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ANALYSIS OF THE FORAGING ECOLOGY OF EUCALYPT FOREST BIRDS: SEQUENTIAL VERSUS SINGLE-POINT OBSERVATIONS

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Abstract. Up to five consecutive prey attacks were recorded for each individual encountered of five species of Australian warblers (Acanthizidae) foraging in eucalypt woodlands near Sydney, New South Wales. A comparison of the first (single-point observations) against all subsequent prey attacks (sequential observations) revealed no significant differences in the use of plant species or foraging heights for the species studied. First observations were biased towards birds foraging in foliage, but the differences between first and subsequent observations were not significant. For all species active prey-attack behaviors (snatch, hover, hawk) were recorded more often on the first than on subsequent observations. However, only a few of these differences were significant: White-throated Warblers (*Gerygone olivacea*) snatched more often ($P < 0.005$), Little Thornbills (*Acanthiza nana*) gleaned less ($P < 0.02$) and hawked more often ($P < 0.02$), and Weebills (*Smicrornis brevirostris*) hovered more often ($P = 0.054$) on the first than the second observations. Differences between the first and subsequent observations were greatest for the more active species [White-throated Warbler, Weebill and Buff-rumped Thornbill (*A. requloides*)] and least for the less active Striated (*A. lineata*) and Little Thornbills. The differences between first and subsequent prey attacks were insufficient to affect interpretations of resource use or of possible interactions between species. Other than for foraging height, where samples of 110–120 individuals were necessary, observations of 60–70 individuals were required to stabilize sample variances of the foraging behaviors of all species, irrespective of the number of consecutive prey attacks recorded. At least for open habitats this suggests that it is necessary to record only one prey attack for each individual encountered. These estimates of minimum sample sizes generally fell within the range required for 90–95% confidence intervals. Greater precision requires much larger samples.

Key Words: Sequential observations; single-point observations; foraging ecology; sample size; prey-attack behavior.

Studies of the foraging ecology of birds usually employ one of two methods: single-point or sequential observations. With single-point observations only one set of data, usually obtained at the first sighting of the bird or whenever it first performs the behavior being studied, is recorded for each individual encountered (e.g., Hartley 1953, Morse 1970). Sequential observations require the bird to be followed and data recorded continuously (e.g., Hertz et al. 1976) or at intervals (e.g., Morrison 1984a). Most observers employing sequential sampling procedures have well-defined rules for stopping and starting which specify minimum and maximum periods of observation (e.g., Morrison 1984a, Recher et al. 1985).

A decision as to which method to use may largely depend on the hypotheses being tested and the ease of studying the birds in question (Bradley 1985). It is also necessary to have information on the extent to which observations may be biased by conspicuous behaviors, the importance of inconspicuous or uncommon events, and the minimum sample sizes required for an acceptable level of precision (Wagner 1981a, Morrison 1984a). Few studies have presented data comparing the two methods (Wagner 1981a, Franzreb 1984, Morrison 1984a) and only Morrison (1984a) has suggested a minimum sample size. These studies are from North America and compare closely related or ecologically similar species.

As part of a study of the foraging ecology of Australian warblers (Acanthizidae) in eucalypt woodland near Sydney, New South Wales (Recher 1989 b), data were recorded for up to five consecutive prey-attacks for each individual encountered. Data were obtained for five species of three genera which differed in their use of substrates, foraging height distribution, and prey-attack behavior (Recher 1989 b). In this paper we compare interpretations of the behaviors of these species based on the first recorded observation (single-point method) to interpretations based on all and subsequent observations (sequential method). Minimum sample sizes required for analysis are also examined.

