Letters

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The Group Strikes Back: Follow Protocols for Behavioral Research on Cetaceans

Recent reviews of the methods used by cetologists to obtain behavioral data (Mann 1999, 2000; Bejder and Samuels 2003) have recommended that in most circumstances data should be collected while following individuals rather than following or surveying groups. I disagree.

The writing of this letter stems partly from personal experience. I have supervised a number of graduate students of cetacean behavior over the past 15 yr. In preparing their project proposals they would read about sampling methods used on terrestrial animals (*e.g.*, Altmann 1974) and conclude that concentrating on individuals was the way forward. They would devise careful focal-animal protocols, go out to sea, and then, usually, abandon them, following or surveying groups instead. Jenny Christal was more persistent. She managed to collect 18.25 h of focal-animal data on sperm whales (*Physeter macrocephalus*) during a 2-mo field season off the Galápagos Islands in 1995. She used these data neither in her thesis (Christal 1998) nor in any of the resulting papers (Christal and Whitehead 1997, 2000, 2001; Christal *et al.* 1998). In preparing a book about sperm whale social structure, I revisited Jenny Christal's focal-animal data, using them to determine joining and splitting rates of short-term clusters of whales at the surface as well as fluke-up synchrony within clusters (Whitehead 2003). Almost everything we have learned about the social structures of sperm whales, including that about relationships between individuals (Christal and Whitehead 2001), comes from data collected when groups were the focus of study.

Mann (1999) usefully distinguishes between the "follow protocol" and the "sampling method" (*e.g., ad libitum* or "point sampling"). Here I am directly concerned with choosing a suitable follow protocol, and, following Mann, will consider three types of follow: the "group-follow" in which the researcher attempts to maintain contact with, and attention on, a spatio-temporally distinct set of animals: the "individual-follow" where an individual animal is the focus of attention; and the "survey" in which the observer encounters groups during a systematic, random, or haphazard survey of a study area, collecting data on each group before moving on. Here I am going to discuss how well the different follow protocols operate in examining cetacean behavior, under the premise that the appropriate approach depends on both the research question, *and* the constraints of the research situation. I consider goals, bias, precision, practicality and the more fundamental issue of the level of investigation.

Behavior is a wide field of enquiry. At the most basic level, we may wish to describe what the animals are doing, perhaps by constructing an "ethogram." A second stage is to compare behavior, between individuals, groups, age and sex classes, geographical areas, environments, levels of disturbance, time periods, populations, species, or levels of any other relevant factor. These descriptions and comparisons can be aggregated into three classes: when the individual identity of the animals on whom the data are collected is important (*e.g.*, studies of individual behavioral development, or research on an anthropogenic impact in which the change in individual behavior is the measure of interest); when groups are the fundamental

level of analysis (as is often the case when examining group-specific behavior in studies of culture); and when specific individual or group information is not needed (*e.g.*, comparisons between the behavior of sexes, sub-populations or populations).

A rather separate goal is the study of social structure. Following Hinde (1976), this is done by collecting data on interactions between identified animals (*e.g.*, touches or simultaneous surfacings), using these data to describe their relationships, and then integrating relationships among members of the population to form a model of social structure. An alternative, which is generally more practical, especially with cetaceans, is to measure dyadic "associations"—circumstances in which interactions are likely to occur (Whitehead 1997). One way to do this is to make "the gambit of the group," and assume that all animals within a spatio-temporal group are in association (Whitehead and Dufault 1999).

An important distinction among measures of behavior is between "events" and "states" (Altmann 1974). An event (such as a breach, vocalization or exhalation) is nearly instantaneous; a state (such as feeding, or traveling) is continuous. When considering dyads, interactions may be thought of as events, and associations as states.

Events seem more firm and fundamental than states: observing that a dolphin has caught a fish being preferable to noting than it is in "feeding mode"; observing two animals touching better than noting that they are grouped. However, even if fish are not caught, animals may have spent considerable energy foraging, and a pair may have an important relationship but not touch. Thus it is not clear to me that events and interactions are fundamentally better measures of behavior than states and associations. And, from the practical perspective, if we rarely see fish being caught or animals touching, states will be more appropriate behavioral measures. The choice of events or states will depend both on the research question, and, especially with hard-to-watch animals like cetaceans, the constraints of the research environment. Sometimes both can be collected.

