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A comparison of survey and focal follow methods for estimating individual activity budgets of cetaceans

CAITLIN KARNISKI,[1] ERIC M. PATTERSON and EWA KRZYSZCZYK, Department of Biology, Georgetown University, 3700 O Street NW, Washington, DC 20057, U.S.A.; VIVIENNE FOROUGHIRAD, Marine Science and Conservation Division, Duke University, 135 Duke Marine Lab Road, Beaufort, North Carolina 28516, U.S.A.; MARGARET A. STANTON, Center for the Advanced Study of Hominid Paleobiology, George Washington University, 2110 G Street NW, Washington, DC 20052, U.S.A.; JANET MANN, Department of Biology and Department of Psychology, Georgetown University, 3700 O Street NW, Washington, DC 20057, U.S.A.

ABSTRACT

Activity budget data are essential for determining behavioral responses to physiological and ecological variables. Yet, few studies are available to investigate the robustness, accuracy, and biases of the methods used to estimate activity budgets for cetaceans. In this study, we compare activity budgets of 55 adult female bottlenose dolphins in Shark Bay, Australia derived from two methods: surveys (n = 6,903) and focal follows (n = 1,185, totaling 2,721 h of observation). Activity budgets estimated from survey data differed in all behavioral states compared to focal follow data. However, when controlling for temporal autocorrelation, only time spent socializing and time spent traveling remained disparate between the methods. To control for biases associated with assigning group-level behavior to individuals, we also compared survey and focal follow activity budgets for lone females. Here we found differences between methods in time spent foraging and traveling regardless of whether we controlled for temporal autocorrelation, which suggests detection biases likely play a role in explaining differences in activity budget estimates between the two methodologies. Our results suggest that surveys are less representative of individual-level activity budgets, and thus, when individual-level knowledge about behavior is needed, focal follows are preferred.

Key words: sampling method, protocol, behavior, observational method, group size, observational bias, detection bias, temporal autocorrelation.

How an animal uses its time, its activity budget, has critical implications for survival and reproduction. Variation in activity budgets across a wide range of taxa has been linked to demographic (Bicca-Marques and Calegaro-Marques 1994), ecological (Cowlishaw 1997), and physiological factors (Matsumoto-Oda and Oda 1998, del Castillo *et al.* 2005, Hamel and Côté 2008). While cetaceans present particular methodological challenges (Mann 1999), activity budget data have shed light on the relationship between behavior and prey ecology, bathymetry, tidal state, time of day,

[1]Corresponding author (e-mail: cbk27@georgetown.edu).

season, and survival (Saayman *et al.* 1972; Shane 1990*a, b*; Ballance 1992; Bräger 1993; Hanson and Defran 1993; Mann and Watson-Capps 2005; Steiner 2011). Several studies have also found links between cetacean activity budgets and human interactions and disturbances (Bejder *et al.* 1999; Lusseau 2003, 2004, 2006; Constantine *et al.* 2004; Bejder *et al.* 2006; Neumann and Orams 2006; Williams *et al.* 2006; Christiansen *et al.* 2013; Foroughirad and Mann 2013). Thus, accurate activity budget data are critical for understanding survival, reproduction, and other aspects of behavioral ecology, as well as for implementing effective conservation strategies. However, despite this importance and previous efforts to address activity budget methodologies (Altmann 1974, Mann 1999), methods for collecting cetacean activity budget data vary widely with relatively little inspection of how such methodological differences might influence results. This study investigates the efficacy of two methods for measuring individual cetacean activity budgets: surveys (sighting records) and individual focal follows.