METHODS

STUDY AREA

The foraging ecology of Australian warblers was studied during 1984 on a 25 ha plot located within a large block (ca. 400 ha) of regrowth eucalypt forest at Scheyville, 40 km northwest of Sydney, New South Wales. The study site was dominated by narrow-leaved ironbark (*Eucalyptus crebra*) (42% of eucalypt foliage) and grey box (*E. molluncana*) (50% of eucalypt foliage). Other plant genera were absent from the canopy and understory. Blackthorn (*Bursaria spinosa*) (>98% of shrub foliage) dominated the shrub layer. Ground vegetation was dominated by exotic grasses and herbs. Total tree canopy cover was 40–45% with the tallest trees emerging to 25 m from an average canopy height of 14–18 m. Patches of dense sapling regrowth of both eucalypts occurred throughout the plot.

The study area was flat and forms part of the Cumberland Plain, an extensive area of low to undulating terrain west of Sydney. Soils in this area were primarily derived from shale formations. The area receives about 775 mm of rain annually with a tendency for spring (August–October) to be drier and for summer (December–March) to be wetter than other months. Summers are hot (January mean maximum 30°C) and winters are mild (July mean minimum 3°C). Recher (1989 b) provided additional details of the plot.

Data were obtained for five species of birds: Little Thornbill (*Acanthiza nana*), Striated Thornbill (*A. lineata*), Buff-rumped Thornbill (*A. reguloides*), Weebill (*Smicrornis brevirostris*), and White-throated Warbler (*Gerygone olivacea*). All foraging data were collected by H. Recher. He recorded up to five prey-attacks for each bird encountered. Most birds were located visually.

Where birds occurred in either single- or mixed-species flocks, data were recorded for as many individuals as possible without repeating observations on the same birds. Generally this meant that fewer than half the birds present in the flock were recorded. Although it is likely that some of the same individuals were observed on more than one occasion, observations were made on different parts of the study site on successive days to reduce the duplication of observations on the same individuals.

As it was not always possible to determine success, all prey-attacks were recorded irrespective of whether or not they were successful. Bird species, type of prey-attack behavior (e.g., glean, snatch, hawk), foraging height, substrate of prey, and plant species, where appropriate, were recorded for each observation. These are the same procedures used by Recher et al. (1985). Prey-attack heights were estimated to the nearest meter and later grouped into height categories (0–0.1 m, 0.1–2 m, 2.1–8 m, >8 m) corresponding to ground, shrub, understory, and canopy vegetation layers.

Observations were made during spring (September–November), summer (January–February), autumn (April–May) and winter (July–August). With the exception of spring, when observations were made over a 6-week period, seasonal data were collected during a 2-week period with most data obtained on 4–6 mornings of fieldwork (20–30 hours). Observations generally began within an hour of sunrise and ceased at 11:00–12:00 EST. Additional details are in Recher (1989 b).

DATA ANALYSIS

We compared the proportions of different foraging behaviors for the first recorded prey-attacks to the proportions for all foraging sequences (i.e., the first through the fifth prey-attack) and also to those calculated from foraging sequences where the first observation was deleted (i.e., the second through the fifth prey attack). The comparison was performed as follows. Suppose prey-attack heights for 0–0.1 m are being considered. Then, for each bird of each species, we calculate the proportion of times the bird is present in the 0–0.1 m height range. An overall or average proportion of birds for the species in this height range may then be obtained. We next calculate the proportion of birds present in the 0–0.1 m height range using the first observation only. If there is no bias in the observation, then this proportion should be substantially similar to that calculated using all the observations. A formal statistical test such as the chi-squared test may then be employed. When the data compared are in terms of proportions, the chi-squared test is identical to a two sample t-test. Each behavior or foraging category was tested separately.

As the inclusion of observations where only a single prey-attack was recorded may influence the results towards conspicuous behaviors, the data were re-analyzed using only sequences where two or more prey-attacks were recorded and the proportions of foraging behaviors recorded for the first observation tested against proportions recorded for the second.

Small changes in the standard error (SE) of the population mean can be used as a simple estimate of minimum sample sizes beyond which further observations provide little additional information relative to the "cost" of obtaining more data. To estimate the SE's of different sized samples (n) (at increments of 5), we assumed the proportion (P) of each foraging parameter for the total sample approximated the proportion (p) for all sample sizes (i.e., 5, 10, 15, . . . n). This is justified by the large sample sizes available for each species. The SE of p was then calculated from

$$\mathrm{SE}(p) = \sqrt{\frac{PQ}{n}}$$

when n is large (i.e., $nP > 5$, $nQ > 5$), $Q = (1 - P)$: "When P is the underlying proportion, the sample p is approximately normally distributed with mean P and standard error" (Fleiss 1981:13).

