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A COMPARISON OF THREE TECHNIQUES FOR ANALYZING THE ARTHROPOD DIET OF PLAIN TITMOUSE AND CHESTNUT-BACKED CHICKADEE NESTLINGS

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Abstract.—Photography, fecal sac and gut analysis were compared for their effectiveness in quantifying the composition of arthropod prey in Plain Titmouse (*Parus inornatus*) and Chestnut-backed Chickadee (*P. rufescens*) nestling diets. Photography produced the most quantitative and taxonomic information. Fecal sac and gut analysis were less reliable for quantitative and taxonomic work but were adequate for determining the presence of prey items. Of the prey identified on film, the Plain Titmouse diet contained a large percentage of Lepidoptera larvae (88%), whereas the Chestnut-backed Chickadee diet contained large percentages of pamphiliid sawfly larvae (63%) and rhaphidophorid camel crickets (17%). Lepidoptera larvae and Orthoptera were the most common prey in both the Plain Titmouse fecal sacs and guts, whereas Orthoptera and Hymenoptera were the most abundant prey in the Chestnut-backed Chickadee fecal sacs and guts. Compared with either fecal sac or gut analysis, photography was considered to be the most effective and complete method for determining the diet of cavity nesting young.

COMPARACIÓN DE TRES TÉCNICAS PARA ANALIZAR LA UTILIZACIÓN DE ARTRÓPODOS EN LA DIETA DE PICHONES DE *PARUS INORNATUS* Y *P. RUFESCENS*

Sinopsis.—Las técnicas de fotografía, análisis de los sacos fecales y análisis de contenido estomacal, fueron comparadas para determinar su efectividad en cuantificar la composición de artrópodos como parte de la dieta de pichones de *Parus inornatus* y *P. rufescens*. El método fotográfico produjo la mejor información taxonómica y cuantitativa. El análisis del contenido estomacal y de los sacos fecales, fue menos confiable para análisis taxonómico y cuantitativo, pero resultó adecuado para determinar la presencia de presas particulares. De las presas identificadas en la dieta de *P. inornatus*, las larvas de lepidópteros resultaron ser las de mayor consumo (88% de la dieta), mientras que en la dieta de *P. rufescens* predominaron las larvas de pamfílidos (Hymenoptera) con un 63% y grillos (Orthoptera) con un 17%. Las larvas de lepidópteros y los ortópteros resultaron ser la presa más común en los sacos fecales y los contenidos estomacales de individuos de *P. inornatus*, mientras que los ortópteros y los himenópteros resultaron ser las presas más comunes en los sacos fecales y el tracto digestivo de *P. rufescens*. Al compararse los tres métodos entre sí, la fotografía resultó ser el método más completo y efectivo para determinar la dieta de pichones de aves que anidan en cavidades.

Numerous methods have been used to assess the composition of insectivorous bird diets. Techniques used for passerine birds have included visual observations, emetics, artificial nestlings, ligatures, gut contents, fecal contents and automatic photography (Calver and Wooler 1982, Otvos and Stark 1985, Rosenberg and Cooper 1990, Royama 1970). Such techniques have been useful for assessing nestling and adult nutrition, foraging behavior, inter- and intra- specific competition for food, and the impact of avian predators upon arthropod populations (Cowie and Hinsley 1988, Crawford and Jennings 1989, Tinbergen 1960).

Rosenberg and Cooper (1990) recently reviewed the advantages and

disadvantages of various approaches to avian diet analysis, but their evaluations were based upon previous studies using single methods. Few studies have simultaneously compared the results of more than one technique to quantify the composition of a birds' diet (but see Jenni et al. 1990). Our objective was to compare three methods of quantifying arthropod composition of nestling diets. The study was unique for we used empirical evidence to make a comparison of fecal sac analysis, gut analysis and automatic photography.