In Table 1 the suitability of the different follow protocols for collecting event or state behavioral data is assessed for situations when populations, groups, individuals or dyads are the unit of interest. State data can come from all three protocols; whereas event data are only collectible when following groups or individuals (as events rarely occur during the short duration of the survey). Furthermore, with cetaceans, it is practically impossible to collect good data on the rate of interactions from group-follows, because we need to know, for each dyad, how long they are visible, and this is usually impossible to know with animals like cetaceans which are frequently not visible (Altmann 1974).

It might be thought that to collect behavior at the level the individual or dyad, as needed for studies of individual behavioral development or relationships between individuals, individual-follow data would be necessary. This is not the case for state data. If individuals can be identified, either in real time or subsequently through analysis of visual or acoustic records, then individual- or dyad-level state data (*e.g.*, proportion of time foraging or association index) are available from either group-follow or survey protocols. Conversely, while carrying out group-follows or surveys, it is not necessary and may not be desirable to collect data at the level of the group, as group-level sampling protocols can introduce bias (see Mann 1999, 2000). For instance, if animals in groups are not all in the same state, then simply recording the predominant state of members of the group ("predominant group-activity sampling"; Mann 1999) can lead to biases against less frequent states. Ideally, during group-follows or surveys, state measures should be recorded for each individual, or dyad. Practical alternatives are to record the proportion of animals in different states, or the states of a randomly or haphazardly chosen subset of individuals. This is effectively what is done when associations are inferred among all animals individually-identified within the group at a particular time.

Examples of research on dyadic associations are Connor *et al.*'s (1992, 1999, 2001) studies of alliances of bottlenose dolphins (*Tursiops* spp.) partially using survey data, and Christal and Whitehead's (2001) examination of relationships within sperm whale groups which entirely used group-follow data.

Table 1. Protocols and measures: ability to measure the incidence of states and rates of occurrence of events in populations (or subpopulations), groups, individuals and dyads using different research protocols during behavioral research on cetaceans. x = feasible protocol; X = optimal?

	Incidence of states for:				Rate of events for:			
	populations	groups	individuals	dyads: association	populations	groups	individuals	dyads: interaction
Survey	X	X	X	X				
Group-follow	X	X	X	X	X	X	X	
Individual-follow	x	x	x	x	x	x	X	X

Bejder and Samuels (2003) repeatedly describe group-follows as producing biased data. If, because of the follow protocol, we consistently over- or underestimate the frequency of particular state or event, there is a bias. Bias could occur because we are more likely to start following or surveying individuals or groups engaging in some kinds of behavior than others, or we are more likely to be able to continue to follow groups or individuals if they are in some behavioral modes than in others.

At the level of choosing subjects, we may be more likely to follow a well-marked individual and rates of scarring may be correlated with behavior, thus biasing individual-follow data. Such bias is less likely for group-follows or surveys, but could be present if groups engaging in more active behavior are more likely to be encountered.

When it comes to the consistency of the follow, then the problems of individual-follow protocols are more severe. Individuals are harder to follow than groups, and following groups is harder than encountering them. For instance, we cannot individually-follow (without tags) female sperm whales during deep dives, but we can do group-follows quite consistently; we may not be able to follow fast-moving groups of pelagic dolphins, but we can record their general behavior in a survey-type protocol. If we relied on individual-follows of female sperm whales, we could conclude that they never dive, if we relied on group-follows of pelagic dolphins we might underestimate their speed of movement.

In general, bias due to selection of, and ability to follow, the focal subject will be *greatest* with individual-follows, intermediate with group-follows and least with surveys. If carrying out individual- or group-follows, the focal individual/group must be selected in an unbiased (group size, behavior, age, *etc.*) fashion or corrections for bias should be applied as needed in the analysis (Mann 1999). These issues of bias are one of the reasons why survey and group-follow protocols, when they are feasible, should generally be preferred to individual-follows (Table 1). While group-follow protocols will rarely be more biased than individual-follows, at the level of the sampling protocols the situation may be reversed, with group-sampling introducing biases not found with individual-sampling (see above; Mann 1999).