As in other analyses, the first recorded observation was used to estimate sample sizes for single-point observations. For sequential observations the mean value for each foraging category was calculated for each foraging sequence and these values used to estimate the proportion (P) for each foraging category. In this instance, P is a weighted average of the proportion of each foraging parameter. A weighted average is preferred as sequential observations are not independent. Thus, for example, we could not observe one bird five times, another three times, and a third once and say we had nine individuals. All observations were used including individuals for which only a single prey attack was recorded. Only sequential data were used in calculating SE's for foraging height data. In this instance SE's were calculated progressively from the field data.

RESULTS

SINGLE-POINT VERSUS SEQUENTIAL SAMPLES

There were seasonal differences in foraging behavior (Recher, 1989 b) and the proportions of behaviors in each foraging category for single-

TABLE 1. COMPARISON OF FORAGING DATA, OBTAINED BY SINGLE-POINT (A) AND CONTINUOUS OBSERVATIONS (2–5) (B) OF AUSTRALIAN WARBLERS (ACANTHIZIDAE)

Species	Little Thornbill		Striated Thornbill		White-throated Warbler		Buff-rumped Thornbill		Weebill	
Method	A	B	A	B	A	B	A	B	A	B
No. individuals	324	200	421	209	84	39	160	110	252	168
No. prey attacks	324	758	421	790	84	207	160	450	252	653
Prey-attack behavior (%)										
Glean	61.7	66.5	40.1	46.3	34.1	43.5	63.7	75.6	28.9	33.7
Hang-glean	2.5	2.4	36.7	33.5	0	0	0	0	4.4	9.8
Hover	11.1	10.9	12.3	12.0	7.1	12.1	16.2	13.3	53.6	42.3
Snatch	19.4	15.3	9.0	6.3	51.8	37.5	13.7	3.6	11.1	12.2
Hawk	5.2	4.9	1.8	1.8	7.1	6.9	6.3	7.6	2.0	2.0
Substrate (%)										
Foliage	80.8	76.5	90.3	87.2	89.5	86.6	53.1	41.8	94.8	92.6
Bark	13.9	18.0	7.9	11.0	3.9	2.6	21.3	25.1	2.4	3.5
Ground	0	0	0	0	0	0	17.5	24.0	0	0
Aerial	5.3	5.5	1.8	1.8	7.0	10.8	8.1	9.0	2.8	3.9
Plant species (%)										
Ironbark	63.9	65.2	62.8	66.4	48.8	51.7	36.7	33.9	87.1	88.8
Box	23.3	19.9	29.3	27.4	39.0	38.6	27.3	26.9	9.5	8.3
Other eucalypts	7.5	7.3	7.9	6.2	12.2	9.7	5.1	4.2	3.3	2.8
Blackthorn	5.2	7.7	2.2	2.0	0	0	30.8	35.0	0.1	0.1
Height intervals (m) (%)										
0	0	0	0	0	0	0	16.4	14.4	0	0
0,1–2	5.0	7.6	5.0	4.0	3.3	2.2	42.1	50.1	2.0	1.7
2–8	32.1	31.5	62.7	62.5	63.7	51.3	37.7	32.8	39.6	42.4
>8	62.9	60.9	32.3	33.5	33.0	46.5	3.8	2.7	58.4	55.9

point and sequential samples were first tested for seasonal effects. As seasonal differences did not affect the proportions of observations recorded in any of the foraging categories for the first observation (single-point method) compared to the total data set or to the second plus subsequent observations (sequential method) (G-tests, P's > 0.05), seasonal data were combined in subsequent analyses.