We examined the nestling diet of two insectivorous, secondary cavity-nesting birds, the Plain Titmouse (*Parus inornatus*) and the Chestnut-backed Chickadee (*P. rufescens*). Both species coexist in the California coastal oak woodlands (Dixon 1954). Their behavioral interactions have been the subject of previous studies but little has been done on the composition of their nestling diets (Dixon 1954, Hertz et al. 1976, Root 1964, Rowlett 1972).

MATERIALS AND METHODS

The study was conducted on the northeastern slope of the Berkeley Hills in the East Bay Municipal Utilities District, Contra Costa County, California, during the months of April and May, 1988–1990. The slope encompasses mature stands of planted Monterey Pine (*Pinus radiata*), adjacent to stands of Coast Live Oak (*Quercus agrifolia*) woodland. The majority of understory vegetation consists of poison oak (*Toxicodendron diversilobum*) and blackberry (*Rubus ursinus*).

Fifty-three artificial nestboxes were established in this area in 1978 (Gold and Dahlsten 1989). They were randomly placed along a series of trails at intervals of 25–50 m, 1.5 m above the ground. The nestboxes were constructed of sawdust and cement and contained a removable front (Schwegler and Sons, Munich, Germany). The diameter of the nesthole was 33 mm with a box height of 25 cm and diameter of 11.5 cm. Nestboxes were checked weekly from March–May and increased to bi-weekly once egg laying had begun.

During the Springs of 1988 and 1989, we collected fresh fecal sacs from young during routine box checks. Once nestlings were considered old enough to be handled safely (about 8 d) we gently pressed the sides of the cloaca until a sac was produced. The procedure did not always guarantee a sac so we obtained additional fecal sacs when handling nestlings during banding. We considered samples independent as the sacs were collected at variable times and dates throughout each nesting season from a minimum of three nests and with a minimum of 24 h between collections from the same nest. We placed each fecal sac in a small labelled plastic vial.

Nest disturbance due to weather, predation, human interference or unknown factors produced a number of abandoned dead nestlings. We examined the gut contents of the dead nestlings with the understanding that some digestion of gut contents would have continued after death. The nestlings were collected within 24 h of death except for two nestlings

collected within 48 h. Their bodies were frozen 1–2 h after collection and their gizzard and intestines were later removed and placed in vials of 70% ethyl alcohol.

Fecal sacs were thawed and placed in plastic petri dishes (60 × 12 mm). Each sac was teased apart in 70% ethyl alcohol with the hardened nitrogenous wastes removed. All identifiable pieces were sorted, coded and placed in a 1-dr shell vial plugged with cotton. Each shell vial was then was placed in a larger screw cap vial containing ethyl alcohol and unidentifiable material. Gizzard and intestine contents were flushed out with ethyl alcohol and treated as above.

We identified arthropod body parts to the lowest taxonomic level possible. Identifications were made by comparing samples to insect parts from a reference collection and to references in the literature (Borror et al. 1981, Essig 1926, Furniss and Carolin 1977, Peterson 1948, Ralph et al. 1985). Identifiable parts were then matched to approximate the number of insects occurring in each sample (i.e., 2 Lepidoptera mandibles = 1 larvae, 3 cicada legs = 1 cicada). As the majority of insect pieces were too fragmented to be counted and identified to Order, we calculated percent composition of the contents from the identifiable material only (Table 1). These percentages are not true representations of the diet composition of Plain Titmouse and Chestnut-backed Chickadee nestlings but are proportions of the identified material that remained intact throughout the digestive process. Extraneous material was noted but not counted. On average it took 30–60 min to process each individual fecal or gut sample. This was dependent upon observer experience and amount of contents. A 2 × 5 contingency table (χ^2 test $\alpha = 0.05$, Statview II, Abacus Concepts, Inc.) was used to compare relative frequencies of the prey Orders (Orthoptera, Homoptera, Lepidoptera, Hymenoptera and other Orders (in total less than 12%)) among the two methods.