Surveys and focal follows differ in both protocol and sampling method. Here, we refer to protocol as the means of determining which, and how many, individual(s) to observe, and for what duration of time, whereas we refer to sampling method as the means of how data are collected (*e.g.*, point sampling, ad libitum, *etc.*). While the effects of sampling method on cetacean activity budgets have been previously examined (Mann 1999, Steiner 2011), less attention has been placed on the importance of protocol. Because the individual is considered the optimal unit of analysis in activity budget studies (Mann 1999), protocols that focus on an individual are recommended so that the unit of data collection parallels that of analysis. In addition, individual-level protocols reduces pseudoreplication (Hurlbert 1984) and allows one to examine behavioral variation of the individual, and with factors such as age and sex. Yet such protocols require real-time, rapid individual identification making them difficult to employ, particularly in species that lack distinctive markings and live in large groups. As such, individual-level protocols (*e.g.,* focal follows) are not often used. In this study, we hope to shed light on the influence methodology has on individual activity budget estimates by comparing adult female bottlenose dolphin activity budgets calculated from focal follow data to that calculated from group survey data.

Methods

Study Area and Subjects

The Shark Bay Dolphin Project has been conducting a longitudinal study of bottlenose dolphins (*Tursiops* cf. *aduncus*) since 1984, and has monitored over 1,600 individuals in the eastern gulf of Shark Bay, Australia (25°47′S, 113°43′E). The relatively pristine study area extends 300 km^2 east of Peron Peninsula and consists of embayment plains (5–13 m), shallow sand flats and seagrass beds (0.5–5 m), and deeper channels (6–13 m).

For this study, researchers collected behavioral data on bottlenose dolphins *via* small motor boats (<5.7 m). Field observers identified individual dolphins using dorsal fin markings and shape, and also matched photographs to a digital identification catalog. Dolphin ages were estimated based on year of birth, the birth of their first calf (Mann *et al.* 2000), or degree of ventral speckling (Krzyszczyk and Mann 2012). Individuals were considered to be adults if they were 12 or more years of age, or for females, if they had given birth to a calf (Mann *et al.* 2000). Finally, sex was determined by visual observation of the genital area, genetic analysis, or the presence of a dependent calf.

Data Collection

Data for this study were collected between 0600 and 1900 during all seasons from 1988 to 2012 using one of two methods: surveys or focal follows.

Surveys—Surveys were short "snapshot" observations of a group or individual. When dolphins were sighted, researchers instantaneously estimated initial activity and distance from the research vessel before approaching to within 100 m. Once the research vessel was close enough for observers to identify individuals, a survey was initiated on all individuals in the group based on a 10 m "chain rule" (Smolker *et al.* 1992). For each survey, observers performed a scan of all individuals to assess their behavioral state as one of six categories: foraging, resting, socializing, traveling, other, and unknown (see below and Table 1 for further details). A "predominant group-activity" was assigned for the first five minutes of the survey based on the activity performed by at least 50% of the individuals (Mann 1999) for at least 50% of the time. It is important that predominant group activity is not confused with predominant activity sampling (PAS), which is the activity that an *individual* performs for at least 50% of the observation interval (Mann 1999).

Focal follows—Focal follows were performed either on an individual or simultaneously on a mother and her dependent calf, and were initiated after a survey that included the focal individual(s). Point sampling was used to record the behavioral activity state of the focal animal (or each focal animal individually in the case of mother-calf follows) at one-minute intervals. Group composition was recorded every minute, and changes in group composition were noted continuously. Prior to 1997, activity states were assessed by PAS of the focal individual for 2.5 min intervals (the average duration of a surfacing-diving bout cycle). After 1997, 1 min point sampling

Table 1. Ethogram of activity states observed in bottlenose dolphins in Shark Bay, Australia.

Activity state	Description
Foraging	Foraging is characterized by directed effort toward locating or capturing prey, often involving rapid and irregular movement and direction changes, in particular, prey chases. The dolphins of Shark Bay have a varied repertoire of over 20 foraging tactics (also see Mann and Sargeant 2003, Mann *et al.* 2008).
Resting	Resting is characterized by a lone individual or a tight group moving at a slow speed (<3 km/h) either in a straight line or varied directions. Resting individuals dive and surface for long bouts (1–2 min). Rest may also include bouts of "snagging" in which a dolphin floats at the surface with its melon and dorsal fin clearly visible.
Socializing	Socializing is characterized by interaction with a conspecific. Socializing behaviors include play, chases, displays at the surface such as leaps or slaps, body contact such as petting or rubbing, sexual, and/or aggressive behavior (*e.g.*, jawing, charges, ramming).
Traveling	Traveling is characterized by regular and consistent spatial progress. Travel is most often in a relatively straight line and is typically observed at moderate to fast speeds (>3 km/h).

