Studies in Avian Biology No. 13:29–37, 1990.

ARTHROPOD SAMPLING METHODS IN ORNITHOLOGY

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Abstract. We review common methods used by entomologists and ornithologists for sampling terrestrial arthropods. Entomologists are often interested in one species or family of insects and use a trapping method that efficiently samples the target organism(s). Ornithologists may use those methods to sample a single type of insect or to compare arthropod abundance between locations or over time, but they are often interested in comparing abundances of different types of arthropods available to birds as prey. Many studies also seek to examine use of prey through simultaneous analyses of diets or foraging behavior. This presents a sampling problem in that different types of prey (e.g., flying, foliage dwelling) must be sampled so that their abundances can be compared directly. Sampling methods involving direct observation and pesticide knockdown overcome at least some of these problems. Trapping methods that give biased estimates of arthropod abundance can sometimes be related to other methods that are less biased (but usually more expensive) by means of a ratio estimator or estimation of the biased selection function.

Key Words: Arthropods; insects; prey abundance; prey availability; sampling.

Numerous techniques exist for sampling insects (e.g., Southwood 1978); many have been used in ornithology. Most ornithological studies use insect sampling to determine types, numbers, and distribution of insects available to birds as prey; many also are designed to examine the use of those prey through simultaneous studies of diet and foraging behavior. Most techniques, however, effectively sample only a portion of the total insect fauna available to birds, and estimates of total arthropod abundance using these techniques will be biased accordingly.

Our objectives are (1) to review a portion of the literature on sampling techniques commonly used in entomological field studies, (2) to describe the advantages and disadvantages of those techniques, (3) to review their use and misuse in ornithological studies, and (4) to make recommendations concerning arthropod sampling methods in light of the objectives of field ornithologists. Our review of the entomological literature is largely limited to sources in which arthropod sampling is a focal point of the paper; it excludes techniques that sample arthropods normally unavailable to passerines, such as light trapping, and techniques that focus on a single species, such as capture-recapture sampling. An excellent review of these techniques is contained in Southwood (1978). Other reviews of interest include Morris (1960) and Strickland (1961).

DEFINING ARTHROPOD AVAILABILITY

The usual objective of most ornithological studies that sample arthropods is to relate some aspect of bird behavior or ecology (e.g., diet, foraging behavior, territory size, productivity) to arthropod abundance and distribution (availability). Simple arthropod abundance, however, may not reflect the prey actually available to birds, because not all arthropods in a bird's foraging area will be eaten by the bird. The size, life stage, palatability, coloration, activity patterns, and other characteristics of arthropods influence the degree to which they are located, captured, and eaten. These are the "translators" (Wiens 1984b) or factors that translate simple arthropod abundance into availability (e.g., see Hutto, this volume; Wolda, this volume). The problem is one of perception; the researcher must assess availability as the bird does. This, of course, is impossible. One approach is to use dietary data to determine availability (Sherry 1984, Wolda, this volume). Using this approach, the prey available to the bird are those it commonly eats. This approach is useful in some types of investigations (e.g., foraging behavior), but it is nonsensical in others (e.g., dietary preference).

Usually, as in this paper, when arthropods are sampled to determine availability, the sampling is designed to estimate the types, numbers, or distribution of some or all arthropods in the foraging area of one or several species of birds. Ornithologists are often interested in locations (e.g., tree species, heights) where birds forage in relation to arthropod availability. In this case, availability would be defined only in terms of the specific prey types in the location(s) of interest. Dietary data can be used to narrow the focus of the sampling effort. If a species eats large percentages of caterpillars a sampling technique specific to caterpillars should be used. Most methods described here are designed to sample one type of arthropod (e.g., flying, foliage dwelling). Such an objective is generally easier to achieve than sampling different types of arthropods for comparison (see Sampling Problem).

If a study seeks to assess "preference," one must estimate the numbers and types of all arthropod prey in the foraging area and compare prey eaten and not eaten by the birds. Reasons for their choices may be found in the ecologies of predator and prey. For example, Robinson and Holmes (1982) and Cooper (1988) found that prey types eaten by different species reflected differences in searching and attack strategies. Aviary studies involving feeding trials (Whelan et al., 1989) or simulated ecosystems (Heinrich and Collins 1983) can also provide information about why certain prey are eaten or avoided.

THE SAMPLING PROBLEM

Estimates of arthropod abundance are either relative or absolute. Relative measures provide only indices of abundance, such as numbers per surface area of sticky trap in a given time period. They have limited utility in studies of arthropod abundance and availability. Absolute measures, on the other hand, permit estimates of arthropod density that can be used for interspecific comparisons and comparisons among different habitats and seasons. Absolute measures usually require an intermediate sampling effort to quantify the density of the unit (plant, leaf, branch, and so on) used to assess arthropod numbers. Arthropod sampling, as used in this paper, covers both types of measures.