To assess adequacy of sample size of numbers of fecal sacs and guts, we used a method for estimating prey diversity described by Pielou (1975) and applied to stomach analysis by Sherry (1984). We randomized the individual fecal sac or gut samples within our 1988–1990 collections for each species of bird. We then calculated the diversity of prey in each individual fecal sac or gut starting with sample 1, then pooled the contents of each successive sample 1 and 2, then 1, 2, and 3 and so on up to the total number of samples in the collection. We used the Brillouin diversity index (H) at each step: $H = (1/N)\ln(N!/n_1!, n_2! \ldots n_t!)$ where there are $n_1, n_2 \ldots n_t$ prey items in each of x different prey categories (insect Orders), with N total prey times per cumulative sample. If enough fecal sacs or guts were collected, saturation curves of prey diversity would result in plateaus at X number samples because additional gut or feces would add little dietary information to increase prey diversity.

We obtained photographs with a camera box recording apparatus patterned after Royama (1970). Each nestbox was fitted with a Minolta® super 8 mm movie camera and Vivitar® flash unit placed in the back of the box (Dahlsten and Copper 1979). Photocells were placed on opposite sides of the entrance hole. As an adult entered the box, the photocell

TABLE 1. Percent of arthropod prey from the total of identified prey items in the diet of Plain titmouse *Parus inornatus* and Chestnut-backed Chickadee *Parus rufescens* nestlings (1988–1990).

	Fecal sacs		Guts		Film	
	P. inornatus 3 nests (n = 14)	*P. rufescens* 8 nests (n = 20)	*P. inornatus* 2 nests (n = 10)	*P. rufescens* 2 nests (n = 10)	*P. inornatus* 31 h (n = 1)	*P. rufescens* 300 h (n = 3)
Orthoptera	30	29	16	33	<1	17
Homoptera	<1	13	12	13	<1	6
Lepidoptera	53	10	58	20	88	4
Hymenoptera	<2	36	4	30	<1	63
Other						
Coleoptera	<2	<2	<2	3	0	0
Hemiptera	0	<2	0	0	0	4
Diptera	<2	0	6	0	6	6
Arachnid	0	10	0	0	5	1

simultaneously triggered the flash unit and camera shutter to photograph the adults' beak full of prey. Either a 6- or 12-v battery powered the operation and a small watch indicating time and date was attached near the entrance hole. Each frame of developed film indicated the time and date and the prey item(s) in the adult birds' beak. The camera nestbox apparatus was used to replace the initial nestbox when nestlings were approximately 8 d old. From experience we have found that transferring Chestnut-backed Chickadee nestlings at an earlier age results in nest abandonment by the adults.

We reviewed developed movie film through a dissecting scope. Prey items were identified from comparisons with photos, reference insects and the literature (Borror et al. 1984, Essig 1926, Furniss and Carolin 1977). Prey items were counted according to the number and category brought in each trip every hour, each 14-h foraging day. Percent abundance of each prey category was then calculated by hour, nestling age and complete filming period. It took approximately 10–20 min to review 1 h of film time. This period was dependent on the reviewer's experience and the frequency of adult bird trips to the nest (# of adult trips = number of frames with prey items).

During 1989, arthropods were collected weekly to create a reference collection for comparative identifications. We removed arthropods from foliage and small branches with pole pruners, beating procedures, and by hand. The majority of arthropods were pinned or placed in 70% ethyl alcohol. Soft bodied larvae were photographed and then reared to adults.

RESULTS

We obtained a total of 14 Plain Titmouse fecals sacs from three nests during 8, 15–20 Apr. 1988, 12 Chestnut-backed Chickadee fecal sacs from four nests during 13, 29 Apr. 1988, and 8 fecal sacs from four nests

during 13–23 May 1989. Nestlings were 9–20 d old. We also collected 11 Plain Titmouse guts from two nests during 12–23 Apr. 1988 and 10 Chestnut-backed Chickadee guts from two nests on 15 May 1988 and 1989. Nestlings were 9–22 d old.