was used for activity state. PAS and point sampling yield virtually identical activity budgets (Mann 1999) and thus were combined in our analyses by weighting each PAS call by 2.5 in order to account for the differences in amount of time each sample represented. Activity states were classified using the same categories as in surveys. Focal follow durations were determined *a priori* based on the quantity of available data for each individual, but occasionally follows were terminated earlier due to weather, equipment malfunction, or if researchers lost the focal individual(s).

Behavioral Categories

Four activity states were assigned based on readily identifiable behaviors according to the ethogram in Table 1. If there was uncertainty in a behavioral call (*e.g.*, the observer indicated forage *or* travel), states were weighted by degree of certainty (0.5 forage, 0.5 travel in the example given). An additional state, "other," was assigned but not included in any analyses because it does not represent a biologically meaningful category of dolphin behavior. "Other" included observed behaviors that did not easily fall into any of the other categories (*e.g.*, bow-riding), and accounted for an average of 0.70% of an individual's point samples in follows, and 0.18% of predominant activity states in an individual's surveys. Finally, an "unknown" activity state was used when observers could not determine an animal's behavior, which accounted for an average of 0.21% of an individual's point samples in focal follows, and 5.67% of predominant activity states in an individual's surveys.

Effect of the Research Boat

Previous studies have shown that exposure to small vessels can affect dolphin behavior (Bejder *et al.* 2006, Neumann and Orams 2006). Due to inherent differences in their respective durations, the survey and focal follow methods used here differed in the amount of exposure to our research vessel. As this difference could impact activity budgets, we examined the effect of research vessel presence in both methods. For surveys, we compared dolphin behavior before the research vessel approached to within 100 m to behavior after approach using a paired McNemar's exact test. For follows, we compared individual female activity budgets in the first 5 min of a focal follow to a 5 min period 1 h into the focal follow using paired permutation tests (10,000 permutations). One hour was chosen as the midpoint between findings from two studies of the start of cetacean avoidant/equivocal behavior in response to a boat (Bejder *et al.* 1999, Neumann and Orams 2006).

Activity Budget Analysis

For all analyses, we restricted our sample to adult females (n = 55) that had ≥5 h of focal follow data and at least 20 surveys (Gibson and Mann 2009, Stanton *et al.* 2011). As consecutively sampled follow data are inherently autocorrelated, we constructed a model to determine an appropriate decorrelation time-scale. For a subset of individuals that had at least one follow of 240 min of more (n = 25) we compared each focal follow point sample to a sample that occurred 1 min away, 2 min away, 3 min away, and so on to a maximum of 240 min for a total 6,521,751 minute-to-minute comparisons. For each unique pair of point samples within a follow we coded the activities as being same (1) or different (0), and calculated the proportion of pairs that were the same for each minute of time shifted from the original point sample.

The effect of time shift on the likelihood of two calls sharing the same activity state was modeled using a piecewise function with two components. This was done with a binomial generalized linear mixed model with same, different (1, 0) as the response, time shift as a fixed factor, and dolphin ID as a random factor using the package *lme4* in R version 3.1.0 (Bates *et al.* 2011). We optimized our model by testing a series of break points from 2 to 239 min and selected the model with the lowest deviance. From this, the optimal breakpoint was estimated to be 10.47 minutes (95% CI, 7.39–12.47) at which point there was a 55% chance (as calculated from the raw data) that two point samples would be the same (Fig. S1). Before this point, the probability of two point samples being the same decreased by 0.11 per additional minute shifted, while after this point the probability only decreased by 0.003 per min shifted (see time shift parameter estimates in Table S1). These data provide support for considering focal follow activity calls that are at least 10.47 min apart as functionally independent. Based on this result, and in order to be as comparable to survey data as possible, we randomly sampled focal follow data to produce subsamples of five consecutive minutes separated by at least 11 min from all other subsamples. This data set will hereafter be referred to as the "decorrelated focal follow data set." However, because autocorrelation is inherent in all animal behavior and removing it can reduce the biological relevance of results (de Solla *et al.* 1999), we also calculated activity budget data using the complete focal data set (hereafter called the "autocorrelated focal follow data set" for comparative purposes).

