CONFRONTING THE DOGMA: A REPLY

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Barclay (1999) criticized the qualitative approach for acoustic identification of species of bats (O'Farrell et al., 1999) on the basis of intraspecific variation due to geography, habitat, and species-assemblage factors. However, variations described to date represent minor variations in specific parameters of call structure and, with experience, present no difficulty in discriminating among species. Certain species, under certain circumstances, emit calls that may be confused with other species. These calls represent a small percentage of the total repertoire. Experience reveals these cases, and such calls should be judged unidentifiable. Barclay was concerned about a qualitative approach but stated that quantification has shown variation sufficient to negate the ability to identify species. The qualitative approach avoids this problem because it is not sensitive to minor quantitative differences.

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The basic assumption in O'Farrell et al. (1999) was that Anabat was a useful tool in identification of free-flying bats. Barclay (1999) apparently misinterpreted this as promoting the idea that all calls of echolocating bats are species-specific and identifiable. There was no intention to imply that all bats could be identified in this way, just as not all birds can be identified by song. There are a number of species known to use low-intensity, short-duration calls that seem to differ little among species (e.g., phyllostomids—Griffin, 1958), and acoustic identification might be inappropriate for those species. However, our extensive experience with Anabat in Australia, North America, and Central America shows that many species can be identified acoustically. We see no reason to assume that bats that were difficult to identify using earlier acoustic methodologies will still prove difficult when Anabat is applied with adequate competence.

We maintain that the reliability of acoustic identification must be determined for each species on a regional basis and that this process is still very much in its infancy. O'Farrell et al. (1999) was an introduction to methods that the authors have found effective, and they hoped that sharing these ideas would assist others in achieving greater competence. It was not intended to present these methods as the final word, and it seems clear that quantitative methods will have a role in refining methodologies and assessing reliability.

We agree with Barclay (1999) that limitations of equipment and methods must be identified. O'Farrell et al. (1999) provided an initial assessment of limitations of equipment and types of questions that are appropriate.

ECHOLOCATION IS NOT SONG

O'Farrell et al. (1999) attempted to justify the use of qualitative methods for acoustic identification of bats by pointing out that such methods are used routinely for identification of other groups in the field, specifically birds and frogs. Barclay (1999) argued exhaustively that the roles of bird songs are fundamentally different from those of the calls of echolocating bats, a point with which we agree. However, Bar-

clay's assumption that these differences should somehow render bat calls less useful for discrimination of species seems unwarranted. Our own observations make it very clear that many species of bats can be identified acoustically using Anabat without recourse to quantitative methods, such as statistical analysis.

We do not think that all species of bats are identified easily by acoustic methods. The difficulty encountered is highly dependent on which confusable species may be found in the same locality or region. This is exactly the same situation presented by birds. As with birds, acoustic identification of bats requires a great deal of experience, and the skill of the investigator will have a major influence on the reliability of the approach. However, approaches used in learning vocalizations of the two groups are different. Vocalizations of birds must be learned acoustically, but with Anabat, most vocalizations of bats are learned visually. Overall, the most significant problem is confirmation of identity, and this is the overriding factor that makes acoustic identification of bats more difficult. We see no compelling evidence that calls of bats are harder to distinguish because of any inherent lack of species-specificity.

We disagree with Barclay's (1999) conclusion that there is no reason to expect the existence of vocal signatures. Species-specific differences have been documented that appear to be genotypic rather than situation-based variations (Simmons et al., 1979). There is ample evidence that the time-frequency structure of calls is correlated with the foraging strategy of individual species (e.g., size of prey, behavior of prey, microhabitat being negotiated—Kalko, 1995; Schnitzler and Kalko, 1998; Simmons and Stein, 1980). Complex species assemblages of bats can be described in terms of niche separation, including type and size of prey pursued and the microhabitat used in hunting activity (Findley, 1993). Kalko (1997) found that aerial insectivorous bats, which rely almost exclusively on echolocation for orientation in space and for foraging, usually emit species-specific types of signals. Inability to discriminate among species within discrete assemblages should be the exception and not the rule. Knowledge of community patterns of guild structure based on echolocation-signal design, in addition to the commonly used criteria of diet, habitat use, and wing morphology, will help clarify these assemblages (Kalko, 1997).

