

Chapter 17

Observing and Quantifying Cetacean Behavior in the Wild: Current Problems, Limitations, and Future Directions

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A subgroup of dusky dolphins “boisterously” leaping. Without behavioral context, it is difficult to know whether these leaping animals represent a mating group, with often several males chasing a female in probable estrus; or whether it is a feeding group, with dolphins leaping to rapidly and simultaneously access a school or shoal of small fish just below the surface. (Off Kaikoura, New Zealand, summer 2011–2012, by Anke Kügler)

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Abstract Behavioral research and analysis is prone to both error and bias, particularly in the early stages of a discipline, in part because it is widely (and erroneously) believed that “behavior” is rather simple and can be easily described or quantified. However, since the 1970s for terrestrial animals, and since the late 1990s for marine mammals, systematic protocols of data gathering and ever more sophisticated modeling and multivariate statistical techniques have been described, largely to reduce problems of bias and pseudoreplication. With modern observational protocols, often enhanced by sophisticated multivariable data-gathering tools, the future for more accurate assessments, and therefore interpretations, of the sophisticated social behaviors of wild cetaceans seems assured.

Keywords Ad libitum • Animal behavior • Behavioral sampling • Data tags • Events • Fission–fusion • Focal animal following • Point sampling • Quantitative methods • Sampling errors • Scan sampling • States

17.1 Introduction

Mapping cetacean behavior is critical to evolutionary approaches and conservation management. How can we understand the basic biology, life history, and evolution of a species, *and* address critical conservation questions, without at least some rudimentary appreciation of their ranging, foraging, social, and parental behavior? Although many people are fascinated with animal behavior, evident by the number and popularity of nature shows, a common misconception of amateur and even senior scientists is the assumption that studying behavior is easy. The premise is that we are all observers of behavior, at least within our own species, so compared to gene sequencing, neuroscience, or biochemistry, mere “behavior” is something with which we are intimately familiar, regardless of training. Historically, such overconfidence plagued field studies of animal behavior until the 1970s, and descriptive studies often overinterpreted behaviors that happened to be noticed. Following Jeanne Altmann’s publication on sampling techniques for behavioral studies (Altmann 1974), which distinguished between ad libitum (“ad lib”) and more quantitative methods, many observers of terrestrial species and systems were more careful and explicit in both defining behaviors with an ethogram and finding appropriate sampling methods to approximate frequency and duration. A similar general shift was later introduced to cetacean researchers (Mann 1999). To date, a large number of papers on cetacean behavior fail to estimate either frequency or duration, except for a limited range of behaviors (e.g., diving intervals), possibly because focal sampling methods require individual recognition of animals, usually from natural marks (Würsig and Würsig 1977). Given the task of observing animals that are difficult to identify, fast moving, wide ranging, leave no scats or tracks, and spend most of their lives out of the sight of surface-dwelling observers, it is no surprise that few studies present basic activity budget data.

17.2 Challenges and Solutions of Behavioral Data Gathering

The challenges confronting students of marine mammal behavioral descriptions are to reduce observer and sampling biases and expand and refine sampling and analytical techniques that yield useful information. Ethologists studying birds, burrowing animals, and forest species have similar difficulties of investigating cryptic species, and their subjects do not have to show themselves: at least cetaceans need to come to the surface at regular intervals to breathe! This need allows for visually tracking individuals or groups, but has several limitations. First, many behaviors, especially foraging, occur at depth, and second, surfacing intervals are strongly influenced by the behaviors themselves. Thus, although it might be important to record surface and dive times, behavior sampling must also account for subsurface periods. Similarly, nocturnal periods are ignored for most cetacean studies, although it is widely recognized that cetaceans are *cathemeral*, that is, active day and night.

When behavioral information is gathered by eye from surface vessels or shore, the limitations of the viewing platform demand careful interpretation of the data. For example, in Shark Bay, Australia, socializing by Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) typically involves prolonged periods at or near the surface where continuous sampling or point sampling is possible. Deep-water foraging involves long dives and short intervals at the surface. During socializing, surface and subsurface behaviors are similar. During foraging, the dolphin sometimes rests at the surface and forages during dives. If sampling records were limited to surface observations, foraging activity budgets would be grossly underestimated. To systematically capture the stream of behavior, the observer must make inferences about what is occurring subsurface, but could indicate which behaviors are directly observed (at or near surface) or based on diving behavior. The validity of the inferences depends on other “confirming” observations, such as fish catches, acoustic behavior, or matching surface with subsurface behavior (Vaughn et al. 2009). For example, if 3-min point sampling intervals are used to quantify delphinid behavior, then the samples might be marked as surface or subsurface (e.g., social-surface, social-subsurface, travel-subsurface, forage-subsurface). In Shark Bay, bottlenose dolphin dives average about 1 min in deep water, and nearly continuous observation is possible in shallower water, enabling us to quantify activity budgets and track behavior at or beneath the surface (Gibson and Mann 2008; Mann et al. 2008).

