Correcting for heterogeneous availability bias in surveys of long-diving marine turtles

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ABSTRACT

Effective conservation requires reliable data on the abundance and distribution of animals in space and time. During ship-based or aerial surveys for diving marine vertebrates such as sea turtles and marine mammals, a proportion of animals in a surveyed area will be missed because they are diving and out of view. While it is likely that dive and surface times vary with environmental conditions, such variation is rarely incorporated into survey-based research and its consequences for analyses of survey data are not well known. We quantified the effects of neglecting to account for variation in the dive-surfacing patterns of green turtles (*Chelonia mydas*) and loggerhead turtles (*Caretta caretta*) when analyzing boat-based survey data from a foraging ground in Western Australia. We found that analyses of turtle sightings data can be confounded by variation in the probability of turtles being at the surface where they are available for detection. For example, during the cold season in deeper areas in Shark Bay, green and loggerhead turtle density was underestimated by 45% and 21%, respectively, if extended dive times relative to population medians were not accounted for. These results have important implications for applications of survey data for a variety of taxa including other sea turtles, marine mammals and large sharks that are surveyed by boat or plane. Diving and depth use studies have much to contribute to the assessment and management of these groups, which include many species of conservation concern.

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1. Introduction

Accounting for detection probability in field-based research is a pervasive challenge that has important implications for conservation applications of field data. When conducting visual surveys to estimate species abundances or analyze habitat–wildlife relationships, some animals will likely be missed (i.e., detection probability will be imperfect) and the proportion missed may be correlated with environmental variables, habitat features or animal characteristics such as age, size or sex (Buckland et al., 2004). If not addressed, non-random variation in detection probability may mask variation in abundance and alter inferences made from analyses of survey data (e.g. Moilanen, 2002; Gu and Swihart, 2004; Mazerolle et al., 2005). Since spatiotemporal analyses of abundance (e.g., time-series or regional comparisons) are fundamental to conservation planning, minimizing bias related to detection probability is an important methodological goal.

Accounting for detection probability in aerial or boat-based surveys of large-bodied, diving marine vertebrates (e.g., marine mammals and sea turtles) is particularly challenging. First, to be detected, an animal must be at a depth where it is visible to observers, which is often referred to as the probability of being 'available'. Availability is primarily a function of the animal's depth use patterns and water turbidity, although survey type is also influential; for example, during boat-based surveys observers often cannot see into the water and only animals at the surface are available, whereas during aerial surveys a proportion of submerged animals may be available. Second, a proportion of available animals will be missed by observers, which may vary with factors such as weather conditions and observer experience. Marsh and Sinclair (1989a) distinguished these components of detection probability for diving taxa and coined the terms 'availability bias' and 'perception bias', respectively, to refer to bias in abundance indices arising as their result. While these definitions are somewhat overlapping, they provide a useful framework for modeling different sources of imperfect detection probability and correcting abundance estimates to account for missed animals.

For taxonomic groups that dive for extended periods and spend a small proportion of time at or near the surface, availability bias is

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highly problematic (Kasamatsu and Joyce, 1995; Barlow, 1999; Okamura et al., 2006). This is because a large proportion of animals present in a surveyed area will be missed since they are submerged and out of view. Failing to account for availability bias for these taxa can therefore cause severe underestimates of abundance (Barlow, 1999). Furthermore, variation in dive and surface times may lead to heterogeneous availability patterns, which can bias or confound analyses of survey data (Kasamatsu and Joyce, 1995; James et al., 2006; Thomson et al., 2012a). Knowledge of dive-surfacing patterns is therefore important for analyses and applications of sightings data.

Two methods of accounting for availability bias during analyses of survey data for diving taxa have been employed. Marsh and Sinclair (1989a) determined an availability correction factor (ACF) for dugongs (Dugong dugon) in aerial surveys by comparing the proportion of animals seen at the surface versus beneath the surface in turbid water with this proportion in clear water. However, this method is not ideal if a clear water habitat is not available to use as a standard and, even in clear water, if some animals are too deep to be seen or are cryptic, using this proportion as a standard will lead to underestimates of abundance (Preen et al., 1997). More recently, diving data have been used to measure the proportion of time animals spend at visible depths and calculate an ACF based on these measurements. This method allows for more accurate estimates of abundance and has been applied in studies of many taxonomic groups including cetaceans (e.g., Laake et al., 1997; Barlow, 1999), sirenians (e.g., Pollock et al., 2006), sea turtles (e.g., Gómez de Segura et al., 2006; Eguchi et al., 2007) and large sharks that spend some proportion of time at or near the surface (e.g., whale sharks, Rhincodon typus, Rowat et al., 2009).

