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EFFICIENCY OF TWO MASS SAMPLING METHODS FOR SAMPLING PHORID FLIES (DIPTERA: PHORIDAE) IN A TROPICAL BIODIVERSITY SURVEY

BRIAN V. BROWN[1] AND DONALD H. FEENER, JR.[2]

ABSTRACT. The period of time necessary for a Malaise trap to collect a given percentage of the susceptible fauna is calculated for females of *Apocephalus,* a genus of small phorid flies that parasitize ants. The 16 Malaise traps operated by the La Selva insect survey are expected to collect about 95% of the *Apocephalus* fauna in 1 year. Comparison of pan traps with Malaise traps in Costa Rica shows that Malaise traps are superior for collecting phorid flies; these results contrast with those from a study done in England. Small pan traps catch relatively more phorids than do large ones. These data provide rough guidelines for biodiversity surveys of phorid flies in tropical forests: presumably these guidelines will be more reliable than those based on Northern Hemisphere studies.

INTRODUCTION

As the numerically dominant forms of terrestrial animal life, insects play key roles in all ecosystems. The loss of insect species through habitat destruction is expected to have profound consequences for other members of natural communities (Wilson, 1987). Therefore, it is vital that we include studies on insects in all major conservation and biodiversity survey efforts. Indeed, some surveys are underway that are dedicated exclusively to the study of insect diversity (Erwin, 1990; Hammond, 1990; Lamas et al., 1991; Longino, 1994).

To date, most information about insects has come from groups that have been well studied in the past, especially butterflies and larger beetles. Recently, mass sampling methods have made the study of many other, less visible groups of insects possible. The use of canopy fogging, in particular, has been found to sample beetles effectively (Erwin, 1990; Stork, 1988). The collecting tools used in this study, Malaise traps, are tent-like structures that intercept large numbers of other groups of insects, notably flies, bees, and wasps.

Currently, little is known about the effectiveness of Malaise traps. Most collectors of our acquaintance use one to four Malaise traps during their collecting trips and capture an unknown fraction of the total diversity of a site. An ongoing insect survey in Costa Rica, the Arthropod Survey of La Selva (ALAS; Longino, 1994), uses 16 Malaise traps. It is not known whether this is an excess of effort or this number of traps will still vastly undercollect the total fauna during the period of the survey.

In this paper, we try to determine how much Malaise trapping is enough. Of course, "enough" can mean many things, and different goals will dictate when this point is reached. We assume that an intensive survey (sensu Castri et al., 1992) will require that 95% of the fauna be identified. Further, we assume that 10 years is the maximum amount of time anyone would reasonably sample a single site. Using species accumulation curves for the group of insects of interest to us (phorid flies, Diptera: Phoridae), we predict roughly how long the 16 ALAS Malaise traps must be operated to collect a given percentage of the trappable species of *Apocephalus,* a genus of ant-parasitizing flies that one of us currently is revising (Brown, 1993, 1994).

Another question we attempted to address was whether or not Malaise traps could be replaced by cheaper, reputedly more efficient collecting devices like pan traps (=water traps). Disney (1986) pointed out the need for sampling methods that produce repeatable results and proposed that mean catches for white pan traps had a lower variance than those from Malaise traps, based on an earlier study (Disney et al., 1982). In this earlier study, however, Disney et al. (1982) compared only two Malaise traps, one of which had a highly dysfunctional design. No useful data are available on whether Malaise trap catches are more or less "repeatable" than those of pan traps, and the only measure of success that was compared by Disney et al. (1982) was total catch. At a site in England, white pan traps were deemed to be more desirable collecting tools than Malaise traps because they collected more speci-

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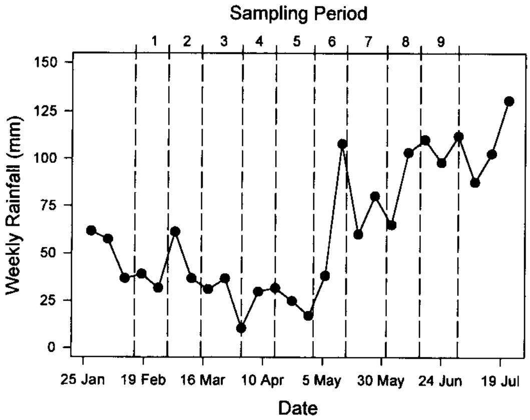