A potential problem with group-follows noted by Mann (1999) is that group composition may change, and a bias will result if, for instance, the more active daughter group is followed after a split. This needs to be guarded against by adopting an appropriate protocol for occasions when groups split (Mann 1999).

Mann (1999) reasonably suggests that individual-follow protocols are suitable when individuals are rapidly identifiable in the field, the group size is <10 and the dive time less than 10 min. How often are these conditions always fulfilled? Evans (1987) gives estimates of group size for 56 cetacean species (with *Mesoplodon* beaked whales considered as one species). Of these, group sizes are given as reaching at least 10 for 43 species. Based on my experience and readings, consistent rapid identification of any individual in the field is not currently possible for 11 of the remaining species (*Balaenoptera borealis*, *B. edeni*, *B. acutorostrata*, *Caperea marginata*, *Kogia breviceps*, *Cephalorhynchus hectori*, *Phocoena spinipinnis*, *Phocoena sinus*, *Lipotes vexillifer*, *Pontoporia blainvillei*), leaving just the blue (*Balaenoptera*

musculus) and humpback whale (*Megaptera novaeangliae*) as candidates for unbiased individual-follows. Of course, there will be circumstances when individual-follows are feasible for some of the other species, but if these circumstances are restricted, as they usually will be, then the resultant data have the potential for bias.

Given a certain amount of field effort, the different follow protocols may be able to give more or less precise estimates of behavioral measures. The precision with which any parameter or measure can be estimated is largely a factor of sample size, with precision roughly proportional to the square-root of the sample size (*e.g.*, Sokal and Rohlf 1981). However, for this relationship to be true the samples must be independent. It will often be reasonable to consider survey encounters with different groups as independent. But with group- and individual-follows, only the follow itself is a clearly independent unit. In some circumstances, if there is much temporal variance and little group-specific behavior, time intervals or points along a group-follow may be considered functionally independent. Similarly, if there is little individual-specificity in behavior and much temporal variance it may be possible to consider points along an individual-follow as independent.

If observations of state (individual state or group state) x time units apart can be considered independent, then group-follows will generally produce more precise estimates of the incidence of different states than surveys in cases when x is less than the mean interval between encountering groups (including the duration of the survey of the group). This leads to the guideline: follow groups if the time taken to encounter a new group is greater than the rate of change of state, and otherwise survey groups.

Sometimes there will be differences between groups in the proportion of time spent in each state. Then no repeat measures of the same group will be independent from the population's perspective, and if we are interested in population measures of state, the balance will be tipped more towards the survey protocol. However, if the interest is in measures of state for individuals or groups, this may redress the balance.

In studies of cetaceans, the guideline "follow groups if the time to encounter a new group is greater than the rate of change of state" can go either way. For instance, in our studies of female sperm whales in the South Pacific, it takes of the order of 24 h to encounter new groups whereas the behavioral mode of sperm whales changes about every 6 h, indicating group-follows. In contrast, when studying males off Nova Scotia, we can encounter new animals every hour or two, making surveys more efficient.

During individual-follows, data are only collected on a particular individual, or dyads containing a particular individual. Thus, state measures using data from individual-follows will almost always be less independent, and so less precise, than those from group-follows of the same duration, in which either data of all members of the group or a randomly or haphazardly chosen subset is used. Thus individual-follows are unlikely to be optimal for collecting state data (Table 1).

The same argument favors group-follows over individual-follows when events are of interest, except perhaps when data on individuals are needed (Table 1). For some purposes, it may be more important to have precise estimates of the rates of events for a few individuals rather than fewer, less detailed, data on many.

Overall then, consideration of the precision of estimates generally favor group-follows or surveys over individual-follows, except when we are interested in estimating the rate for occurrence of events for individuals, or interactions within dyads.