An obvious problem is comparing results from one or more methods involving different sampling units. This is especially the case if one wishes to compare arthropods eaten by birds with those available. Because various foraging sites and maneuvers differ among bird species, many sorts of arthropods may have to be sampled simultaneously in a given habitat, including flying insects, foliage-dwelling forms (e.g., spiders, Homoptera, some beetles), caterpillars, and litter-dwelling insects (e.g., ground beetles, ants). Because most of these groups require a unique sampling technique, one cannot easily relate results from one group to another. For example, how might we compare a frequency of two caterpillars/100 leaves with a density of 10 ichneumonid wasps/400 cm^2 of sticky-trap surface per week? The problem requires either (1) a technique that equivalently samples all types of arthropods in a given habitat (defined as unbiased measurement of the abundance of all arthropod taxa on experimental units that completely cover the habitat of those arthropods), or (2) a method that permits unbiased comparison of results from one technique with those of another. The first solution can sometimes be achieved in arthropod sampling by using methods that allow estimates of density, instead of indices of relative abundance. The second solution involves relating one estimator to another, as commonly done in entomology and other fields by using a ratio or regression estimator (Cochran 1977), which takes the form

$$\bar{y} = \left(\frac{\bar{y}_1}{\bar{x}_1}\right)\bar{x}_2$$

where $\bar{x}_1$ is the estimate of mean abundance from sampling technique 1, $\bar{y}_1$ is the estimate of mean abundance from sampling technique 2 when applied to the same study site, and $\bar{x}_2$ is the estimate of mean abundance from sampling technique 1 when applied by itself in a second study site.

Usually x is less costly and less accurate than y. Both x and y are measured on several sampling units and the relationship between them is expressed as a ratio ($\bar{y}_1/\bar{x}_1$). Then a larger number of samples is taken measuring only x. An estimate of y for the entire study area can then be obtained by using the general formula above. This method is mentioned frequently in the following sections. McDonald and Manly (1989) consider an alternative to ratio (regression) estimation in which an attempt is made to calibrate a biased sampling procedure by estimating a selection function.

ESTIMATING RELATIVE ABUNDANCE (INDICES)

The following techniques are designed to give indices of relative abundance, not to estimate absolute abundance or density of arthropods. Most of the methods use a trapping device, such that the sampling unit is insects per trap or time period.

Sticky traps

Sticky traps of various design (see Southwood 1978:250–252) are commonly used to sample flying insects inexpensively; an insect settles on or strikes an adhesive surface and is trapped. Trap size and shape (Heathcote 1957a, b; Younan and Hain 1982) and color of the trap surface (Purcell and Elkinton 1980; Weseloh 1972, 1981) are important. The traps are messy. Temperature can affect the consistency and effectiveness of the adhesive, and large insects tend to bounce off or escape.

Sticky traps have been compared with other flying insect traps or sampling techniques mostly with unfavorable results, in that certain insect taxa, or sizes, or both, were underrepresented (Trumble et al. 1982, Younan and Hain 1982). Because trap color alters the effectiveness of the traps for many insects, between-species comparisons of abundance may be biased. However, strong correlations were documented between sticky traps and absolute counts (Heathcote et al. 1969) and suction traps (Elliott and Kemp 1979), suggesting that sticky traps could be used in a ratio or regression estimation scheme, given a common sampling unit.

Despite the considerable shortcomings, sticky traps have been used widely in ornithological field studies, probably because of their simplicity and low cost. Cody (1981) used them to study the relationship between precipitation patterns and the insects available to birds. Given the extremely low sampling intensity (5 days/year), results should be viewed with caution. Blake and Hoppes (1986) used them to determine prey abundance in treefall gaps, and Hutto (1980, 1981a, 1985b) used them in several habitats. These authors recognized that their sampling schemes did not sample the same arthropods that foliage-gleaning insectivores capture, but assumed that the numbers of insects captured in the traps were correlated with actual prey availability. Given that sticky traps do not capture larval Lepidoptera, an important prey source for birds in many areas, that assumption is questionable.

Moreover, because sticky-trap catches cannot be meaningfully related to a sampled area, and because comparisons of catches between arthropod taxa are biased for various reasons, we doubt that sticky traps are useful in ornithological studies, especially because more reliable methods exist.