In order to account for differences in observation time between the two methods, activity budgets for each method were calculated using an equal amount of time by randomly sampling without replacement 5 min of data from either the surveys or one of the two focal follow data sets (decorrelated or autocorrelated) until all samples from one of the two methods had been selected. This was done while simultaneously controlling for possible seasonal changes in activity budgets, by sampling with equal seasonal distributions of observations across the two methods for each individual (season estimated based on Mann *et al*. 2000 and Heithaus and Dill 2002). This resulted in a total of 524 h of observation (mean hours per female $\pm$ SD = 9.53 $\pm$ 10.47 for each method) when using the decorrelated focal follow data set, and 591 h of observation (mean hours per female $\pm$ SD = 10.74 $\pm$ 11.05 for each method) when using the autocorrelated focal follow data set. From these data, we determined activity budgets for each female by calculating the proportion of calls each activity state represented, and then compared these proportions between methods using paired permutations tests (10,000 permutations) using package *coin* (Hothorn *et al.* 2008) in R version 3.1.0.

Because survey data are collected soon after an initial dolphin sighting, and larger groups are easier to spot compared to small groups or solitary individuals, surveys are biased towards larger groups (*e.g.*, Mann 1999, Gibson and Mann 2009; also see Results). Furthermore, in surveys observers assign a single behavior to the whole group even if some individuals are not performing this behavior. To control for differences in survey and focal follow activity budgets that may relate to these differences in group size and group-level behavior assignment, we compared activity budgets for a subset of females (n = 19) with enough data using only solitary data (hereafter, solitary activity budgets). Females were considered to be "solitary" when they were alone and/or with a dependent calf. As before, we used an autocorrelated solitary focal follow data set (95 total hours, mean hours per female $\pm$ SD = 5.02 $\pm$ 3.72 for each method), and decorrelated solitary focal follow data set (82 total hours, mean hours per female $\pm$ SD = 4.32 $\pm$ 2.93 for each method). These data were sampled to produce activity budget estimates of equal observation time and seasonal distribution and were compared using paired permutations tests (10,000 permutations). Because females have no associates to socialize with when they are solitary (other than a dependent offspring if present), we excluded socializing from these analyses.

In all methodological comparisons, we recognize that activity budgets are interdependent by nature and should theoretically sum to 1 for each individual. However, we are specifically interested in examining how each activity changes between the two methods separately, and have thus run independent tests comparing all behavioral states. However, Bonferroni adjustments were applied to P-values where appropriate to maintain an experiment Type I error rate of $\alpha = 0.05$. Finally, because the decorrelated focal follow data set is smaller than the autocorrelated one, and all comparisons between focal follows and surveys are sampled to represent the same total time and seasonal distribution, the surveys compared to decorrelated focal follows are not the exact same as surveys compared to the autocorrelated focal follows. Activity levels between these two sets of survey data for both nonsolitary and solitary activity budgets were virtually identical so for brevity, all figures in the text represent survey data that were compared to the decorrelated focal follow data set. Both survey data sets can be seen side by side in Figures S2 and S3.

Results

Effect of the Research Boat

For surveys, dolphin behavior before and after the research vessel approached did not differ for any activities (Table 2). Likewise, activity budgets in the first 5 min of a focal follow were no different from a 5 min period 1 h into the follow for any activity states (Table 3). Combined, these results indicate that the approach and continued presence of our research vessel were not associated with behavioral changes.