Critiques of group-focused behavioral work invariably reference the key paper in this field, "Observational study of behavior: Sampling methods," by Altmann (1974). Altmann has one three-paragraph section (of a 40-page paper) entitled "Focal subgroups" which considers focusing on groups. She notes two problems with the group-focused approach:

1. "Such sampling will be practicable only when it is possible to keep every member of the focal subgroup under continuous observation during the sample period." She applies this restriction because, as noted above, in order to estimate dyadic interaction rates from group-follow data it is necessary to know the amount of time that each dyad is visible,

and this will generally only be known if all animals are always visible. However, this only refers to the estimation of dyadic interaction rates, a rare goal in studies of cetaceans.

2. Altmann also notes that individuals are not observed if they move out of sight away from the main group, and therefore there is a bias against more cryptic behavior in group-follows, whereas in individual-follows the individual is observed whatever its behavior. In cetacean research, we have to face the frequent disappearance of our subjects underwater, whichever the protocol, so we are not losing anything by focusing on the group.

Thus, Altmann's (1974) arguments against group-follows are not generally relevant for cetacean research.

Mann (1999) notes that "Selection operates at the level of the individual (Williams 1966) . . ." implying that individuals are thus intrinsically the most appropriate focus of analysis. However, selection may also operate at other levels, including the gene, the species, and the group (Stearns and Hoekstra 2000). There are good theoretical reasons for believing that group selection is generally unimportant in genetic evolution (Stearns and Hoekstra 2000), but the situation in cultural evolution is very different: theoretically, group selection can easily drive cultural evolution (Boyd and Richerson 1985) and it is believed that this has been a vital element in the recent evolution of human societies (Richerson and Boyd 1998). Evidence is growing that culture is also an important determinant of the behavior of cetaceans (Rendell and Whitehead 2001), and some species, such as killer whales (*Orcinus orca*) and sperm whales seem to have social structures, including substantially-closed, conformist groups, which provide an ideal substrate for cultural group selection (Whitehead 1998). In other species, long-term cohesive groups may be elements of higher levels of social structure. An example is the second-order alliances (alliances of alliances) of bottlenose dolphins (Connor *et al.* 1992). Thus, in some cetacean species, there is reason to examine the behavior of long-term groups *per se* as they are themselves fundamental elements of social systems.

In conclusion, individual follows, if carried out carefully and in appropriate conditions, can provide wonderfully detailed accounts of dyadic interactions. However, the appropriate conditions are rare and cetologists will generally achieve more useful results over a wider range of research topics by using group-follows or surveys. In some circumstances groups themselves may be of fundamental interest, and describing their behavior gives a more revealing model of a social system than one focused on individuals. Even when individuals are fundamental, data on them may be collected by following groups or surveying different groups, and usually, such data will give less biased and more precise measures of behavior than those collected during focal-animal studies. There are undoubtedly factors influencing choice of follow-protocol which I have not considered here, but I cannot think of any which will fundamentally tip the balance towards one or another of the protocols. Thus, the low rate of individual-follow protocols in studies of cetacean behavior (12% in the review of Mann 1999) has been an adaptive response to the difficulties of obtaining data on highly mobile animals who spend much of their time out of view, but often maintain well-defined groups.

Studying cetaceans is different from work on terrestrial animals in a number of ways. Dives, high mobility and, frequently, highly-cohesive groups mean that lessons gained from research on model terrestrial animals, such as Altmann's (1974) primates, cannot necessarily be translated to the ocean. Cetologists tend to rely much more on technology and inference than their terrestrial counterparts (Read 1998, Whitehead *et al.* 2000). Among the more basic observational techniques, we also need different emphases. As on land, individual-follow protocols give the most fine-scale image of cetacean social behavior. But, if used indiscriminately, such techniques can produce biases and they are often inefficient in measuring much cetacean behavior.

The follow protocols are not mutually exclusive. Jenny Christal's focal-animal follows, each lasting a few minutes, were done within follows of groups of sperm whales lasting periods of days (*e.g.*, Christal and Whitehead 2000). The group follows were much more productive, but the focal-animal work did produce useful results, and took nothing away

from the larger-scale work. I suspect that there will often be cases in which focal-animal studies can be embedded within group follows. They may possess biases, but if these are recognized they can provide valuable information. Surveys are less compatible with the other protocols, but hybrids in which only short individual and/or group follows are carried out after encountering a group may sometimes be useful.

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