Figure 1. Ten-year average rainfall at La Selva (from Sanford et al., 1994), superimposed on the nine trapping periods sampled for Malaise traps 8 and 10.

mens and because sorting the catch required less effort. It is not clear whether or not these results can be relied upon for other areas, especially in the tropics. The study of Disney et al. (1982) was a pioneering effort in this type of analysis, and the paucity of data from other areas makes it likely that others will uncritically use these results for designing biodiversity surveys. We replicated the methods of Disney et al. (1982) in a tropical forest in Costa Rica to see if the same results would be obtained.

A final question we addressed was one suggested by Disney et al. (1982) as a further study: whether a single large pan trap or several small pan traps were better for sampling phorids. Their data suggested that the number of specimens collected was approximately proportional to the surface area of traps. We tested this finding during the Malaise trap versus pan trap experiment.

METHODS

The catch from 10 Malaise traps operated by the ALAS project for one sampling period, 1–15 April 1993, was examined. Also, the catch for two traps (traps 8 and 10) was analyzed for nine trapping periods, each trapping period being approximately 2 weeks in duration. This time span, from 15 February to 1 July 1993, extended through the dry and early rainy season at La Selva (Fig. 1). All female *Apochephalus* specimens were removed from the samples and identified to morphospecies. Records were entered into a computer database. Specimens are currently housed at the Natural History Museum of Los Angeles County, but most will be returned to the Instituto Nacional de Biodiversidad, Costa Rica.

The number of *Apocephalus* species collected by all possible combinations of the 10 traps was tabulated. All two-arrangements, three-arrangements, . . . , to nine-arrangements of the 10 traps were averaged, to find the mean number of species collected per one trap, two traps, three traps, . . . , 10 traps. These means were used as separate observations to build a species accumulation curve and to estimate the total "Malaise-trappable" fauna (Lamas et al., 1991; Soberón and Llorente, 1993).

The catch from two individual Malaise traps operated over 18 weeks was also identified. This allowed us to examine the interplay between spatial and temporal heterogeneity; in other words, do 10 traps operated for 1 week collect the same number of species as one trap operated for 10 weeks?

Soberón and Llorente (1993) recently reviewed and justified three models for estimating the rate of species accumulation and asymptotic species richness based on repeated sampling of an area. According to these authors, the exponential model is appropriate for small areas or those with a well-known fauna that will eventually be completely collected. This model was clearly inappropriate for our data, since La Selva, with its connection to Braulio Carrillo National Park, certainly is not a small area, and the phorid fauna is anything but well known. The Clench model was the second model examined by Soberón and Llorente (1993). It specifies that as more time is spent in the field experience will increase the number of species collected. Our observations, however, are based on collections made by Malaise traps, which do not gain experience. We therefore rejected this model as well. We selected the logarithmic model as the most appropriate model for our Malaise trap data. Soberón and Llorente (1993) described this model as being appropriate for large areas with poorly known faunas, where the probability of adding new species decreases during sampling but never entirely disappears. A major disadvantage of the logarithmic model relative to the other two models is that no asymptote, or estimate of the total size of the fauna, can be generated. Instead, we only can calculate the number of species expected at a given point in time. Thus, we cannot state unequivocally when 95% of the estimated fauna has been sampled. However, we can make statements about how rapidly we can collect 95% of the fauna estimate for a fixed period of sampling (e.g., 10 years).

The logarithmic model takes the form

$$S(t) = 1/z \ln(1 + zat),$$

where $S(t)$ is the predicted number of species at time t, z is the slope of the species/sampling-effort curve (a straight line when plotted on a log/log graph), and a is the list increase rate at the beginning of the collection period (Soberón and Llorente, 1993). We used non-linear regression to estimate z and a for our Malaise trap samples. The NONLIN procedure in SYSTAT Version 5.03 was used to obtain these estimates (SYSTAT Inc., 1992). Model evaluation was based on least-squares with quasi-Newton optimization (SYSTAT Inc., 1992). Reliable estimates of z and a were achieved after 7–12 interactions. Once we obtained estimates of z and a, we used them to predict $S(t)$ at various times.