Activity Budgets and Group Size

Female activity budgets estimated from surveys had higher foraging, resting, socializing, and lower traveling than did activity budgets estimated from the autocorrelated focal follow data set (Fig. 1). The activity budget differences for socializing and traveling persisted when comparing surveys to the decorrelated focal follow data (Fig. 1). Female group sizes estimated from all surveys were also significantly different when compared to both autocorrelated (mean group size ± SE, surveys = 6.05 ± 0.24, focal follows = 4.58 ± 0.25) and decorrelated focal follows (mean group size ± SE, surveys = 6.16 ± 0.26, focal follows = 4.56 ± 0.26), suggesting that differences

Table 2. Results of paired McNemar's exact test between initial and predominant activities of surveys within each activity category. A subset of 1,599 surveys with available data were used. Because all P-values are Bonferonni-adjusted, any P-values > 1 are reported as $P > 0.85$.

Initial activity category	P-value	Odds ratio	Lower CI 95%	Upper CI 95%
Foraging	>0.85	0.8446	0.6275	1.1346
Resting	0.4144	0.7766	0.5725	1.0503
Socializing	0.5920	1.4642	0.8838	2.4586
Traveling	0.3132	1.2954	0.9723	1.7308

Table 3. Results of paired permutation tests of each activity category within individual focal follows between subsets of 0–5 min and 60–65 min. A subset of 861 individual focal follows with available data were used. Because all *p*-values are Bonferonni-adjusted, any *P*-values > 1 are reported as *P* > 0.85.

Activity category	*Z*-score	*P*-value
Foraging	−1.3990	0.6264
Resting	−0.6272	>0.85
Socializing	−0.8828	>0.85
Traveling	−0.2010	>0.85

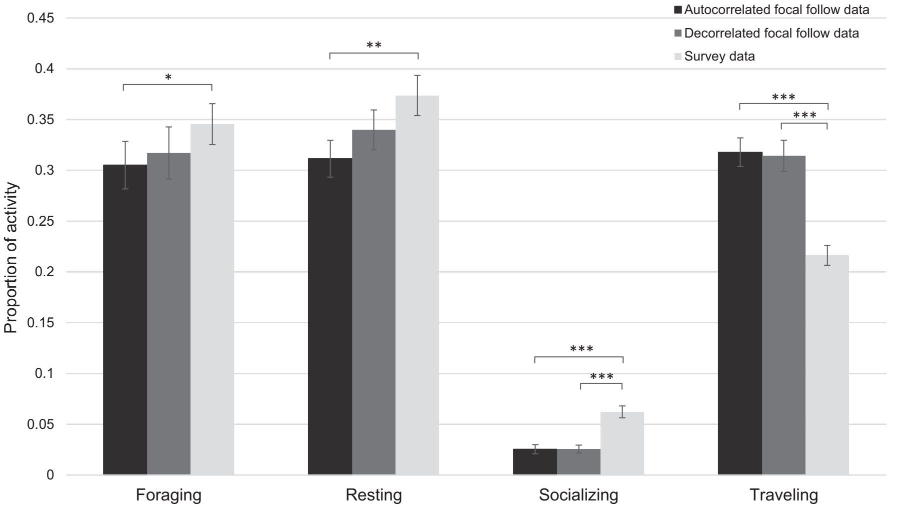

Figure 1. Female activity budgets from autocorrelated focal follow data, decorrelated focal follow data, and surveys. Figure shows mean ± SE proportion of time in each behavioral state. Paired permutation tests comparing autocorrelated focal follow data set and surveys: foraging: $Z = -2.2785$, $P = 0.0448$; resting: $Z = -3.1010$, $P = 0.004$; socializing: $Z = -4.6290$, $P < 0.0001$; traveling: $Z = 4.6739$, $P < 0.0001$. Paired permutation tests of decorrelated focal follow data and surveys: foraging $Z = -1.8385$, $P = 0.2856$; resting: $Z = -2.2324$, $P = 0.1040$; socializing: $Z = -4.5670$, $P < 0.0001$; traveling: $Z = 4.4974$, $P < 0.0001$. All permutation tests performed with 10,000 permutations. * = $P < 0.05$, ** $P = < 0.005$, *** = $P < 0.0001$.

in activity budget could be driven by biased survey sampling of larger groups. That said, we also found that female solitary activity budgets differed between the two methods. As in the nonsolitary activity budgets, solitary surveys estimated lower traveling than did both the autocorrelated and decorrelated focal follow data; however foraging budgets also differed between solitary surveys and both autocorrelated and decorrelated solitary focal follow data (Fig. 2).