Malaise traps

The Malaise trap is an interceptive device made of fine-meshed netting that uses a series of baffles to herd insects into a closed chamber that may or may not contain a killing fluid (see Steyskal 1981 for an excellent bibliography). Malaise traps have been used effectively to sample a variety of flying insects in a variety of habitats (Evans and Murdoch 1968, Matthews and Matthews 1970, Walker 1978). Results indicate that these traps perform well for larger Hymenoptera, adult Lepidoptera, and some Diptera, but they are unsatisfactory for Coleoptera and Hemiptera, which tend to be less common in collections than expected, because they usually drop when encountering obstacles (Juillet 1963, Tallamy et al. 1976, Reardon et al. 1977). Although more comparative studies are needed, the trap's advantages are clear. It samples most flying insects except the Coleoptera and Hemiptera with roughly equal intensity. Collections are funneled into a jar that is easy to handle and process. The jars may be removed if only a portion of the day is of interest. However, they are expensive (approximately $300/trap), transportation is difficult, and they often must be operated for some time to obtain large numbers of insects.

Malaise traps have been used to sample flying insects assumed to be available to a variety of aerial-hawking birds. Often diets of such species have been compared with availability as determined solely from Malaise trap captures (e.g., Beaver and Baldwin 1975, Davies 1977b), or in concert with sticky traps and direct observation (Blancher and Robertson 1987), or together with sweep net samples (Blendon et al. 1986). At least Davies (1977b) recognized that Coleoptera and perhaps other taxa were underrepresented but assumed that trapping results were acceptable because the flycatchers he studied seldom eat beetles. Robust analysis of use versus availability (Johnson 1980) can be helpful when one is unsure of including questionable prey items.

A viable alternative to Malaise traps that operates on a similar principle (i.e., interception) is the stationary tow net, a large net that swivels around to face into the wind. Quinney and Ankney (1985) and Quinney et al. (1986) used them to assess use versus availability of flying insects by Tree Swallows (*Tachycineta bicolor*). These nets have an advantage over Malaise traps because they capture insects that fall when striking an object. Such insects may also be sampled with a window trap—basically a sheet of glass held vertically with a fluid-filled collecting trough below (Chapman and Kinghorn 1955).

Beating or shake-cloth methods

These methods have been in use for a long time in a variety of situations. Typically, a cloth supported by a frame is placed underneath a branch or plant. The vegetation is then shaken or beaten to dislodge insects, which collect in the cloth below. The technique is seldom considered to result in an accurate estimate of absolute density, although the number of leaves in a selected plant or branch can be counted to arrive at a density estimate. Boivan and Stewart (1983) found that while most individuals were dislodged from struck branches, many missed the cloth or moved off too quickly to be counted. Similarly, Rudd and Jenson (1977) found that the technique did not sample highly mobile species efficiently. Frequently, therefore, this method is used together with a more expensive but accurate technique in the form of a regression estimator (Bechinski and Pedigo 1982, Linker et al. 1984), although Marston et al. (1976) were not satisfied with the results of the ratio estimators they derived using shake-cloth sampling. Ornithologists that have used versions of shake-cloth sampling to obtain a measure of relative arthropod abundance include Boag and Grant (1984) and Brush and Stiles (1986).

Sweep-net sampling

The sweep net is probably the most widely used device for sampling arthropods from vegetation. Its advantages are simplicity and speed. Sweep netting has been used in numerous ecosystems where plants of interest are short. Strong positive correlations between sweep netting and more accurate but expensive procedures suggest that the technique may be useful in a regression estimation scheme (Bechinski and Pedigo 1982, Fleischer et al. 1982, Linker et al. 1984). However, others have found regression estimators employing sweep-net sampling to be generally unacceptable (Byerly et al. 1978, Purcell and Elkinton 1980, Ellington et al. 1984). Marston et al. (1982) found sweep netting to collect some groups of insects more efficiently than others, so resulting ratio estimators varied in precision. They also provide some sample size guidelines for sweep netting in ratio estimation schemes.

Sweep netting does not provide a measure of absolute density and it is biased in several ways. It collects only arthropods located in the upper portions of plants. The method is ineffective in tree foliage or extremely short vegetation. The taller a plant is, the smaller the proportion of the plant that is adequately sampled, so arthropods differing in their vertical distributions cannot be compared using sweep netting. Because of the effect of foliage height on the efficiency of sweep netting, it is not useful for comparing the abundance of arthropods between different habitats or between seral stages on the same site (Southwood 1978:240–242).