Results from our analysis of sample size adequacy (no. of fecal sacs or guts) differed for each species and method (Fig. 1). Saturation curves for prey diversity plateaued between seven and 10 pooled samples for both Chestnut-backed Chickadee guts and Plain Titmouse fecal sacs. Rate of change of the saturation curves for both Chestnut-backed Chickadee fecal sacs and Plain Titmouse guts differed little in the proximity of 10 samples but appeared to be climbing steadily rather than reaching a plateau.

We obtained 31 h of film from one Plain Titmouse nest during 9–11 Apr. 1988. The nest contained six nestlings, 9–12 d old. In 1989, we did not obtain film on Plain Titmice. We attempted to film three nests, but two nests were abandoned by the parents and the third was lost to predation. We did not obtain film of Chestnut-backed Chickadee nests in 1988. Attempts were made to film three nests, but film was lost due to technical difficulties and parental abandonment.

During 1989–1990 we obtained a total of 300 h of film from Chestnut-backed Chickadee nests. We obtained 110 h of film during the 14–25 May 1989 for nestlings 10–13, 16, 17, 20 and 21 d old (Nestbox 34) and 112 h of film during the 12–19 May 1989 for nestlings 10–17 d old (Nestbox 36). We suspect as evidenced from visual observation, film and lack of nest sanitation that box 36 was raised by one adult whereas box 34 had two adults. Box 36 also experienced nestling mortality from an initial five nestlings to two fledglings. A third Chestnut-backed Chickadee nest had been equipped with a camera but failed due to parental abandonment. In 1990, we recorded 78 h of film from one Chestnut-backed Chickadee nest during 11–17 May. It contained seven nestlings, 11–16 d old. Parents of all nests were recorded bringing in prey on average 14 h a day from 0.600 to 2000 hours.

Though several hours of film and prey records were obtained from each nest, we did not consider three nests a representative number of samples for statistical comparison with either fecal sacs or guts. Instead, we used the film as a baseline for interpretation because it was a record of every prey item brought to an individual nest over a specified time.

Pooling the Plain Titmouse fecal sacs and guts separately, we identified 54 prey to Order in the fecal sacs and 108 prey to Order in the guts. In our photographic analysis, Plain Titmouse adults brought a total of 730 prey to the nest. Approximately 620 of these prey were identified to Order and more than half of these were green larvae not identifiable to species but likely one of the following: Noctuidae, unknowns and *Cosmia calani*; Geometridae; Plutellidae, *Ypsolopha cervella*; Tortricidae, *Epinotia emarginana, Pseudexentera habrosana* and *Decodes fragarianus*. The remainder of the items were mostly geometridae larvae belonging to the genus *Hydriomena*. These are probably *H. nubilofacicatus*, which were commonly found on Coast Live Oak.