Discussion

Our results demonstrate that activity budgets derived from surveys and focal follows differ, which can be explained by three possible factors. First, due to individual

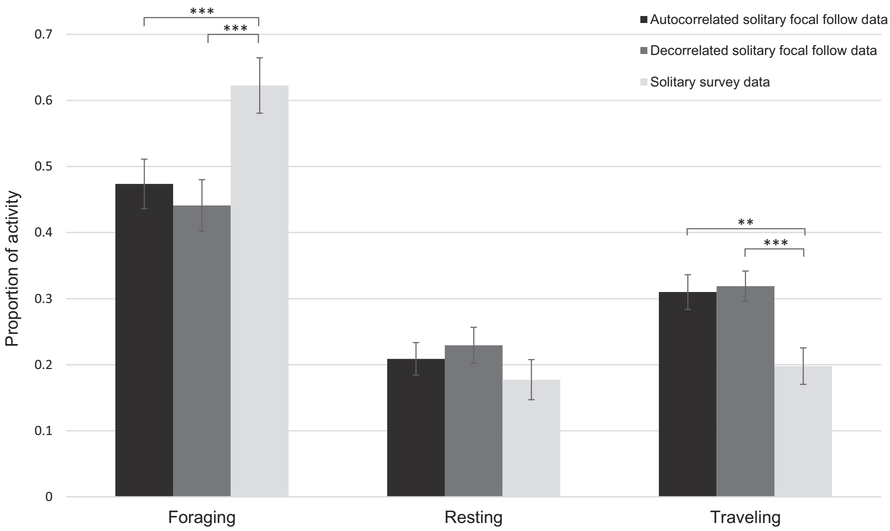

Figure 2. Female solitary activity budgets from autocorrelated solitary focal follow data, decorrelated solitary focal follow data, and solitary surveys. Figure shows mean ± SE proportion of time in each behavioral state. Paired permutation tests comparing autocorrelated solitary focal follow data set and surveys: foraging: $Z = -3.6547$, $P < 0.0001$; resting: $Z = 1.6460$, $P = 0.3171$; traveling: $Z = 2.9995$, $P = 0.0027$. Paired permutation tests comparing decorrelated solitary focal follow data set and surveys: foraging: $Z = -3.6593$, $P < 0.0001$; resting: $Z = 2.2120$, $P = 0.0777$; traveling: $Z = 3.2106$, $P < 0.0001$. All permutation tests performed with 10,000 permutations. ** = $P < 0.005$, *** = $P < 0.0001$.

differences in behavior, predominant group activity determined in surveys does not accurately represent the behavior of each individual, as dolphins in the same group are not necessarily all engaged in the same activity. Second, surveys are likely biased towards more visible activity states and larger group sizes since surveys are always the first method conducted following the initial sighting of dolphins. Finally, characterizing a group's activity in surveys requires observers to divide their attention among multiple individuals, which may lead to some behaviors going unnoticed that are otherwise apparent during individually-based behavioral assessment as in focal follows.

The first issue, that of predominant group activity not representing an individual's activity, concerns differences in protocol. In focal follows, the level of observation is equal to the level of data analysis, *i.e.*, the individual; however, in survey data the observation unit is the entire group. By converting the survey scan to a predominant group activity, observers are assigning one state to all individuals in a group defined by spatial (and not necessarily behavioral) association (Smolker *et al.* 1992). In this scenario, intragroup behavioral variation is disregarded. While it is possible for all members of a group to engage in the same behavior, groups of mixed activity state often occur, especially in groups of mixed age and sex classes (*e.g.*, bottlenose dolphins: Mann and Smuts 1999, Mann and Watson-Capps 2005, Mann 2006, Foroughirad and Mann 2013; bighorn sheep, *Ovis canadensis*: Ruckstuhl and Neuhaus 2001; black-and-gold howlers, *Alouatta caraya*: Prates and Bicca-Marques 2008; chimpanzees, *Pan troglodytes*: Wrangam and Smuts 1980). Furthermore, even within age and sex classes Shark Bay dolphins show pronounced individual variation in behavior (Mann and