Sweep-net sampling is extremely popular in ornithology, undoubtedly because it is easy. Murphy (1986) used sweep netting to relate breeding biology of Eastern Kingbirds (*Tyrannus tyrannus*) to food availability, noting that arthropods commonly eaten by kingbirds were located in the upper portion of the field vegetation. Many ornithologists have also used sweep netting in woody vegetation, either to track abundance of arthropods in the same location over time (Sealy 1979, 1980; Biermann and Sealy 1982; Rosenberg et al. 1982; Boag and Grant 1984), to compare abundance of arthropod prey between different areas (Blenden et al. 1986), or to compare availability and use of arthropod prey (Root 1967, Beaver and Baldwin 1975, Busby and Sealy 1979). Because sweep netting of woody vegetation undoubtedly captures more active prey and relatively few caterpillars, which adhere to leaves and twigs more readily than active prey, use-versus-availability estimates using sweep-nets are probably biased, perhaps severely so.

Pitfall traps

Pitfall traps are designed to capture surface-dwelling arthropods, especially such active forms as spiders (Uetz and Unzicker 1976, Doane and Dondale 1979) and ground-dwelling beetles (Thomas and Sleeper 1977, Shelton et al. 1983). The pitfall trap is a receptacle (e.g., cup, jar, can), usually with killing or preserving fluid, sunk into the ground with its opening level with the ground surface. One improvement provides a cover to prevent rain from filling the receptacle (Shubeck 1976), and another uses plastic cups placed one inside the other to prevent escape (Morrill 1975). Barriers leading to the receptacles can increase captures significantly (Durkis and Reeves 1982). Like other trapping techniques discussed in this section, absolute population density cannot be estimated from pitfall traps alone. Frequently, if a single species is of interest, pitfall trapping is used as part of a capture-recapture study (Rickard and Haverfield 1965, Brown and Brown 1984).

The method has been seldom used in ornithological studies, probably because it effectively samples only actively crawling arthropods, and not larvae in the litter layer. Pitfall traps have been used to compare numbers of different arthropod taxa that were known prey of insectivorous birds in pesticide treated and untreated areas (Johnson et al. 1976, Sample 1987), and to compare abundance of surface-dwelling arthropods among Wheatear (*Oenanthe oenanthe*) territories (Brooke 1979), objectives for which the technique is appropriate.

ESTIMATING ABSOLUTE ABUNDANCE (DENSITY)

Methods that allow density estimates are usually labor intensive and expensive and differ in several ways from those previously discussed. First, they depend upon instantaneous measures, whereas most trapping methods measure relative abundance over a period of time. Second, results can be expressed in numbers per unit area, volume, or weight. An intermediate sampling step is usually needed to relate the sampling unit to area sampled, so arthropod counts can be converted to a density estimate. Unlike measures of relative abundance, of course, density estimates allow direct comparisons between different taxa in the same habitats, or between the same or different taxa in different habitats. Certain ways of sampling arthropods in vegetation and in the air also allow density estimates.

Sampling arthropods in vegetation often involves collecting all or part of a plant, with determination of the number of arthropods per leaf, leaf area, shoot, branch, or plant. Arthropods may also be collected from whole plants without collecting the vegetation as well (e.g., by fumigation or careful examination of plants and physical removal of organisms). If the collection technique is efficient, a reasonable estimate of numbers per plant or other unit of vegetation can be obtained. In some cases, arthropods can be counted directly on foliage without collecting vegetation or removing the organisms. In all of these instances, knowledge of the density of the collection unit then allows conversion of arthropod counts to density estimates. Another approach that allows density estimation uses suction traps to capture flying insects, with counts being expressed in terms of a given volume of air.

Collecting vegetation

Counting arthropods on collected whole plants is usually restricted to relatively small plants, frequently crops such as cotton and soybeans. Because it can be time consuming, whole plant assessment is often used as a basis of comparison for other sampling techniques, such as vacuum and sweep-net sampling (Smith et al. 1976, Byerly et al. 1978), shake-cloth and vacuum sampling (Fillman et al. 1983), and shake-cloth and sweep-net sampling (Linker et al. 1984).

Pole pruning or branch clipping is similar to whole plant sampling, but the vegetation of interest (usually trees) is too large to allow collecting the entire plant; branches are pruned and collected instead. This is often done with a pole pruner, featuring a cutting device at the end of one or several extendable poles that is operated from the ground. The cut branch is either collected in a basket suspended beneath the cutter or it crashes to the ground, usually onto a tarpaulin, where it and any expelled arthropods are collected.

Because more active arthropods often escape or are expelled when a branch is disturbed, pole pruning is largely restricted to use with caterpillars and other relatively sedentary arthropods. It has been used widely in ornithological research to study bird-insect relationships associated with caterpillar populations (e.g., Morris et al. 1958; Tinbergen 1960; Buckner and Turnock 1965; Royama 1970; Morse 1973, 1976a; and Emlen 1981). It seems to be the preferred technique for mid- to upper-canopy caterpillar sampling and has been used to sample larval stages of spruce budworm (*Choristoneura fumiferana*) (Carolin and Coulter 1971, Torgersen et al. 1984a), Douglas-fir tussock moth (*Orgyia pseudotsugata*) (Mason and Overton 1983), gypsy moth (*Lymantria dispar*) (Martinat et al. 1988), leaf miners (Pottinger and LeRoux 1971) and others (Markin 1982, Martinat et al. 1988).