As was pointed out by Mann (1999), it is important that types of behaviors are broadly but accurately categorized. *Events* (brief behaviors such as surface displays, or dive types) are usually not timed and can be readily converted into rates, either rate per unit time (e.g., an individual dives 13 times per hour) or as a rate during another behavior. For example, dolphin A dives 22 times per hour of foraging and 13 times per hour of resting. *States* are typically longer behaviors that are either timed (e.g., onset and offset of foraging bouts) or estimated using quantitative measures such as scan or point sampling (Altmann 1974). Behavioral events such as fish catches, dive types, and particulars of interactions help confirm the behavioral state. Events are easily missed unless they regularly occur at the surface, but states should not be.

To interpret event rates fairly, researchers need to be careful to avoid observer bias (systemic, nonrandom sampling errors). Such biases might be implicit or explicit but are especially likely for animals that conduct much of their behavior subsurface or otherwise out of sight and have therefore plagued many cetacean studies (Mann 1999). For example, calves might catch small fish that are less visible to observers than adult fish catches. Thus, one might underestimate the rate at which calves catch fish relative to juveniles or adults. Or, if juvenile mating behaviors were raucous and tended to occur at the surface, but adult matings were subsurface and less obvious, then comparing mating rates between different age-sex classes would be futile. This bias might be exaggerated further if there were other interactions by age and sex (e.g., season). If, however, individual traits did not affect the likelihood of observing a behavior, then one could determine relative differences in mating behavior by age, sex, or season. How one interprets events largely depends on the sampling protocol (group or individual), how visible or obvious the behavior is, intrinsic biases to observability, and the sampling method (i.e., did the observer record all events of one type or just a subset for an individual or group?).

Even ad lib event sampling can add to a dataset and, as Altmann (1974) pointed out, these samples can be used for sociometric analysis, especially if direction is important. For example, in many delphinid societies, fission–fusion is a central feature. Often one group or individual clearly is the “joiner” and others are “joined.” Similarly, a subgroup or individual may leave a group and the others are left. Such directionality might be extremely informative and can be used for social network analyses (i.e., in-degree or out-degree; see Stanton and Mann 2013). In Indo-Pacific bottlenose dolphins, adult males might join females, and females might often leave males, but females almost never join up with males. This type of information can reveal much about male–female relationships. An observer might not always be able to record who leaves and who joins during individual or group follows, but so long as ad lib join–leave events are not biased (e.g., the observer is biased by recording leaves only if they are females or joins only when they are males), then directionality can be quantitatively analyzed.

Given the difficulty in following most cetacean species, observers must first select an appropriate sampling protocol that captures the behavior(s) of enough individuals to be representative. There is a tradeoff between the number of individuals sampled and how often or intensively the same individuals are sampled. Typically, researchers use surveys (transect or opportunistic) to increase the number of individuals sampled in the population, or they follow groups (group-follow) or individuals (focal animal sampling) and collect more detailed and repeated measures on the same individuals (see Mann 1999). Surveys are useful for keeping track of individual life histories, ranging, and significant events. Group follows tend to be most useful when individuals cannot be tracked or the main research question focuses on group behaviors, as is particularly likely when animals stay in relatively stable groups (e.g., pilot whales, false killer whales, killer whales, sperm whales). Under these conditions, scan sampling can be a good relative measure of behavior. If fissions and fusions are common, then it is critical to have clear protocols to guide the observer on the “group” with which to stay. Otherwise, the observer might have

a tendency to always stay with the larger or more interesting group, or not even notice if an individual or several animals left. Biases are likely to emerge if one always stays with the larger group, for example, so techniques for capturing the diversity of group behavior would be needed. Recently, we found that surveys of mothers and calves grossly underestimated the amount of time they spend separated relative to focal follows (Gibson and Mann 2009). The probable explanation is that observers are more likely to approach and sample adults, and if the calf joined at some point, observers might infer that the calf had been there all along.