The proportions of foraging behaviors for single-point observations were similar to those recorded for sequential observations (Table 1). This was the same whether single-point data were compared to sequential observations with the first prey-attack deleted (Table 1) or to the total data set. None of the species studied had rare or unusual behaviors that required prolonged study (i.e., >20–25 observations) to observe or that affected interpretations of their use of resources and interactions with other individuals (see Recher 1989 b, for details).

There were no significant differences in the use of foraging substrates, plant species or height intervals (P's > 0.05) between the first and subsequent observations. However, there were some consistent, although not significant, differences in the proportions of foraging behaviors recorded for the first and subsequent prey-attacks. For most species foliage was over-represented whereas bark and aerial foraging were under-represented on the first observation (Table 1). The exception was the White-throated Warbler, for which the proportion of bark foraging decreased with subsequent observations.

Apart from Buff-rumped Thornbills, the proportion of prey-attacks by birds foraging in ironbarks increased after the first observation, whereas the proportion in grey box and other eucalypts decreased (Table 1). Ironbark has smaller leaves and denser foliage than grey box and the other eucalypts on the plot, which made the detection of birds in ironbark more difficult. Buff-rumped Thornbills were the only birds to forage extensively in blackthorn and there was an increase in the use of blackthorn and a decrease in the use of ironbark and grey box subsequent to the first observation (Table 1). The foliage of blackthorn is much denser than that of the eucalypts and the detection of birds foraging in blackthorn more difficult. The increased use of the shrub layer by Little and Buff-rumped thornbills with the second and subsequent observations (Table 1) reflects their use of blackthorn.

Active prey-attack behaviors (i.e., snatch, hover, hawk) were recorded more often and less active behaviors (i.e., glean, hang-glean) less often on the first compared with subsequent observations (Table 1); these differences were significant for two species. Buff-rumped Thornbills snatched and hovered more often and gleaned less often on the first than subsequent observations ($P < 0.001$). Weebills gleaned and hang-gleaned less often and hovered more often on the first than subsequent observations ($P < 0.025$).

Testing the first against second prey-attacks, there were no significant differences for any species in the proportions of plant species, foraging heights, or substrates recorded for the first and second prey-attacks (P's > 0.1). However, there was a tendency for active behaviors to be recorded more often and less active behaviors to be recorded less often on the first than on the second prey-attack. Little Thornbills gleaned less often ($P < 0.02$), but hawked ($P < 0.02$) and snatched more often ($P = 0.1$) on the first than second observation. White-throated Warblers snatched more often ($P < 0.005$) and gleaned less often ($P = 0.1$) on the first than second observation. Weebills hovered ($P = 0.054$) more often and hang-gleaned less often ($P < 0.004$) on the first than second observation. Buff-rumped Thornbills snatched more often on the first than the second observation ($P = 0.07$). Other differences were not significant (P's > 0.1).

Estimate of Sample Size

The standard error of the mean for different sized samples stabilized (i.e., a small change in value with increasing sample size) at about ±0.05 for single-point and sequential methods for all foraging categories and all species (Figs. 1–3). This value can therefore be used to estimate sample sizes beyond which additional observations add little information on the proportions of different foraging behaviors. Although sample sizes differed between species, generally observations of 60–70 individuals were needed before standard errors stabilized (Figs. 1–3). For the proportional data reported here, samples of 60–70 individuals fall between the sample sizes estimated for 90 and 95% confidence intervals (15–365 individuals) (Snedecor and Cochran 1980: 441–443). For a 99% confidence interval, samples exceeding 5900 individuals are required.