A variation of this technique involves placing a plastic bag over a branch and clipping it with shears. The sample is then fumigated and the arthropods are collected. Majer et al. (this volume) found that few arthropods escaped using this method. Schowalter et al. (1981) used a long-handled insect net fitted with a closeable plastic bag and a long-handled pruning hook to cut the sample.

Few studies have compared the effectiveness of pole pruning with other sampling methods. Mason (1970, 1977), who developed sampling techniques for the Douglas-fir tussock moth, concluded that pole pruning at midcanopy was an ineffective technique when populations were low, because of the small sample sizes. His preferred method involved beating lower canopy branches over a shake cloth on which dislodged larvae could be counted. Majer et al. (this volume) compared branch clipping with pesticide knockdown for sampling canopy arthropods in eucalypt forests. Branch clipping gave a much better representation of sessile arthropods, such as psyllids, caterpillars, and web-spinning spiders, but was inadequate for sampling mobile arthropods.

The value of pole pruning depends on study objectives. The technique is appropriate for determining caterpillar abundance, but not for determining use versus availability of all prey by birds. Further, pole pruners are difficult to operate at heights >15 m, thus precluding sampling of taller forest canopies. Those problems can largely be overcome by bagging, clipping, and fumigating samples, but the investigator must gain access to canopy foliage. Schowalter et al. (1981) used platforms to reach canopy foliage, and Majer et al. (this volume) used a mobile cherry picker.

In addition to collecting live foliage by pole pruning, researchers have measured arthropod fauna available to birds by collecting dead foliage. Gradwohl and Greenberg (1982b) collected dead leaves inside and outside of exclosures to determine the effect of avian predation on dead leaf arthropods. Smith and Shugart (1987) related prey abundance and territory size of ovenbirds (*Seiurus aurocapillus*) by collecting litter samples within a circular hoop and sorting arthropods from the litter. Berlese funnels considerably facilitate this process (Southwood 1978: 184–186).

Stationary suction traps

First developed by Johnson (1950) and Taylor (1951), stationary suction traps vacuum flying insects into a collection device in a fixed spot. The trap usually features an electric fan that pulls or drives air through a fine gauze cone, which filters out insects. The trap may be fitted with a device that separates the catch by time intervals. Taylor (1955, 1962) standardized air flow and trapping results of numerous suction traps, and estimated their absolute efficiency. Based largely on those results, Southwood (1978) considered the suction trap to sample a fixed unit of habitat and thus provide an estimate of absolute abundance. Because they are believed to sample most flying insects in an unbiased fashion, suction traps are a substantial improvement over sticky and Malaise traps. The primary disadvantage is cost.

Suction traps have been used to sample aphids, lacewings, Coleoptera, Diptera, and Hymenoptera (Taylor 1951, 1962). Johnson (1950) compared his suction trap with sticky traps and tow-nets (Broadbent 1948) and found that it performed best for aphids and other small, airborne insects. Elliott and Kemp (1979) also used suction traps for aphids and developed regression estimators to compare them with sticky-trap results.

Suction traps have been used effectively to determine abundance of flying insects in several studies. Holmes et al. (1978) used them to determine diurnal change in flying insect abundance and response in foraging behavior by American Redstarts (*Setophaga ruticilla*). Catchability bias associated with insect size was calibrated using Taylor's (1962) correction factors. Bryant (1973, 1975b) used suction traps to assess use versus availability of flying insect prey of House Martins (*Delichon urbica*). Bryant (1975a) also used suction traps to relate breeding biology of House Martins to food supply. Because suction trapping is efficient and its bias can be calibrated, we believe the above procedures resulted in good estimates of the flying insects available to the birds of interest.

Portable vacuum sampling

Also called suction sampling, this procedure uses a portable vacuum. It was first applied by Johnson et al. (1957) and Dietrick et al. (1959). Dietrick's model was later improved (lightened to approximately 27 lbs.) and is now known as the d-Vac sampler (Dietrick 1961).

The d-Vac has been used widely in agricultural and other ecosystems, such as for Homoptera in flooded rice fields (Perfect et al. 1983) and cherry orchards (Purcell and Elkinton 1980), weevils in thistle plants (Trumble et al. 1981), mosquitos in salt marshes (Balling and Resh 1982), aphids on peaches (Elliott and Kemp 1979), and various arthropods in cotton (Leigh et al. 1970, Smith et al. 1976, Byerly et al. 1978) and soybeans (Bechinski and Pedigo 1982, Culin and Yeargan 1983).