Sargeant 2003, Gibson and Mann 2008, Sargeant and Mann 2009). In contrast to surveys, focal follows capture this individual variation in behavior because data are recorded on each individual independently. Nevertheless, the assignment of group activity was not the only factor leading to differences in activity budgets between methods, as solitary activity budgets also differed between surveys and focal follows (Fig. 2). Thus, there must be other factors aside from interpolating individual behavior from group-level observations producing these incongruent data sets.

The second possibility that may explain the differences between focal follow and survey activity budgets concern differences in sighting biases, which result from the fact that surveys are recorded soon after an initial sighting. Initial sightings are biased towards large groups (group-size sighting bias) and conspicuous surface behaviors (activity sighting biases). Because survey data are recorded during the first 5 min of an encounter, most behavioral data collected during surveys likely represent what the individual(s) was doing at the time of this initial sighting. This is supported by the fact that dolphins did not significantly alter their activity between initial observation and the 5 min survey sampling period (Table 2). Focal follows avoid both group-size sighting biases and activity sighting biases for several reasons. First, focal follows occur after a survey and last for up to several hours allowing them to capture smaller group sizes and less obvious activity states. Second, during focal follows observers focus their attention on a single (or pair of) individual(s), decreasing the likelihood that they miss more subtle behaviors and are overly influenced by conspicuous behaviors. The higher activity budget estimates for socializing in surveys could be due to the fact that socializing is characterized by relatively visible behaviors (*e.g.*, splashing and displays), and often occurs in larger groups (socializing group size was greater than group sizes in all other activity states for all data sets with $P < 0.05$ except traveling in decorrelated focal follows, and resting in all data sets, paired permutation tests, 10,000 permutations, Bonferroni-corrected), making it easily observed from afar. Conversely, traveling, which had a lower incidence in survey activity budgets, mostly occurs in smaller groups (Daura-Jorge *et al.* 2005) and consists of few surface behaviors, making it more subtle and difficult to observe. Yet, even when controlling for group size differences through solitary activity budgets, the difference in traveling between the two methods remained (Fig. 1, 2), suggesting that the difference in traveling may be mostly driven by activity sighting biases rather than group-size sighting biases. Furthermore, foraging budgets also differed between methods for solitary activity budgets, highlighting an additional activity sighting bias between the two methods that is independent of group size.

The final possible factor driving the differences in activity budgets between surveys and focal follows is that at small intervals, point sampling better captures activities that occur intermittently and punctuate other activities. For example, foraging bouts are often interspersed with bouts of travel. Unless an observer is focused on a single individual, these subtle changes in behavior might not be noticed. In surveys an observer's attention is often divided among many individuals, a situation which increases the chance that conspicuous behaviors will be disproportionately noticed. Travel, which is a relatively subtle behavior, is less likely to be identified as a predominant group activity in surveys unless it is performed exclusively for the entire 5 min sampling period. Thus, surveys in which animals travel from one foraging patch to another are likely to be assigned a foraging activity state, as traveling might escape an observer's notice. Because the sampling methods of focal follows better capture the sequence and transition of behaviors, they yield a more complete picture of an individual's activity budget.

Finally, it is important to consider the role temporal autocorrelation plays in animal behavior, and to what extent the choice of observational methodology incorporates this inherent autocorrelation. While it is true that subsampling of point-sampled focal follow data at a discrete interval ("time to independence") may reduce autocorrelation in attempts to achieve statistical independence of samples (Swihart and Slade 1985), this removal could be destructive to the accuracy and precision of activity budget estimates (de Solla *et al.* 1999). This reduction may instead eliminate nuanced patterns and "intrinsic properties" of behavior (Rooney *et al.* 1998, de Solla *et al.* 1999, Cushman *et al.* 2005). As animals rarely behave in a sequentially random fashion, to render behavioral samples independent by removing valuable autocorrelation may be misrepresenting an individual's true activity budget. Because our autocorrelated focal follow data set had significant differences in activity compared to surveys where our decorrelated follow data did not (foraging and resting, see Fig. 1), complete focal follow data appear to retain relevant behavioral autocorrelation that is otherwise not revealed in surveys or subsampled follow data. Since the full set of point samples in the focal follow data set more closely reflects an individual's true activity budget, *i.e.*, its complete and continuous behavioral patterns, it is a better representation of the way an individual partitions its time.