For the Malaise trap versus pan trap experiment, we placed a Malaise trap in the La Selva forest (Clark, 1990; Hartshorn, 1983) and placed 14 white pan traps in the surrounding area. The Malaise trap was of the Townes (1972) design, black, with a white roof, purchased from D.A. Fochs Company (Gainesville, Fla). The killing and preservation agent used was 70% ethanol. The pan traps were white plastic, rectangular refrigerator compartments and were of three sizes: (1) small: 7.6 cm × 7.6 cm = 58.1 cm^2, (2) medium: 22.9 cm × 15.2 cm = 349 cm^2, and (3) large: 38.1 cm × 30.5 cm = 1,161.3 cm^2 (large pans were composed of two 38.1 cm × 15.2 cm pans joined together). The pans were distributed about 1.5 m apart in the vicinity of the Malaise trap; the total area

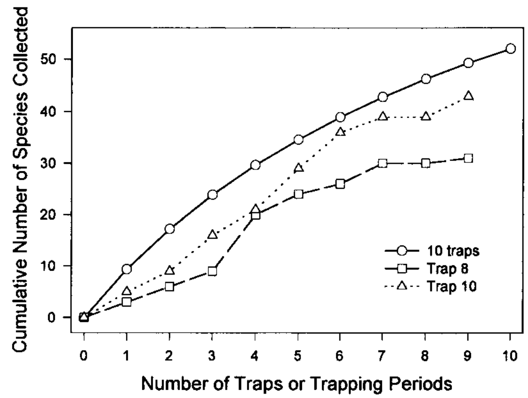

Figure 2. Cumulative catch of *Apocephalus* species at La Selva by means of all combinations of 10 traps sampled once (top line) and by Malaise traps 8 and 10 over nine trapping periods.

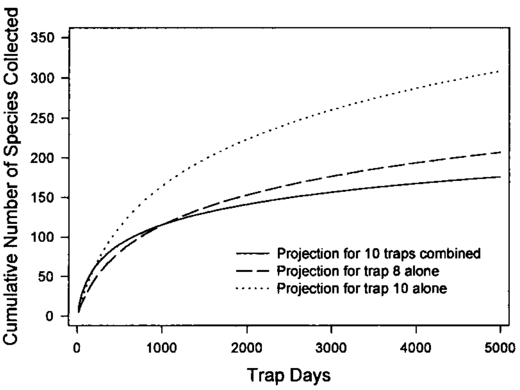

Figure 3. Extrapolated species accumulation curves for *Apocephalus* species at La Selva.

covered by these pans was 4,765.2 cm^2. The following number of traps were operated: two large, six medium, and six small. Pan trap fluid was water with several drops of dishwashing detergent added to lower surface tension. The traps were operated from 6 to 9 July 1993. An overall difference in the number of specimens collected by pan traps of different sizes was assessed by a one-way analysis of variance. Post-hoc differences in means of small, medium, and large pan traps were detected by the least-square mean procedure with a Bonferroni adjustment to ensure an experimentwise error rate of $\alpha = 0.05$ (Sokal and Rohlf, 1981).

RESULTS

SPATIOTEMPORAL VARIATION IN MALAISE TRAP CATCHES

The ten ALAS Malaise traps collected a total of 52 *Apocephalus* species, ranging from 1 to 19 species per trap (see the Appendix). The 1,023 possible combinations of the ten traps produced the results shown in Table 1. A species accumulation curve was plotted (Fig. 2, "10 traps"), with the numbers extrapolated out to over 5,000 days (approximately 15 years; Fig. 3, "10 traps combined"), using the parameter estimates in Table 2. The extrapolated numbers of species collected after 1, 2, 3, 5, and 10 years are given in Table 3. In 10 years of sampling, these traps are predicted to catch a total of 164 species of *Apocephalus*.