Portable vacuum samples are closely correlated with direct counts (Ellington et al. 1984) and have even exceeded whole-plant visual sampling of thistles (Trumble et al. 1981). Although they have been used to estimate densities (Perfect et al. 1983), Wiens (1984b:404) found that d-Vac sampling of arthropods on sagebrush was only 55% efficient, and that different taxa were sampled with differing effectiveness. Leigh et al. (1970) also concluded that suction sampling alone cannot estimate density; they recommended using the d-Vac with a sampling cube for such an estimate.

Portable vacuum sampling has not been used extensively in ornithological research. The cost of suction samplers (about $1000; Dietrick, pers. comm.) precludes their use in many studies, and their bulk makes them unsuitable in certain situations, such as forest canopy sampling. Suction samplers are especially efficient in shrubby or field-like habitats. For example, K. G. Smith (1982) used a portable vacuum sampler with a sampling cube to collect herbaceous and understory arthropods in a standardized area and time period in a study of drought-induced changes in a bird community. Rotenberry (1980b) used a portable vacuum sampler and a quicktrap (Turnbull and Nicholls 1966) to sample shrubsteppe arthropods.

Direct observation

Occasionally it is feasible to count arthropods directly. Use of more than one observer introduces observer bias, and direct observation is especially time consuming and requires well-trained observers. Furthermore, not all types of arthropods are equally observable, due to activity or crypsis. However, the method has the major advantage that all observable arthropods are measured in the same units (e.g., insects per leaf, leaf area, or plant). Also, many ancillary data (location, substrate, plant species association, or escape behavior of arthropods) can be recorded, most of interest to ornithologists (e.g., Greenberg and Gradwohl 1980, Holmes and Robinson 1981, Cooper 1988, Holmes and Schultz 1988).

Direct observation is rarely used in entomological field studies to sample arthropods of forest canopies. The objective of much entomological research is to sample populations of one species or family of arthropod, which can generally be sampled more efficiently by using one or a combination of the previously mentioned methods. Ornithologists, however, are usually more interested in the entire arthropod community in terms of its availability to birds as prey. Often relative numbers of different prey taxa are compared with the frequency of those taxa in bird diets. Thus, a sampling method is required that targets all arthropod taxa. This is accomplished with direct observation methods, if performed carefully. Not surprisingly, then, the method has been used frequently in ornithological research to count arthropods on herbaceous vegetation (Schluter 1984, Blancher and Robertson 1987), tree trunks (Cooper 1988), understory tree foliage (Holmes et al. 1979c), dead leaves (Gradwohl and Greenberg 1982b), and mid- to upper-canopy foliage (Greenberg and Gradwohl 1980, Holmes and Schultz 1988). Access to canopy foliage has been done using towers (Greenberg and Gradwohl 1980) or tree-climbing gear (Cooper 1989, Holmes and Schultz 1988).

MISCELLANEOUS TECHNIQUES

Many other arthropod sampling methods do not fit under the above categories but have been used in ornithological research. Some are designed especially to sample a single species. For example, frass traps have commonly been used to sample larval Lepidoptera (e.g., Betts 1955). They are funnel-shaped structures placed on the forest floor to collect arthropod excrement, providing an index of abundance. If mean daily production of excrement can be calculated, absolute abundance can be estimated (Liebhold and Elkinton 1988). Use of frass traps requires prior study of frass from target species, so it can be distinguished in the field from that of other insects.

Pheromone traps are commonly used for adult Lepidoptera of pest species and were used by Crawford et al. (1983) to sample spruce budworms in a study of avian predation. Some species, such as the gypsy moth, lay conspicuous masses of eggs that overwinter and can be counted as an index of abundance (Smith 1985). Burlap bands wrapped around trees have also been used to count late instar gypsy moth larvae, which hide beneath the burlap during the day (Campbell and Sloan 1977).

Emergence traps, which are cone-shaped nets erected with the circular end flush to the ground, were used to estimate the emergence rate of periodical cicadas (Homoptera : Cicadidae) in a study of avian response to this superabundant prey source (K. Smith, pers. comm.). Buckner and Turnock (1965) trapped emerging larch sawfly (*Pristiphora erichsonii*) adults and Orians and Horn (1969) trapped emerging damselflies in similar studies using emergence traps.

A method that seems to be gaining popularity among ornithologists working in forest habitats is the pan or water trap (Southwood 1978:252–253). These are plastic containers filled part way with water and a preserving solution (e.g., salt or antifreeze) and placed on the ground or hung in the canopy. They effectively capture many arthropod taxa (Morrison et al. 1989). Although pan traps are undoubtedly biased against certain types of arthropods and are likely to be affected by trap color, they are an inexpensive way to assess canopy arthropod abundance over time or between locations.