In recent years, technological advances have greatly improved behavioral data collection for cetaceans (*e.g.*, DTAGs, Johnson and Tyack 2003; satellite telemetry, Balmer *et al.* 2010). Yet these methods are not currently feasible for studying large numbers of individuals or for smaller cetaceans, meaning that observer-based methodologies are still necessary and important. Our study is one of few that explicitly examine how methodology influences individual activity budgets estimates. While group-level behavioral data may still be appropriate for certain questions (*e.g.*, Gero *et al.* 2005), our results indicate that activity budgets derived from focal follows, particularly data sets that include relevant behavioral autocorrelation, likely reflect a more accurate representation of an individual's activity budget than surveys. That said, although survey and follow data were statistically different, the biological relevance of these disparities is not known. For example, the methods appear to yield differing relative proportions of activities: from low to high, surveys order socializing, traveling, then foraging and resting (tied), whereas both decorrelated and autocorrelated focal follows have socializing as the lowest activity, with traveling, foraging, and resting as tied (see Fig. 1, non-ties $P < 0.0001$, paired permutation tests, 10,000 permutations, compared to all other states, Bonferonni-corrected). Whether or not these discrepancies could yield meaningful impacts for management decisions depends on many behavioral and ecological variables. Regardless, it is important to consider these discrepancies when comparing activity budgets calculated from different methods. Given the importance of activity budget data and what behavioral patterns they may reveal, it is crucial that investigators interested in collecting activity budget data take great care in deciding upon a methodology appropriate for their research questions, and critically consider how the possible biases associated with each method might impact results and the inferences made.

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Supporting Information

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Figure S1. Proportion of paired activity calls in focal follows that are the same for each minute of time shifted from the original point sample. Dashed line represents the optimal breakpoint (10.47 min), at which point the probability that the two activity calls would be the same was 0.55.

Figure S2. Female activity budgets from autocorrelated focal follow data, decorrelated focal follow data, survey data that were compared to autocorrelated focal follow data set, and survey data that were compared to decorrelated focal follow data set. Figure shows mean ± SE proportion of time in each behavioral state. Both survey data sets are virtually identical (paired permutation tests): foraging: $Z = 0.2791$, $P > 0.85$; resting: $Z = -0.7561$, $P > 0.85$; socializing: $Z = 1.3188$, $P > 0.85$; traveling: $Z = 0.3258$, $P > 0.85$. All permutation tests performed with 10,000 permutations, and because all P-values are Bonferonni-adjusted, any P-values > 1 are reported as $P > 0.85$. * = $P < 0.05$, ** = $P < 0.005$, *** = $P < 0.0001$.

Figure S3. Female solitary activity budgets from autocorrelated solitary focal follow data, decorrelated solitary focal follow data, solitary survey data that were compared to autocorrelated solitary focal follow data set, and solitary survey data that were compared to decorrelated solitary focal follow data set. Figure shows mean ± SE proportion of time in each behavioral state. Both survey data sets are virtually identical (paired permutation tests): foraging: $Z = 0.6189$, $P > 0.85$; resting: $Z = -1.5215$, $P = 0.5031$; traveling: $Z = 1.2649$, $P > 0.85$. All permutation tests performed with 10,000 permutations, and because all P-values are Bonferonni-adjusted, any P-values > 1 are reported as $P > 0.85$. ** = $P < 0.005$, *** = $P < 0.0001$.

Table S1. Results of binomial generalized linear mixed model before and after the optimal breakpoint (10.47 min).