Foliage and bark were the two most commonly used foraging substrates (Recher 1989 b). For Little and Striated thornbills, which took 70–80% of their prey from foliage, standard errors

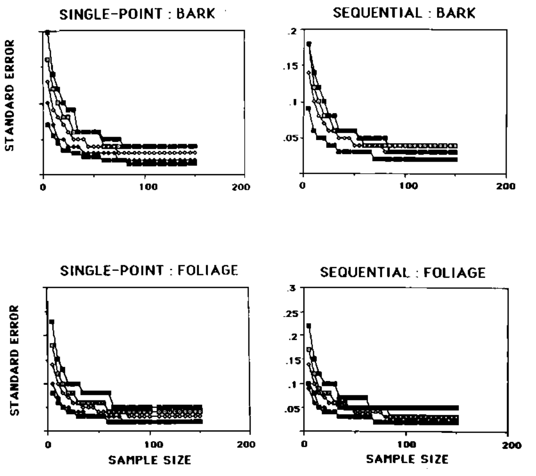

FIGURE 1. The standard error of the mean for the proportions of foraging substrates used by Australian warblers at Scheyville is plotted against sample size for foliage and bark.

stabilized at a maximum of 50–60 individuals (Fig. 1). Smaller sample sizes (30–40 individuals) were required for Weebill and White-throated Warbler which took more than 85% of their prey from foliage. The largest sample sizes (65–70 individuals) were required for Buff-rumped Thornbills which used the greatest diversity of substrates and often foraged on the ground and among debris as well as taking prey from foliage and bark.

Snatch, glean, and hover were the most common foraging behaviors used by Australian warblers at Scheyville (Table 1; see also Recher 1989 b). Gleaning was the most frequently used prey-attack behavior (35–70% of observations). Standard errors for the proportion of gleaning stabilized for all species at 60–70 individuals (Fig. 2). Hovering by Weebills and snatching by White-throated Warblers were the most common behaviors (40–50% of prey-attacks) used by these two species. Standard errors for these behaviors stabilized at 65–70 individuals for Weebills and White-throated Warblers and for the other species at 45–50 individuals (Fig. 2).

Ironbark and grey box dominated the study site and accounted for >90% of foraging by Australian warblers on eucalypts at Scheyville (Recher 1989 b.) Weebills foraged almost exclusively on ironbark (>90% of observations). For Weebills foraging on ironbark single-point observations stabilized at 55–60 individuals and sequential observations at 65–70 individuals (Fig. 3). For all other species standard errors for the use of ironbark as a foraging substrate stabilized at 60–70 individuals.

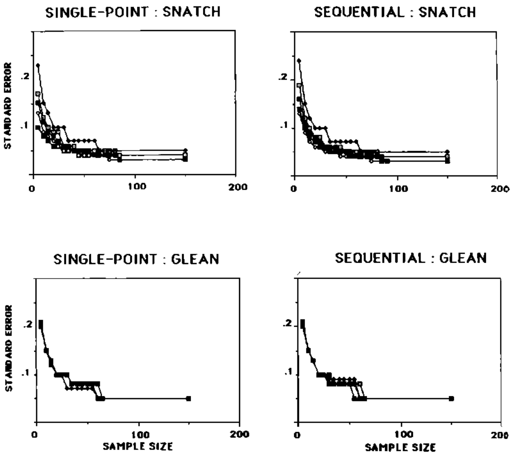

FIGURE 2. A plot of standard error against sample size for the three most commonly used prey-attack behaviors: snatch, glean, and hover.

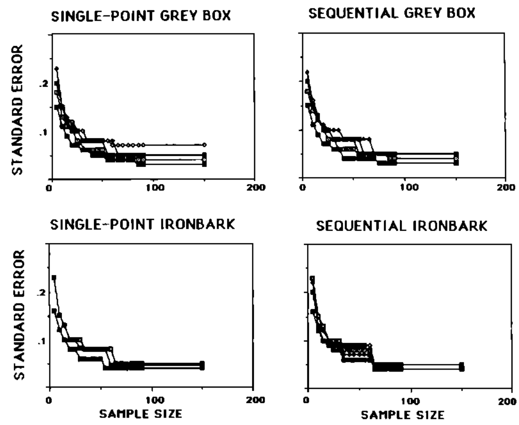

FIGURE 3. The standard error in the use of the two dominant eucalypts at Scheyville by Australian warblers is plotted against sample size.