The single Malaise traps, 8 and 10, collected fewer species for the same trap effort than the the traps together. In nine sampling periods, traps 8 and 10 accumulated 31 and 43 species, respectively, substantially less than the mean number of species (49.30 ± 2.54) collected in nine traps for one sampling period. A mean of 16.4 ± 5.55 species per sampling period was collected by a combination of traps 8 and 10, compared to 17.24 ± 7.28 for the mean of 2 of 10 traps sampled during a single period (Table 1).

Extrapolation of the species accumulation curves for traps 8 and 10 separately and together over a duration of 10 years gave predicted species richness values of 188–278 (Table 3). While these values appear to be considerably higher than the 164 species predicted by the 10 traps sampled simultaneously in time, it is perhaps surprising that the estimates were not even more disparate, given the fact that we projected the data up to 261 times beyond the periods sampled.

The higher mean and predicted values of species richness for the aggregate collecting effort of traps 8 and 10 is almost certainly a product of the increased time span over which these traps operated. Their trapping period encompassed both wet and dry seasons, and the collections from these traps strongly suggest that seasonal changes in abun-

Table 1. Number of *Apocephalus* species collected by all combinations of ten Malaise traps.

No. of traps	No. of combinations	Average No. of species collected	SD	Range
1	10	9.40	6.62	1–19
2	45	17.24	7.28	2–31
3	120	23.89	7.20	4–41
4	210	29.63	7.76	10–46
5	252	34.62	6.10	17–48
6	210	38.99	5.33	25–50
7	120	42.85	4.48	31–51
8	45	46.27	3.56	38–52
9	10	49.30	2.54	44–52
10	1	52.00	—	—

Table 2. Parameter estimates (±SE) for the logarithmic model for the accumulation of species during repeated sampling.

	z	a
Trap 8		
Nine sampling periods	0.016 ± 0.013	0.331 ± 0.063
Trap 10		
Nine sampling periods	0.010 ± 0.006	0.418 ± 0.050
Traps 8 + 10		
Nine sampling periods	0.014 ± 0.004	0.308 ± 0.033
Ten traps		
One sampling period	0.026 ± 0.001	0.737 ± 0.010

dance, species richness, and activity of individual species are common.

There is some evidence for seasonality in La Selva *Apocephalus*, similar to strong seasonality reported for *Apocephalus* activity at other tropical sites (Feener, 1988; Feener and Moss, 1990). Total catch of *Apocephalus* specimens (Fig. 4A) and species (Fig. 4B) showed an increase at the beginning of the rainy season (cf. Fig. 1). Totals for trap 8 increased sooner than those from trap 10, probably because of differences in the microhabitat sampled by each trap. Similar variation among different habitats has been shown for other phorids (Disney, 1994, p. 195). Because most *Apocephalus* species were represented by few specimens, most of the variation in numbers of specimens can be attributed to a few species, namely, species 21 and 130 in trap 8 and species 130 and 143 in trap 10 (Fig. 5).

COMPARISON OF WHITE PAN TRAPS VERSUS MALAISE TRAPS

Over a 3-day sampling period, the Malaise trap collected a total of 261 phorids, while the combined total catch for all of the pan traps was 182 phorids (Table 4). The number of flies collected by small, medium, and large pans varied significantly ($F = 9.50$, $df = 2, 11$, $P = 0.004$). Small pan traps collected significantly more specimens per unit area (0.123 ± 0.053 flies/cm^2) than did medium traps (0.047 ± 0.013 flies/cm^2; $P = 0.012$) and large traps (0.018 ± 0.007 flies/cm^2; $P = 0.014$). Medium pan traps did not differ significantly from large pan traps in number of specimens collected per unit area ($P > 0.5$).

DISCUSSION

Our data contrast the effect of sampling with 10 traps over one time period versus sampling with one trap for approximately 10 periods of time. Are they equal, and can our estimates based on a single time period be used with any justification?

