analysis	Neck-collar method	Fecal analysis	Differences
Diptera (adult)	5	7	0.398 ± 0.112	0.243 ± 0.098	0.097 ± 0.101
Hymenoptera (adult)	21	19	1.021 ± 0.372	0.677 ± 0.192	0.344 ± 0.198
Carabidae	9	9	0.653 ± 0.220	0.352 ± 0.132	0.301 ± 0.251
Other Coleoptera	19	17	0.978 ± 0.179	0.628 ± 0.190	0.350 ± 0.299
Larvae	18	17	0.954 ± 0.032	0.628 ± 0.092	0.326 ± 0.153
Hemiptera	4	8	0.301 ± 0.251	0.304 ± 0.187	0.003 ± 0.038
Araneae	22	19	1.041 ± 0.392	0.677 ± 0.263	0.364 ± 0.170
Others	2	4	a	_	_

TABLE 1. Diet composition and log-ratios assessed using neck collars and fecal analysis (n = 32). No significant difference between methods was detected.

* "Others" taxonomic group used as denominator in calculating log-ratios.

chicks were wearing neck collars. The mean compositions of the diets measured by neck collars and by fecal analysis and associated mean log-ratios and log-ratio differences, are given in Table 1. The MAN-OVA revealed no significant difference in diet composition measured by the two methods ($F_{1,30} = 0.21$, P = 0.39). In both cases, the bulk of the diet consisted of adult Hymenoptera, other Coleoptera, larvae, and Araneae: 80 and 81% from using neck collars and fecal analysis, respectively.

Discussion .- The lack of detectable differences in the diet composition, for Skylarks, between fecal samples and neck-collar samples is not in accordance with the findings in Johnson et al. (1980). They found, during a study of Gray Catbirds (Dumetella carolinensis) and Brown Thrashers (Toxostoma rufum), quantitative differences in the amount of food delivered when neck collars were and were not applied. With neck collars in use, feeding frequency was reduced because the collars prevented the chicks from begging for food from their parents, resulting in part of the food intended for the chicks eaten by the parents instead. No incidence of this was recorded in our study. Johnson et al. (1980) also stated that small insects may pass through the esophagus when the neck collar is in place. Either this did not occur in our study, or else the effect was negligible and produced no detectable bias. The same held for the problem of differential digestion and its effect on the contents of the fecal samples (Hartley 1948, Owen 1975), possibly because passage through the gut is relatively quick in Skylark nestlings (O'Connor 1984).

In conclusion, it appears that for Skylarks the indirect, noninvasive method of fecal analysis produces the same assessment of nestling diet composition as the direct, but invasive, neck-collar method. Given the risks of using neck collars, we recommend fecal analysis as the sampling method in future research on this species.

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Sunning by Black Noddies (Anous minutus) May Kill Chewing Lice (Quadraceps hopkinsi)

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Birds are hosts for ectoparasites such as lice (Clayton et al. 1992), mites (Rothschild and Clay 1952, Møller 1993, Clayton and Tompkins 1994), bugs (Brown and Brown 1986, Møller et al. 1994), ticks (Duffy 1983), flies (Shields and Crook 1987, Whitworth and Bennett 1992), and fleas (Oppliger et al. 1994). The possible adverse effects of these ectoparasites are well documented. Infestation can cause a bird to attract fewer mates (Clayton 1990, Johnson and Boyce 1991), increases nest desertion (Moss and Camin 1970, Duffy 1983, Oppliger et al. 1994), lowers hatching success (Clayton and Tompkins 1994, Oppliger et al. 1994), and reduces clutch size (Møller 1993), as well as reduces the survival of nestlings (Møller 1987, Shields and Crook 1987, Richner et al. 1993), fledglings (Clayton and Tompkins 1994), and adults (Borgia and Collis 1989, Clayton 1989). Because ectoparasitic infestation may decrease fitness, avian behavior that minimizes infestation typically has a selective advantage (Møller et al. 1990, Hart in press).

Avian sunning may be a strategy for controlling ectoparasite populations (Dathe 1964, Fry 1972, Horsfall 1984, Simmons 1986, Blem and Blem 1992). Despite decades of interest in this behavior, however, no one has tested the hypothesis that sunning adversely affects ectoparasites (Blem and Blem 1993). We demonstrate experimentally that conditions experienced during normal sunning are lethal to chewing lice, which is consistent with the ectoparasitecontrol explanation of sunning.

Methods.—We studied the sunning behavior of Black Noddies (Anous minutus) at the Heron Island Research Station (HIRS; 23°26'S, 151°55'E) on the Great Barrier Reef of Australia. At this location, Black Noddies sun gregariously on bare sand and on the rooftops of HIRS buildings.

From 30 October through 2 November 1991, we investigated the relationship between sunning activity and temperatures at the sunning site. The typical sunning posture used by Black Noddies is a standing position with tail fanned and one wing extended (Fig. 1). To estimate the thermal environment experienced by a Black Noddy wing during sunning, we mounted thermometers about 6 cm above each of three sunning sites. The thermometers were exposed to the sun and mounted so they could be read from a distance with a spotting scope. The number of sunning noddies and the temperature at each site were noted periodically over two days. Any noddy that alighted on the exposed sunning sites was considered to be sunning. The longest time we observed any individual sunning

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