Apart from White-throated Warblers, which used grey box as a foraging substrate more frequently (39% of observations) and Weebills which used it less often (9% of observations) than other species (Table 1), standard errors for single-point and sequential observations for grey box stabilized at 55–60 individuals. For White-throated Warblers 70–75 individuals were required for sequential observations and 65–70 individuals for single-point observations (Fig. 3). Standard errors for the proportion of foraging on grey box by Weebills stabilized with observations of only 40–45 individuals for both single-point and sequential observations.

The most variable foraging parameter measured was mean foraging height. All species foraged from the shrub layer into the canopy and the Buff-rumped Thornbill foraged extensively on the ground (Table 1). Relative to other foraging categories, large samples were required to stabilize standard errors. After weighting for the number of observations per individual (see Methods), sequential data were used to calculate the standard error of mean foraging height with increasing sample size (Fig. 4).

For all species the rate of change in foraging height standard error decreased markedly after 70–80 observations with standard errors between ±0.2 m for Buff-rumped Thornbills and ±0.4 m for Little Thornbill. Standard errors stabilized between ±0.2–0.3 m for all species after 110 observations. Estimates of the minimum required sample sizes (Snedecor and Cochran 1980: 53) for an 80% confidence interval about the mean with standard errors between 0.2 and 0.3 m range from 110 to 140 individuals. For a confidence interval of 95% the required sample size is 440 and for a 99% interval it is 725.

DISCUSSION

Sequential observations of the same individual are not independent, posing problems for the statistical analysis of the data (Wagner 1981a, Morrison 1984a, Bradley 1985). In addition, results may be biased towards individuals or behaviors that are easy to follow (Franzreb 1984, Bradley 1985). Single-point observations have the advantage of statistical independence, but may be biased towards particularly conspicuous individuals (e.g., singing males) or behaviors (e.g., hawking) (Wiens 1969, Wagner 1981a). Single point observations are also useful in that details of the substrate (e.g., plant species, substrate height, prey concentrations) can be recorded without the necessity of following the bird and losing track of the foraging stations that had been used. Sequential observations have the advantage that a large amount of data can be collected for each bird, and uncommon or inconspicuous behaviors are more likely to be recorded (Hertz et al. 1976, Sturman 1968, Austin and Smith 1972). Thus it is tempting to use sequential recording techniques when little is known of a species' behavior or when individuals are difficult to locate. For these reasons sequential observations have generally when preferred (e.g., Hertz et al. 1976, Wagner 1981a, Morrison 1984a, Recher et al. 1985), but with the caveat that large sample sizes may be necessary to overcome problems of the lack of statistical independence (Morrison 1984a) or that special methods are needed to analyze the data (Bradley 1985).

Data collected over 12 months for five species of Australian warblers suggests that there may be a tendency for the first recorded prey-attack to be of particularly conspicuous individuals. Despite the openness of the habitat in which observations were made, birds that foraged in foliage were more readily detected than those foraging on bark. Probably this is because eucalypt foliage tends to be clumped and clustered towards the ends of branches. Foliage gleaners are seldom concealed by leaves and the terminal position of the foliage makes them easy to detect. Similarly, conspicuous foraging behaviors such as snatching and hovering were over-represented on the first recorded prey-attack. The reduced frequency of aerial foraging (an active behavior usually associated with hawking and/or hovering) on first compared to subsequent observations may have resulted from a tendency by the observer to avoid recording particularly conspicuous behaviors when birds were first sighted. For Weebills the greater frequency of hovering on first observations and the increased incidence of gleaning and hang-gleaning with sequential observations results from hovering being an exploratory as well as a prey-attack behavior, with hovering birds landing to feed after locating prey.

With the exception of the White-throated Warbler, none of the species studied was sexually dimorphic. Male White-throated Warblers were the only birds studied that sang and which were located by sound. Although there was a tendency for singing males to forage in the upper canopy (Recher 1989 b), first observations tended to be biased towards individuals foraging in lower vegetation (Table 1). Thus, there is no indication that the detection of some birds by song affected results. Probably this is because of the small numbers of males located while they were singing. All other birds were located visually. This probably contributed to the tendency to first see birds that were in the outer foliage of trees or that were foraging actively. The greater proportion of first observations of birds in grey box than in ironbark may result from the more open foliage and larger leaves of grey box than ironbark, where birds were more easily concealed.