Single traps, 8 and 10, collected only 63% and 87%, respectively, of the expected number of species based on 10 traps sampled once (Fig. 2). We see this lower number as a reflection of the initial disadvantage of lower spatial heterogeneity, or fewer microhabitats, sampled by the two traps, as opposed to the larger area sampled by 10 traps. Combining the catches from the two traps gave an average of 16.3 species per period, a number that is close to the mean value of 17.24 species collected by two randomly selected traps in the 10-trap sample (Table 1).

The single traps predict a larger number of species than the 10 traps sampled once (Fig. 3). Presumably, this is because they sampled a longer period of time, including the period of the dry-wet season rainfall change. Apparently, temporal het-

Table 3. Extrapolated Malaise trap catch (number of species) using the logarithmic model and parameter estimates in Table 2.

	Year				
Trap(s)	1	2	3	5	10
Trap 8					
Nine sampling periods	67.25	98.89	119.80	147.94	188.26
Trap 10					
Nine sampling periods	92.65	139.91	171.87	215.51	278.85
Traps 8 + 10					
Nine sampling periods	67.53	101.61	124.59	155.90	201.27
Ten traps					
One sampling period	79.95	104.13	118.85	137.79	163.91

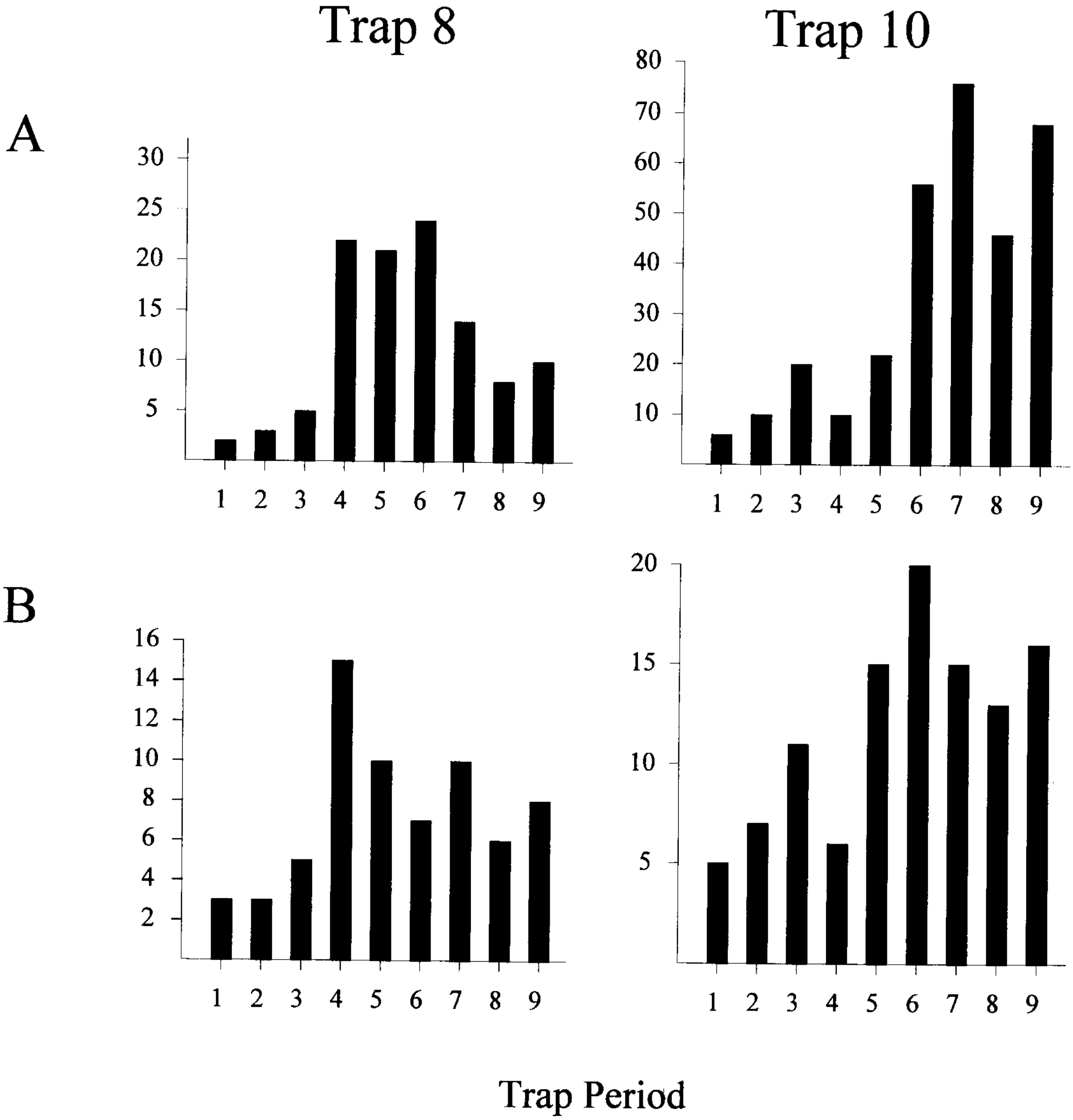

Figure 4. **A.** Number of specimens of *Apocephalus* collected by traps 8 and 10 during each trapping period. **B.** Number of species of *Apocephalus* collected by traps 8 and 10 during each trapping period.

erogeneity is more important than spatial heterogeneity, at least over the time periods we sampled.

All of the projections predict that after 10 years the number of species of *Apocephalus* present at La Selva will exceed 150. This number, about 1.5 times the number of described species in the entire genus, was much larger than we originally anticipated and reflects our true ignorance of the actual size of the fauna. Obviously, collecting over short periods of time, such as the 2-week length of our typical visit to a site, with four Malaise traps will not intensively sample the La Selva fauna, but what about the 16 traps that the ALAS survey is currently using? If we assume that 10 years is the maximum amount of time anyone would reasonably sample a single site, we can predict the amount of time necessary for an intensive survey. Different data sets give different answers (Table 5), but generally we predict that it takes 8–9 years for a single Malaise trap to collect 95% of the 10-year total at La Selva. Because there are 16 traps operating, however, we have to divide the 8–9 years by some constant that represents the increased catch of 16 traps over a single trap. Using the accumulation curve for all traps (Fig. 3), we calculate that 16 traps would catch an average of 66.25 species, or 7.048 times the average amount collected by a single trap. Therefore, if we divide the amount of time predicted by