Intraspecific Variation in Design of Echolocation Calls

Barclay (1999) argued that intraspecific variation in calls of echolocating bats makes it difficult to use these calls for identification of species. We agree because intraspecific variation complicates any identification process. Most of Barclay's comments consisted of generalizations that apply in some situations but not others, and these comments suggest a lack of experience on his part with the methodologies being discussed, specifically with Anabat. Each case must be treated on its own merits, and we stress that an unskilled user may encounter formidable problems that a skilled user will regard as trivial.

Variation within an individual.—Barclay (1999) implied that variation in calls given by a single individual would confound the process of acoustic identification. As an example, he cited the well-known variation in calls that accompanies the process of detecting, approaching, and attacking prey (Griffin et al., 1960). Although this pattern varies among taxa, it is predictable and easy to take into account when trying to identify bats using Anabat.

We agree with Barclay (1999) that calls produced in different situations by one species may cause confusion with other species. However, this is not a universal truth, and problems that result must be assessed in each case. For example, high-clutter search-phase calls of *Eptesicus fuscus* closely resemble low-clutter calls of *Antrozous pallidus*. Nevertheless, such calls represent only a small percentage of the calls

obtained from either species, and an experienced investigator should recognize this potential problem and place such calls into the category of "unidentifiable." Inability to identify some calls given by a particular species in no way reduces the value of the technique—just as the inability to catch every bat that passes close to a mist net or harp trap does not render those techniques invalid.

Barclay (1999) stressed that calls recorded from bats flying in rooms cannot represent calls of bats in natural habitats. O'Farrell et al. (1999) indicated that only certain species (e.g., mormoopids) or individuals of uncommon or rare species were recorded within large enclosures. Mormoopids emit identical calls in enclosures and under free-flight conditions. The reason for applying the technique to less common species of other families involved the overwhelming need to establish a baseline no matter how crude. We know that bats in enclosures generally produce calls of shorter duration, broader range of frequency, and higher minimum frequency than during free flight in less constrained conditions. Data obtained from enclosures provide a starting point.

Barclay (1999:292) further claimed that "reference calls need to come from bats flying in the habitat(s) being studied." We have seen no indication that habitat is an important factor in determining the types of calls given by bats. Rather, bats vary their calls continuously as they respond to their immediate surroundings on a much smaller scale than that of habitat (Kalko, 1995; Kalko and Schnitzler, 1993; Obrist, 1995; Schnitzler and Kalko, 1998). Awareness of these changes and the ability to observe the proximity of clutter while monitoring with Anabat provides the observer with contextual information that assists in identifying species. An observer wishing to identify bats acoustically must be aware of such subtleties and learn to cope with them.

Variation within a population.—Barclay (1999) stated that some intraspecific variation is caused by differences in age or sex. However, O'Farrell et al. (1999) emphasized that determination of such inter-individual variation is fundamental to identification of any organism.

Variation between populations.—Barclay (1999) claimed that geographic and subspecific differences in structural characteristics of calls are well documented, citing Parsons (1997) and Thomas et al. (1987). However, differences in critical characteristics of species presented by these authors are miniscule and well within variation found in one or several individuals at the same location (O'Farrell et al., 1999). For example, we stated that minimum frequencies varied by several kHz for each individual when multiple bats of the same species were flying in close proximity to each other. Nevertheless, shape of calls remained consistent and such individual variation did not hinder identification of species. Likewise, a single sequence of calls will not contain all variability inherent within a species. Experience and an expanding library of vocalizations across a species' range will account for such variation during the identification process.

Without voucher recordings in a recognized repository, it is difficult to assess previous work. Barclay (1984, 1985, 1986) used a simple dichotomy in call structure to identify *Lasiurus cinereus* and *Lasionycteris noctivagans.* However, we have documented a range of variation in those species (O'Farrell et al., 1999) suggesting that Barclay's criteria for identification was not complete. If recordings of the calls on which future investigators based their identifications were available in a repository, it might be possible to confirm, or refute, past identifications and reassess conclusions accordingly. At present, we have little indication of the magnitude of incorrect identifications from past research.

Variation due to recording differences.—We agree with Barclay that exact recording circumstances will have a profound effect on the nature of an Anabat display of a se-

quence of calls. However, use of any tool requires that the user understand how the tool performs under different circumstances. A user of Anabat must understand how the system works to get meaningful results from it.