Another method, pesticide knockdown, can be used to sample all types of arthropods in a less biased manner than many of the previously mentioned techniques. Using a fogging machine and a pyrethroid pesticide, which has strong knockdown ability but breaks down quickly and has low vertebrate toxicity, the forest canopy can be fogged in a systematic fashion. Pyrethrin killed virtually all arthropods in patches of foliage examined before and after fogging (Cooper, unpubl. data). Majer et al. (this volume) found that pesticide knockdown missed some types of sessile arthropods obtained in branch clipping samples. Some flying insects were also able to escape at the time of spraying. Dead insects fall to the ground and are collected in jars at the bottoms of funnels made of canvas or plastic (Wolda 1979; Majer et al., this volume) or on collecting cards (Raley 1986). The percent composition of each arthropod taxon can then be computed and compared with the percent of each taxon in bird diets. The drawbacks of this method are that arthropod densities are difficult to compute and that arthropods are not observed until they are collected, so an understanding of their location and behavior must be obtained in some other way. Foggers and pesticides are also expensive. A major advantage is that large numbers of arthropods are collected per sample in a short period of time. Also, in forests with extremely tall canopies, such as tropical rain forests, fogging may be the only way to sample arthropods from the upper layers (Wolda 1979).

DISCUSSION

If the objective is to measure the abundance of a particular arthropod taxon or overall abundance of all arthropods in the same location over time, or to compare the abundance of a particular taxon or all arthropods between different locations, then almost any of the techniques described above will suffice, because the inherent biases of a sampling method against certain prey taxa should be more or less constant. However, if the objective is to assess the relative abundance of different prey taxa available to birds, the method of choice must sample all relevant arthropods with equal intensity. This is relatively easy for some bird species, such as swallows and some flycatchers, which feed almost entirely on flying insects that can be sampled with a stationary suction sampler or stationary tow nets (Bryant 1973, 1975b; Quinney and Ankney 1985).

Because most bird species do not entirely feed on one type of arthropod, but use a variety of foraging behaviors and different substrates to capture several types of arthropod prey, this presents a formidable sampling problem; different types of arthropod prey (i.e., flying, foliage-dwelling, bark-dwelling) must be sampled in a consistent fashion that allows the researcher to compare the abundances of all types.

TABLE 1. SUMMARY OF SOME ARTHROPOD SAMPLING TECHNIQUES COMMONLY USED IN ORNITHOLOGY

Method	Arthropods sampled	Advantages	Disadvantages
Sticky trap	Flying or otherwise active	Inexpensive; able to cover large area	Messy; influenced by trap color, temperature; small interceptive surface
Malaise trap	Flying	Easy to maintain; large interceptive surface	Expensive, bulky; biased against Coleoptera; few catches per unit time
Stationary tow-net	Flying	Inexpensive; captures most flying insects with equal probability	Small interceptive surface
Shake-cloth	Foliage-dwelling	Inexpensive; good for sessile arthropods	Active arthropods can escape; hard to sample in canopy
Sweep-net	Foliage-dwelling	Simple, inexpensive; good for active arthropods	Biased by foliage height and against sessile arthropods
Pitfall trap	Ground-dwelling	Simple, inexpensive; can estimate density of single population using capture-recapture	Biased against inactive litter arthropods; captures affected by density and type of ground cover
Pesticide knockdown	Foliage-dwelling	Samples many types of arthropods with approximately equal probability	Foggers, pesticide expensive; affected by wind; can miss attached or extremely active arthropods
Frass traps	Caterpillars	Field methods simple, inexpensive; absolute density estimable	Requires arthropods be kept in captivity
Emergence traps	Arthropods emerging from soil or water	Inexpensive; can estimate density of emerging arthropods	Large number often required to adequately cover area of emergence
Pole pruning	Sessile, foliage-dwelling	Inexpensive method of reaching forest canopy	Biased against active arthropods; few arthropods per sample
Branch-clipping	Foliage-dwelling	Captures many arthropods missed by pole pruning; inexpensive but must gain access to forest canopy	Biased against active arthropods; few arthropods per sample
Suction	Foliage-dwelling	Gives good estimates of abundance when used with sampling cube or quick trap	Expensive; can miss some arthropods
Stationary suction	Flying	With correction factors gives good estimates of abundance; can sort samples by time	Expensive; difficult to sample large area
Direct observation	Foliage-dwelling	Can directly compare abundances of different arthropod taxa; many ancillary data on arthropod ecology collected; arthropods "collected" quickly on tape recorder	Observability bias likely for both arthropods and observers; must gain access to forest canopy, strenuous; identification to species level often difficult

In field-like ecosystems, for example, sweep netting is often used. It is fast, simple, and efficient, but it is biased against arthropods located near the ground. This bias can be corrected by using a more accurate method, such as portable vacuum sampling, on a subset of the units sampled by sweep netting and relating them by means of a ratio or regression estimator. Of course, if possible for all samples, portable suction samplers would be more desirable than sweep netting.