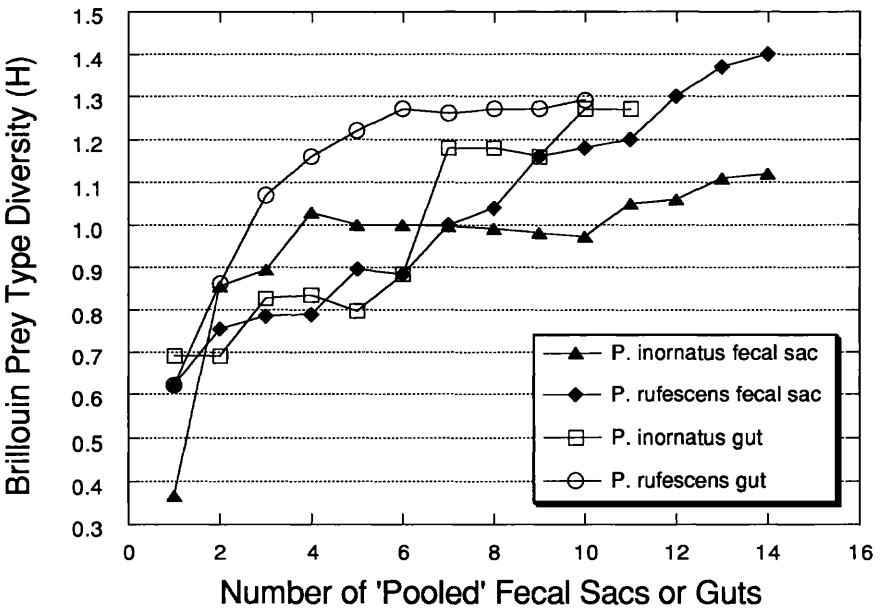

FIGURE 1. Diversity of prey items (H) in the fecal sacs and guts of Plain Titmouse *Parus inornatus* and Chestnut-backed Chickadee *P. rufescens* nestlings.

Lepidoptera accounted for the majority of the identified contents in the Plain Titmouse fecal sacs (53%), guts (58%) and film (88%) (Table 1). The frequency of all prey orders did not significantly differ between the fecal sac and gut analyses (2 × 5 Contingency table, $\chi^2 = 6.36$ df = 4, $P > 0.05$).

In the diet of the Chestnut-backed Chickadee, we identified 86 prey in the feces and 32 prey in the guts. From the film of the Chestnut-backed Chickadee nests, approximately 6212 prey were identified from a total of 7239 items brought to the nests. The frequencies of prey did not differ among the fecal sac and gut analyses (2 × 5 Contingency table, $\chi^2 = 3.1$, df = 4, $P > 0.05$). Within each of the methods, Hymenoptera (36%) accounted for the largest proportion of prey in the fecal sacs, while Orthoptera (33%) comprised the largest proportion in the gut. *Acantholyda* sp. (Hymenoptera: Pamphiliidae) comprised the majority (63%) of prey on film. A smaller percentage (17%) of the prey were Orthoptera, a majority of which were the tree camel cricket, *Gammarotettix bilobatus* (Orthoptera: Rhaphidophoridae) (Table 1). The majority of contents in all fecal sacs and guts for both species was uncounted fragments of exoskeleton, leg segments, eggs, setae, spiracles, vegetable material and pebbles.

In addition, we did find a significant difference in the frequency of prey orders between the Plain Titmouse fecal sacs and Chestnut-backed Chickadee fecal sacs (2 × 5 Contingency table, $\chi^2 = 33.2$, df = 4, $P <$

0.05) and between the Plain Titmouse guts and Chestnut-backed Chickadee guts (2×5 Contingency table, $\chi^2 = 24.5$, df = 4, $P < 0.05$).

DISCUSSION

Our results show that there is little difference between fecal sac and gut analyses for determining proportions of insect Orders in Plain Titmouse and Chestnut-backed Chickadee nestling diets. Both methods are adequate for detecting the presence of particular prey when identifiable prey structures remain intact; however, the methods are less desirable for complete and precise taxonomic identification and quantitative composition of a birds' diet. Estimates of prey abundance from nestling feces and guts are unreliable because both methods entail dissection and identification of arthropod pieces and rough estimations of prey abundance from matching pieces of prey. Furthermore, individual nestling diets may differ because food intake is controlled not only by the amount of prey brought by the parent but also by the aggressiveness of the nestling. Gut and fecal contents represent a bird's recent dietary intake obtained over an unknown period, unless fecal sacs are collected from a known individual after every parent's delivery of prey (Hespenheide 1971). Also the diet contents are biased toward prey items such as mandibles that remain intact (Jenni et al. 1990, Ralph et al. 1985). Mandibles are convenient to count because they are schlerotized and less likely to disintegrate during the birds digestive process. Using items such as Lepidoptera or Hymenoptera larvae mandibles for prey abundance estimates may be a problem, however, as some adult birds have been observed to decapitate distasteful prey before feeding them to their young (Dahlsten and Herman 1965).

Given the similarity of results from the two methods, we recommend fecal sac analysis rather than gut analysis. Fecal sacs are easily obtained and are of little risk to nestling survival, whereas gut analysis requires killing nestlings. Digestive rates also differ between individuals and digestion of gut contents may continue after death, a factor not controlled in our study (Koersveld 1950). In addition, fecal sacs are advantageous in that samples from the same individuals may be collected through time.