One advantage of a real-time display, such as that provided by Anabat, is that it allows the user to gain quickly an appreciation of effect of changes in settings and setup. Such changes will affect only those parts of a call that the Anabat detector will detect reliably. Most recorded sequences will contain a number of calls that are detected with varying effectiveness. Those detected well will result in whole calls being displayed on the screen. Those detected poorly will be displayed as fragments representing only the loudest parts of those calls (O'Farrell et al., 1999:14; figure 1).

In practice, the only issue affected will be how close a bat must be before its calls are detected completely and displayed on the computer screen. Nearly all recorded sequences include calls that are recorded from too far away to be detected completely, so only parts of those calls will be displayed. Such fragments of calls may or may not show all characters that would help in identification. Therefore, O'Farrell et al. (1999) emphasized the need for the user to learn how to distinguish fragmentary recordings and to treat them accordingly. As with all aspects of acoustic identification, the usefulness of such fragments will depend on which species is being recorded, which species it might be confused with, and experience of the investigator.

Calls of bats vary for a variety of reasons. Understanding that variation is key to successful acoustic identification—just as understanding variation is key to identification of any organism, no matter what characters are being used. We regard it as essential that anyone attempting acoustic identification of bats be thoroughly aware of all sources of variation described by O'Farrell et al. (1999) and reiterated by Barclay (1999). Future investigators also must distinguish situations where this variation becomes a problem to identification and when it can be ignored.

Uses Of Identification By Echolocation In The Field

Barclay (1999) focused attention on the stringency of tests reported in O'Farrell et al. (1999) and appeared troubled that error rates were often >5%. We stress that those error rates involved two observers trying to identify recorded sequences of good quality, for a wide range of species, from the southwestern United States. Less experienced users dealing with recordings that typically result from use of fixed recording stations, and especially those recorded via analog tape-recorders, should be expected to fare much worse. Conversely, someone working in real time probably could achieve better results, especially if visual observations are combined with acoustics.

Most importantly, we stress that identifiability varies among species and geographical regions because these factors influence which species may be confused. The development of criteria for acoustic identification is still at a very early stage. The value of tests, such as those described in O'Farrell et al. (1999), is that they help identify where problems exist in acoustic identification and suggest ways to improve performance.

Much of Barclay's (1999) discussion concerned sampling biases. We agree that acoustic sampling will not work with equal effectiveness across all species of bats. We also agree that different recording methods will affect biases imposed. However, O'Farrell et al. (1999) were not trying to convey the impression that acoustic sampling was devoid of bias, and they identified limitations of acoustic identification with Anabat. As far as we can tell, every method ever used to sample bats has been subject to biases. By using a variety of sampling techniques, the bias is reduced, but that has not prevented useful data from be-

ing collected using a subset of techniques available.

Surveys will be most comprehensive when investigators use multiple methodologies (Kalko et al., 1996; O'Farrell and Gannon, 1999), but in some situations, practical considerations make that infeasible. In this situation, an acoustic survey conducted by sufficiently experienced personnel often will result in a more comprehensive survey over a broader area than conventional capture techniques alone. Interpretation of the results of such a survey should be tempered by the limitations inherent in the technique, but this is equally true of all surveys using any technique.

Overall, we suggest that, in many situations, acoustic sampling may be much less biased than methods that involve capturing bats. As techniques of acoustic identification improve, effectiveness of acoustic surveys will inevitably increase.

The Qualitative Method Versus Quantification

Barclay (1999) took issue with the way that O'Farrell et al. (1999) emphasized the need to discriminate between fragments of calls and calls that were recorded more completely by the Anabat hardware. He suggested that the criteria used to make this discrimination were subjective and would not be agreed upon by different workers, arguing that such fragments "may in fact be complete variants of calls" (Barclay, 1999:294). Not all calls are detected equally by the Anabat system, but we consider it easy to recognize the difference between fragments and complete calls. We further contend that experienced operators will agree. Anyone lacking the experience to make this distinction should not attempt to identify bats acoustically.

Finally, Barclay (1999) pointed out that precise quantification often has failed as a tool for distinguishing among species because of combined inter- and intrapopulational variability. This is exactly why we adopted a qualitative approach that is less sensitive to such variation.

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