In forest ecosystems, canopy-dwelling, foliage-gleaning birds feed upon a variety of arthropods associated with bark, foliage, and air. Most of the aforementioned sampling methods work best on only one of these substrates and would be inappropriate for assessing use versus availability. Two methods, direct observation and pesticide knockdown, are effective for comparing relative frequencies of different arthropod taxa available to and used by foliage-gleaning birds. While those methods are not unbiased, they are preferable for sampling canopy arthropods.

Most ornithological studies have used arthropod sampling in an effort to relate some aspect of avian feeding ecology to arthropod availability. Yet few studies have done this adequately. Typical shortcomings include inadequate sample sizes and inappropriate extrapolation from a specialized technique to make inferences about total arthropod availability. Sample size is more likely to be a problem with methods like branch clipping or direct observation that obtain only a few arthropods per sample than with methods that obtain large numbers of arthropods per sample (Gibb and Betts 1963, Cooper 1989; Majer et al., this volume). Many types of arthropods have clumped distributions, which can greatly inflate variance estimates using methods that sample a small volume of foliage or airspace. Sample-size problems like these are offset by the larger number of samples usually obtainable per unit time and the shorter amount of sorting time required using branch clipping and direct observation. Sorting time can reach mountainous proportions in techniques that obtain large numbers of arthropods per sample (Table 1).

Not surprisingly, many studies that have meaningfully associated some aspect of avian ecology with arthropod availability have either been done in structurally simple habitats such as shrubsteppes or pine plantations or have involved birds known to feed almost exclusively on one type of insect. Other studies have concentrated on a single type of insect known to be especially important to the bird species of interest.

The few meaningful studies (see Root 1967, Holmes and Robinson 1981, Robinson and Holmes 1982, Rosenberg et al. 1982, Holmes et al. 1986, Holmes and Schultz 1988) have several things in common. First, most lasted three or more years. Second, sampling procedures were frequently directed towards only one type of prey such as caterpillars (Holmes and Schultz 1988) or cicadas (Rosenberg et al. 1982). Sampling methods used for assessing arthropod availability, such as sweep-net sampling of woody vegetation (Root 1967, Rosenberg et al. 1982) were often biased. However, the methods were sufficient to demonstrate seasonal changes in arthropod abundance, which is often all that is needed. Third, the authors all performed dietary analyses to convincingly establish which prey birds were selecting, and which strengthened the conclusions concerning arthropod availability and foraging or reproductive behavior.

Studies of bird-insect relationships have long been of interest to avian ecologists and seem to be gaining popularity. Because this area of ecology involves insects as much as birds, knowledge of insect ecology and behavior is important, as it clarifies how and why birds capture and eat certain types of prey. Sampling methods involving direct observations can be particularly insightful.

Virtually all techniques in this paper have been developed by entomologists. Comparison of methods, advantages and disadvantages, calibration of biases, and required sample sizes appear in the entomological literature. Other methods, such as direct observation and pesticide knockdown, which are likely to gain favor with ornithologists, should be similarly assessed (e.g., Majer et al., this volume). No single, magic sampling method exists. Each has strengths and weaknesses, and each is biased to some extent. Bias can be tolerated in certain situations and corrected in others. An appropriate sampling design depends upon study objectives and the scale of investigation. In general, more time and effort should be devoted to arthropod sampling in ornithological research than has been done in the past. We encourage ornithologists to investigate, compare, and report the efficacy of different methods and designs as they pertain to the objectives of ornithological research.

ACKNOWLEDGMENTS

This research was supported by funding through the McIntire-Stennis program and, in part, by USDA Forest Service Cooperative Agreements 23-972, 23-043, and 23-144, and a Sigma Xi grant-in-aid of research. We thank L. Butler, L. L. McDonald, M. L. Morrison, C. J. Ralph, J. T. Rotenberry, K. G. Smith, and J. Verner for reviewing the manuscript. P. W. Brown, K. M. Dodge, and P. J. Martinat provided many helpful comments. Published with the approval of the Director, West Virginia University Agriculture and Forestry Experiment Station as Scientific Article No. 2120. This is contribution No. 7 of the Forest Arthropod Research Team.