Sherry (1984) suggested that 10 stomachs is an adequate sample size for diet analysis of neotropical flycatchers. Our results indicate that 10 guts or fecal sacs were adequate for analysis of Chestnut-backed Chickadee guts or Plain Titmouse fecal sacs, but that more than 10 samples should be collected for Chestnut-backed Chickadee fecal sacs or Plain Titmouse guts. We are skeptical of such variable results for both methods, which raises the topic of appropriate sampling size and unit. To avoid problems of independence in samples collected from the same nest (i.e., parents favoring particular prey), it may be better to have individual nests serve as individual sampling units with an adequate number of fecal sacs collected from each nest within designated time periods.

In comparison with both fecal sac and gut analysis, we found photography to be a more thorough method for the diet analysis of Plain Titmice

and Chestnut-backed Chickadees. We obtained a complete record of all prey delivered to individual nests during the filming period. Time spent analyzing film was tedious; however, 1 h of film review was equal to several hours of nestling dietary intake.

Unlike fecal sac and gut analysis, a greater number of prey recorded on film can be identified to species and the percentage of particular prey items determined from a total number of items brought over time. We consider identification of arthropods to the family and species level better for quantifying predation and for identification of inter- and intra- specific differences in prey choice. Presence of prey identified to Order or Operational Taxonomic Unit (OTU) would not be as adequate (Otvos and Stark 1985). In addition, film can provide information on other aspects of the birds' biology, such as size of prey loads carried by adults, number of trips over a specified time period, parental sex differences, information on preferences for prey at particular times or nestling age, and prey sequences (Grundel 1984).

The main disadvantages of film analysis are initial expenses of set up and film development, need for constant camera maintenance and limited sample size. Initially, a prototype camera unit with accessories costs between $500.00 and $1000.00 and each roll of film including development averages $15.00. The expense is obvious when considering the number of units necessary to have an acceptable number of samples (nests). Further limits on samples size are due to camera failures and nest abandonment. We found some adult birds to be sensitive to the photographic units and abandon a nest within 24 h. As with the collection of fecal sacs, we recommend obtaining several hours of film from as many nests as is feasible within a designated time period.

In both the Plain Titmice and Chestnut-backed Chickadees, the largest percentages of prey recorded on film were also the largest percentages found in both fecal sacs and guts with the exception of Orthoptera in Chestnut-backed Chickadee guts. In contrast, the film percentages of other prey were less than those estimated for fecal sac and gut analysis. We assume this variability was due to variation in sampling units, methodology or recognition of prey (Jenni et al. 1990). Some of the inconsistencies in the proportions of prey that resulted from the same methods between the two species are explainable. In the Chestnut-backed Chickadee film there was an underestimation of Lepidoptera but in the Plain Titmouse film there was an overestimation of the Order. The latter was assumed to be due to sample size (1 nest, 31 h) or possible decapitation of larvae. The overestimation of Orthoptera in the Plain Titmouse film was possibly due to the early date or shortness of the filming period. The Chestnut-backed Chickadee film also had an underestimation of Homoptera. On film, aphids and immature leafhoppers were in clumps and individuals could not be counted; however, in fecal sacs and gut pieces of individuals could be identified and counted. In contrast, and assuming the film to be more "correct," the birds fed large numbers of *Acantholyda* larvae (63%)

to their young. If we were to base our observations on fecal or gut contents alone a much smaller percentage of *Acantholyda* (identified from mandibles) would have been recorded.

In conclusion, film analysis allowed us to be nearly species specific in description of prey items and quantification of prey brought to a nest over time. It gave us a relatively complete record of what the parents were feeding their young compared to either fecal sac or gut analyses. From our comparisons we recommend photography for analyzing the diet of cavity-nesting nestlings and the use of fecal sacs rather than guts for supplementary information or for when photography is not feasible.

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