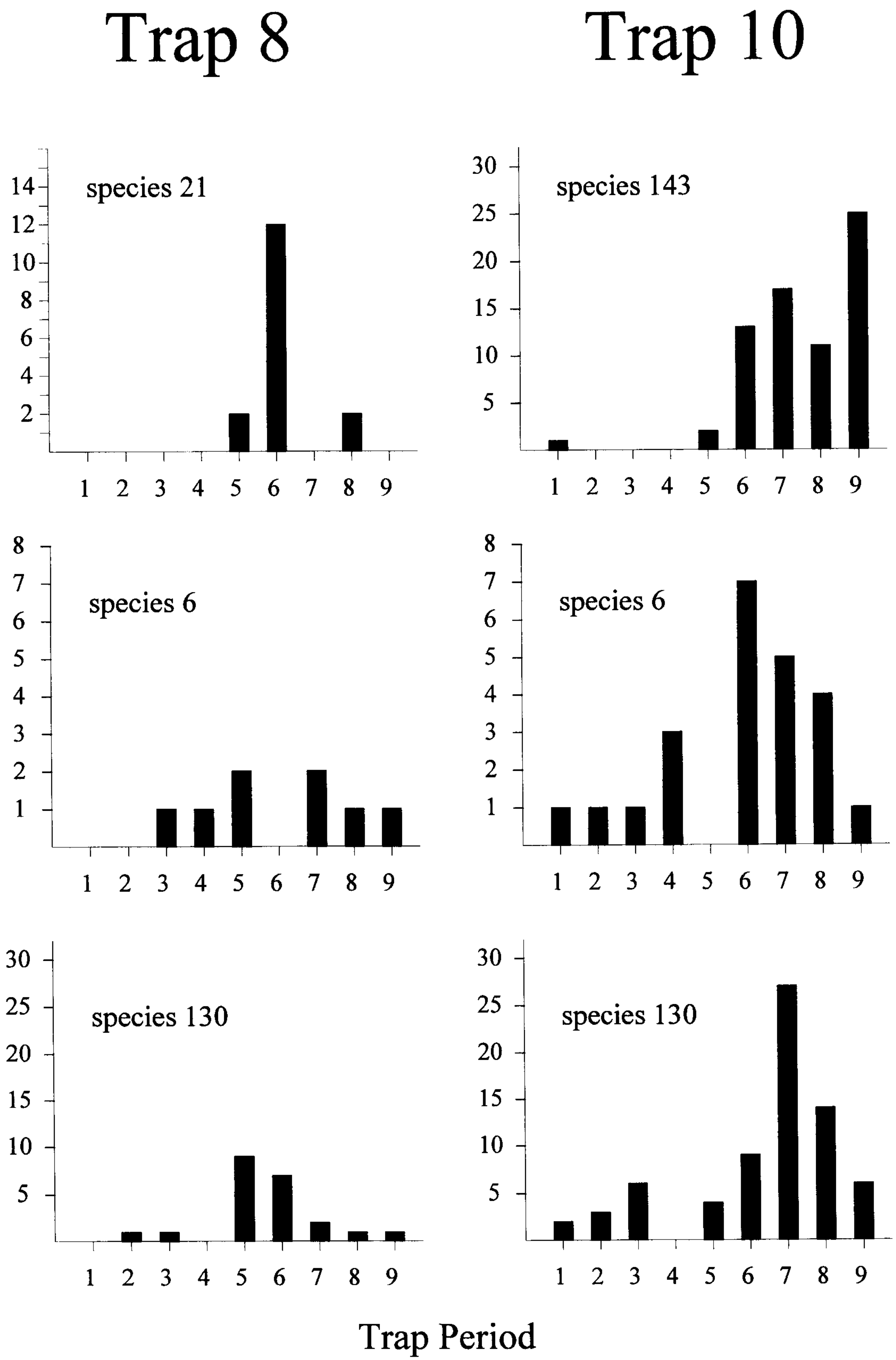

Figure 5. Number of specimens of some common *Apocephalus* species collected by traps 8 and 10 during each trapping period.

Table 4. **Number of Phoridae collected by fourteen pan traps.**

Pan trap No.	Size	No. of phorids collected	Phorids per cm^2
1	Small	9	0.155
2	Small	11	0.189
3	Small	7	0.120
4	Small	6	0.103
5	Small	8	0.138
6	Small	2	0.034
7	Medium	10	0.029
8	Medium	12	0.034
9	Medium	18	0.052
10	Medium	22	0.063
11	Medium	18	0.052
12	Medium	17	0.049
13	Large	27	0.023
14	Large	15	0.013

Size	Mean number of phorids per cm^2
Small	0.123 (SD 0.053)
Medium	0.047 (SD 0.013)
Large	0.018 (SD 0.007)

Table 5. **Years to collect 95% of the 10-year total at La Selva, based on different data sets.**

Data set	Years (1 trap)	Years (16 traps)
Trap 8		
Nine sampling periods	8.53	1.21
Trap 10		
Nine sampling periods	8.61	1.22
Traps 8 + 10		
Nine sampling periods	8.60	1.22
Ten traps		
One sampling period	8.05	1.14

the various data sets for the traps to collect 95% of the 10-year total by 7.048, we calculate that an intensive survey will be completed in 1.14–1.22 years. Naturally, these numbers are rough estimates and are limited by the limited sampling used for their calculation. They give some sort of time period over which a Malaise trap can be operated for the specific goal of collecting a given percentage of *Apocephalus* females, or of a taxon with a similar number of species and similar susceptibility to Malaise trap capture.