Surveys are good for sampling a large number of individuals and across different time periods. Although each sampling point for an individual might be considered independent on a given day, surveys can inflate association patterns, that is, the “gambit of the group” where all individuals in a group are considered associated even though there might be strong preferences within the group (Whitehead 2008). One way to reduce this bias is to use weighted data (e.g., half-weight coefficients) and only consider those above a certain threshold to be associated (Franks et al. 2010). Regardless, sample size (sighting record per individual) has an immense impact on the validity of such estimations. We recently used bottlenose dolphin surveys over a 22-year period to determine social preferences between tool-using (with marine basket sponges) and non-tool-using dolphins. We took several precautions to reduce bias. We used weighted coefficients (affinity indices) with a very large sample size (average of 75 surveys per individual), and if individuals were not alive at the same time, the data for that dyad were coded as missing. Because we wanted to control for factors such as sex, maternal kinship, and range overlap, we used a multiple regression quadratic assignment procedure (Dekker et al. 2007). This permutation method allowed us to discriminate between the multiple factors that are likely to influence association by incorporating multiple matrices into one analysis while accounting for the structural autocorrelation that is inherent to social networks (Mann et al. 2012). Our analysis showed a clear pattern where sponger (tool-using) dolphins preferentially associated with each other over non-spongers (Mann et al. 2012). Such methods are likely to gain popularity as long-term datasets grow in size and complexity.

Ranging estimates are best achieved with systematic (e.g., transect) survey sampling, but are also plagued by inadequate sample sizes and pseudo-replication when groups are moderately stable. Fixed kernel densities (Gaussian distribution) are commonly used (Worton 1989; Seaman and Powell 1996), but a new adaptive local convex hull method outperforms traditional kernel density (KD) methods (*a*-LoCoH; Getz and Wilmers 2004; Getz et al. 2007). Urian et al. (2009) found that more than 100 points were needed to capture home range estimates using traditional methods, but few studies achieve this. For Shark Bay dolphins, we found that beyond 50 points, KD home range sizes did not change in a systematic way, but *a*-LoCoH home ranges did. Thus, to examine relative home range sizes (e.g., to compare males and females), we selected a random subset of 50 points for each animal (Patterson 2012). This method is recommended because any differences between groups cannot then be attributed to differences in sample size. Although it is tempting to use all one’s data, randomized subsampling is preferable when variation in

sample size biases the analysis. Long-term information on ranges of known animals and their mothers can provide important insights to bisexual philopatry, mother–son avoidance, and the role of fission–fusion societies (Tsai and Mann 2013).

For detailed behavioral information, individual focal follows are optimal because the observer is less likely to make sampling errors while observing the stream of behavior of one animal. However, such follows depend on individual identification or at least being able to identify the same animal throughout the follow. For example, a calf might not be “identifiable” by photo-identification but can be followed because it is distinctive enough from others in the group. Follows can also be quite short (e.g., 5 min) if longer follows are too difficult. Short sequential follows of all individuals in a group can provide information similar to scan sampling and are sometimes easier if behaviors are difficult to identify. When aggregations are very large (sometimes hundreds or even thousands), systematic sampling can still occur, but might involve sampling smaller clusters within the larger group or scan-sampling every tenth dolphin in view. The important point is to establish clear protocols that minimize bias regardless of sampling conditions.

Central to all these issues is establishing protocols that yield adequate sample sizes for drawing inferences about the population or group of interest. To reduce sampling error (variation from one sample to another, usually the standard error of the estimate, or the coefficient of variation, which expresses the standard error as a percentage of the estimate) and bias (e.g., selection bias, measurement bias, statistical bias), care must be taken to repeat samples, avoid pitfalls in the selection of subjects and measurement of behavior, and finally, apply appropriate statistical techniques. On the last point, which has received little attention here, pseudoreplication is a particular problem with many animal behavior studies, and cetacean studies in particular (Milinski 1997).

17.3 Technological Advances in Studying Behavior

In this overview, we have concentrated on the kind of behavioral information that can be gleaned from watching animals quite close up, as from a small boat near an individual or group. We acknowledge that the mere presence and (usually) noise of the boat engine can cause some degree of disruption of the “normal” behavioral repertoire of the watched animals. With careful boat approaches by experienced operators, such disruption is usually minimal (Bejder et al. 2006). For some species of cetaceans, observations can also be made from shore, with binoculars, still cameras with long lenses, digital video cameras, and theodolite tracking (the latter for more accurate positional information), and with the advantage that no disruption is made; however, shore-based observations provide a less intimate view of the animals or group (Würsig et al. 1991; Lundquist et al. 2012). Observations can also be made from circling aircraft, but this technique has been used mainly for large whales that can be identified from above, although some successful group-structure data have been gained on delphinids in clear waters of the open Pacific Ocean. This

technique can also disturb animals, and care must be taken while circling (from an altitude of at least 450 m) to stay outside of the “cone of sound” of airplane noise underwater and to ensure that the plane’s shadow does not fall onto the animals being observed.