Despite the tendency to locate individuals that were conspicuous, there were few significant differences between the proportions of the various foraging parameters recorded on the first prey-attack (single-point method) versus subsequent behavior (sequential method). Such differences did not affect any of the conclusions relating to the use of resources by these birds or their interactions with each other. At least in the open eucalypt habitats where this work was done, problems of conspicuous behavior or individuals might be minimized by rejecting the first prey-attack observed for each bird encountered or having a set waiting period before recording the

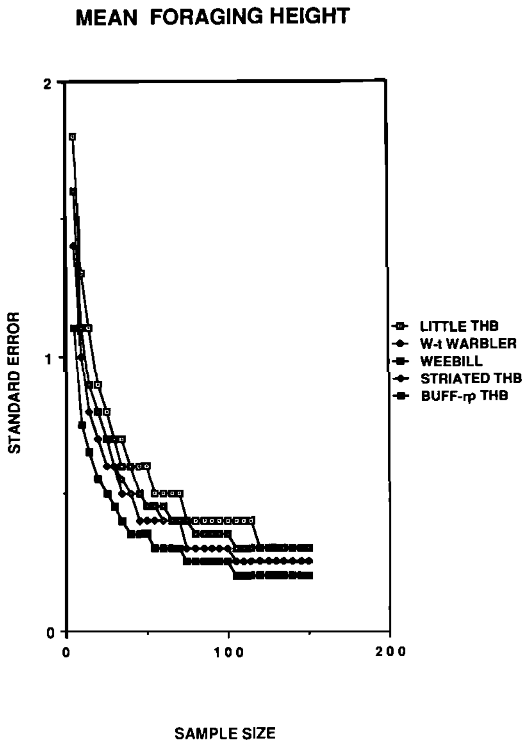

FIGURE 4. A plot of standard error against sample size for mean foraging height. In this plot standard errors were calculated for all prey attacks as the data were collected in the field.

first observation. Either procedure could be used without greatly increasing the effort required to obtain adequate sample sizes.

Regardless of the sampling procedure a minimum of 60–70 individuals was required to stabilize sample variances for most foraging parameters by both single-point and sequential methods. This estimate of minimum sample size assumes that the proportion of each foraging behavior recorded for the total sample approximates the underlying proportion for the population (Fleiss 1981). As such, the estimate of sample size is independent of the time period over which the sample is obtained. Where there are significant temporal or spatial changes in the proportions of foraging behaviors within a population, similar sized (i.e., 60–70 individuals) samples are required for each time period or area.

The estimates of minimum sample size presented here are greater than Morrison's (1984a) estimate of a minimum of 30 individuals or 150 sequential observations. Inspection of Morrison's data suggests a sample size of 30–40 individuals is required for single-point observations and 60–180 observations is required for sequential sampling, although more than 200 observations may be needed to ensure that some rare behaviors are sampled. Both our estimates of minimum sample sizes and those of Morrison (1984a) fall within the range required for 90-95% confidence intervals. Greater precision requires much larger samples.

Although Morrison (1984a), Wagner (1981a), and Hertz et al. (1976) advocated sequential sampling, unless the objective of the study was to record series of events (e.g., rates of movement, search and quitting times), there appears to be little justification for these procedures in habitats where it is easy to locate birds. Similar numbers of individuals are required for both procedures and sequential recording failed to detect rare and/or unusual behaviors that might affect interpretations regarding the use of resources or the ways in which species interacted with each other.

The large sample sizes needed to stabilize sample variances for mean foraging height can be used to establish an upper limit for data recording, which is easily calculated progressively in the field. The time saved by recording only a single prey-attack for each individual located can be used to obtain other habitat data (e.g., details of substrate) or to reduce the time taken to obtain a sample, thereby reducing effects of weather, time of day or seasonal changes in food resources on avian behavior.

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