The comparison of the Malaise and pan traps showed that the Malaise trap collected 43% more phorids than did the pan traps, but comparison with the study of Disney et al. (1982) shows that the Malaise trap was relatively even more superior. In one experiment, Disney et al. (1982) found that three pan traps collected 106 phorids, while the Malaise trap caught only 15, but the total area of pan traps was only about 1,845 cm^2. Thus, although we used more than 2.5 times the surface area of pan traps used by Disney et al. (1982), our Malaise trap was still superior in number of phorids collected.

A further criticism of Malaise trap samples given by Disney et al. (1982) was that they collect so many other insects (non-phorids) that they are tiresome to sort. This problem has been greatly reduced by an idea of Dr. Lubomir Masner and the other hymenopterists at the Biosystematics Resources Division in Ottawa, Canada: samples are gently screened by 0.25-inch and then 8-inch mesh in a large tub of alcohol. Phorids are found almost exclusively in the fraction that goes through the 8-inch mesh, although the other fractions should be scanned quickly to find odd specimens stuck to larger insects. Screening eliminates at least 75% of the bulk of the sample, making phorid sorting much easier.

In the comparison of different-sized pan traps, small pans were found to collect a relatively larger number of phorid specimens than large and medium pans. Based on these results, a collector should take many small pans, rather than a few larger pans, into the field.

SUMMARY

Biodiversity surveys in tropical countries eventually will be more streamlined and efficient, when we know more about the effectiveness of our sampling methods. Guidelines based on studies in tropical regions presumably will be more reliable for tropical biodiversity studies than guidelines based on studies from the temperate Northern Hemisphere.

Based on results obtained from Malaise trap samples at La Selva, sixteen Malaise traps operated for about 1 year hypothetically should collect about 95% of a 10-year survey of the *Apocephalus* fauna, probably satisfying the criteria for an intensive survey (Castri et al., 1992). Other taxa of similar species richness and susceptibility to being caught in Malaise traps should require a similar period of trapping time.

Pan traps are distinctly inferior to Malaise traps for collecting phorids at La Selva, in contrast to the preference for pan traps found in a study in England. Additionally, Malaise traps are much more convenient, because they require only weekly or biweekly attention once deployed. Pan traps in the warm tropics must be emptied daily to prevent rotting of their contents, and new water must be carried to the pans every few days. If pans are to be used, however, many smaller pans should be used rather than a few large ones.

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APPENDIX

Species of Apocephalus collected by Malaise traps at La Selva.
Each species is represented by a number; Malaise trap numbers are those of the ALAS project.

Malaise trap 8

15.ii-1.iii.1993
3061
3073
3168

1-15.iii.1993
3180
3194
3202

15.iii-1.iv.1993
3022
3144
3180
3202
3211

1-15.iv.1993
160
910
3022
3073
3105
3144
3148
3167
3177
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15.iv-1.v.1993
910
2701
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3180
3202

1-15.v.1993
110
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3222

15.v-1.vi.1993
76
110
152
157
3022
3166
3167
3180
3194
3211

1-15.vi.1993
76
160
3022
3068
3180
3211

15.vi-1.vii.1993
76
110
152
3022
3102
3144
3168
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Malaise trap 10

15.ii-1.iii.1993
2701
3022
3148
3180
3227

1-15.iii.1993
152
3022
3103
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3188
3202

15.iii-1.iv.1993
2701
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1-15.iv.1993
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15.iv-1.v.1993
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1-15.v.1993
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15.v-1.vi.1993
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1-15.vi.1993
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15.vi-1.vii.1993
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Appendix continued

Malaise trap 3

1-15.iv.1993
3105
3167

Malaise trap 4

1-15.iv.1993
96
157
2701
3022
3151
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3211
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Malaise trap 5

1-15.iv.1993
110
121
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Malaise trap 7

1-15.iv.1993
3171
3201

Malaise trap 11

1-15.iv.1993
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910
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Malaise trap 12

1-15.iv.1993
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Malaise trap 15

1-15.iv.1993
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Malaise trap 16

1-15.iv.1993
3167

NATURAL HISTORY MUSEUM
OF LOS ANGELES COUNTY
900 EXPOSITION BOULEVARD
LOS ANGELES, CALIFORNIA 90007