Nowacek and colleagues (Nowacek 2002; Maresh et al. 2004) used a helium-filled aerostat (blimp) fitted with a videocamera and tethered to a boat, with two hydrophones, to record detailed foraging sequences in bottlenose dolphins. These innovative methods greatly expand our view into the world of smaller cetaceans. We predict that the recent rapid development of remote-controlled (“drone”) mini-copters equipped with high-resolution cameras, operated from shore or vessel, will become a modern staple of group formation and behavioral research (NOAA 2012).

“Observations” of behavior do not need to be only by eye, but can involve acoustic studies of the especially soniferous delphinids, and various techniques of developed or developing electronic monitors (on the animals) or remote sensing devices. An up-to-date example is the use of so-called DTags (for “data tags”) that can be placed onto a cetacean by suction cup or small barb attachment. Such tags have provided valuable insights. For example, exciting new information has become available with such tags for short-finned pilot whales (*Globicephala macrorhynchus*) that were discovered to echolocate for prey many hundreds of meters below them and then rapidly plunge-dive to depth to attack (Aguilar Soto et al. 2008). The DTag to accomplish this was outfitted with high-frequency echolocation detection and storage capability, as well as a depth sensor, triaxial accelerometer, and magnetometer for pitch, roll, and heading information in three-dimensional space. Because such devices fall off the animal and float, they can be recovered for data retrieval, and used again. A future application could be on multiple animals of a group, so that better social data can be obtained for animals at depth. At any rate, one device on one animal can already be thought of as an extension of a “focal follow” beyond that possible by visual assessment alone.

Other technological advances have greatly expanded research potential for marine mammals. However, most of the devices placed on animals have to date been used largely on pinnipeds and larger whales, and their development for smaller delphinids is just becoming practical as the result of miniaturization. The tried-and-true technique is conventional radio-tracking, but larger-distance satellite tracking is becoming practical for even small delphinids. Video chips, memory storage, and battery systems are becoming ever smaller, so that it is now feasible to use video recorders for underwater swimming, foraging, and social behavior information of even smaller cetaceans, although such devices have been used for more than 10 years on pinnipeds (Williams et al. 2004) and large whales. Anything put onto an animal can also be built to gather environmental data and can therefore enhance not only our understanding of behavior but of ecology as well. An overview of modern data acquisition systems (and their promise) is provided by Read (2009).

As can be the case for observations from surface vessels, a device put onto an animal, even for short times or by what seems a benign attachment technique (such as a suction cup system for delphinids), can be bothersome to the animal and change its behavior. One technique of gathering dive and foraging information that has been

used for spinner (*Stenella longirostris*) and dusky (*Lagenorhynchus obscurus*) dolphins uses a sophisticated multi-beam “fish-finder” sonar array and mathematical algorithms to reconstruct information on potential prey and the depths and kind of dives of dolphins (Benoit-Bird et al. 2004, 2009). However, the high-frequency sonar itself might cause some behavioral change, and at any rate, one needs to be directly over the diving animals of interest for such information. Another technique not yet fully explored for delphinids is three-dimensional array passive listening of their own acoustics, for positional data during different behavioral states (Schotten et al. 2004), and for determination of which dolphin is vocalizing when incorporated with a video camera (Schotten et al. 2005).

17.4 Conclusions

Observation and quantification of behavior can proceed in many different ways, with and without enhancement by modern data acquisition techniques. Direct and remotely sensed data can also be augmented by, for example, scat samples or protein analyses relating to diet, and genetic sampling to examine relatedness and mating patterns. Such samples can be gleaned directly from behind or on the swimming animals, or from short-term captures in special situations (Wells et al. 1999). A practical set of research directions will probably involve more integration of variable data-gathering platforms, so that, for example, a group of cetaceans with several DTags or other electronic devices can be watched by eye from shore (in special situations), from a surface vessel, or via a remote-controlled mini-copter at the same time that detailed biological and oceanographic data are gathered. The future of behavioral observations of cetaceans is bright, and we only caution that behavioral patterns be well defined and data gathering be as representative as possible.

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