Currently, corrections for the diving component of availability bias are often hindered by limited dive data. As a result, ACFs are often poorly resolved, abundance estimates are uncertain and spatiotemporal analyses of survey data rest on the tenuous assumption that availability is uniform across all survey conditions (e.g., Kasamatsu and Joyce, 1995; Barlow, 1999; Gómez de Segura et al., 2006). Thus, applications of survey data are typically limited relative to their full potential. In particular, the effects of variation in dive-surfacing patterns on spatiotemporal analyses of survey data, which are fundamental to ecological and conservation applications, require quantitative evaluation (Kasamatsu and Joyce, 1995; Preen et al., 1997; Thomson et al., 2012a).

Here, we present a case study focusing on marine turtles on a coastal foraging ground in Shark Bay, Western Australia. Previously, we collected a large set of dive records for green turtles (Chelonia mydas) and loggerhead turtles (Caretta caretta) in Shark Bay and found variation in their dive and surface times related to habitat depth and seasonal water temperature (Thomson et al., 2012a). We concluded that this variation could confound or bias spatiotemporal analyses of transect survey data for turtles. Here, we quantify the effects of failing to account for such variation in availability when analyzing survey data. To do so, we use Bayesian statistical methods to incorporate depth- and temperature-related variation in marine turtle diving into several analyses of boat-based transect survey data from Shark Bay. We compare the results of each analysis with those obtained without accounting for variable availability – that is, using a single ACF for each species based on median dive and surface times for all availability corrections. We thereby illustrate the effects of unmodeled variation in availability on analyses of survey data and demonstrate analytical methods by which these effects can be minimized.

## 2. Materials and methods

2.1. Study site and species

Shark Bay, Western Australia (~25°45′S, 113°44′E) is a shallow (mostly <15 m), subtropical bay located approximately 800 km north of Perth, Western Australia. Our study area in the bay's Eastern Gulf near the Monkey Mia Resort (Fig. 1) is characterized by expansive shallow (<4.5 m) seagrass-dominated habitat separated and surrounded by deeper (>6.0 m) sand-dominated habitat. There are also extensive, shallow sand–seagrass flats near shore. Green and loggerhead turtles use Shark Bay as a feeding ground year round. Green turtles may forage for a variety of seagrasses, algae, scyphozoan jellyfish and ctenophores (Heithaus et al., 2002; Seminoff et al., 2006; Burkholder et al., 2011) while loggerhead turtles are known to feed generally on benthic invertebrates, particularly molluscs and crustaceans (e.g., Dodd, 1988; Limpus et al., 2001; Thomson et al., 2012b).

2.2. Boat-based strip transect surveys

Strip transect surveys were conducted at thirteen sites, each bisecting either a shallow, seagrass-dominated habitat (six sites) or a deep, sand-dominated habitat (seven sites). Transects were between ~3 and 4.5 km long and were initially established to measure the relative density of large marine vertebrates including bottlenose dolphins Tursiops aduncus and dugongs under predation risk from tiger sharks Galeocerdo cuvier in each habitat (e.g. Heithaus and Dill, 2002). Transects were run in small (<5 m) boats during warm and cold seasons (February–April and June–August, respectively) in 2003, 2004, 2006 (cold season only), 2007, 2008 and 2009 (warm season only). Transects at a given site within a single month were conducted at different times of day and in different directions (i.e., reversing start and end points), organized haphazardly, to minimize these possible biases. Observers were assigned quadrants to search so that all waters within 30 m of the boat, parallel to or ahead of the boat's position, were being viewed. A sighting was logged when one or more observers saw a turtle. Only turtles at the surface were counted because, from the low height of our small boats, it was often difficult or impossible to see into the water, especially as distance from the transect line increased. Furthermore, in Shark Bay, which is shallow and has a fine sand-silt substrate, turbidity conditions can change rapidly over short distances, making accounting for this aspect of availability bias very difficult. Sightings for which the species of turtle could not be confidently identified (6% of sightings) were excluded from analyses.

2.3. Availability bias related to dive-surfacing behavior

Dive-surfacing patterns have been quantified for green and loggerhead turtles in Shark Bay (Thomson et al., 2012a). Briefly, short-term (1–7-day) time-depth recorder (MK9, Wildlife Computers, Redmond, Washington, USA) deployments were used to collect dive data for 29 green and 46 loggerhead turtles between 2005 and 2008. The software MultiTrace Dive (Jensen Software Systems, Laboe, Germany) was used to analyze dive profiles. Hierarchical Bayesian regression models revealed a positive effect of habitat depth (estimated from maximum dive depths, see Thomson et al., 2012a) and a negative effect of daily water temperature (i.e., seasonal variation between ~18 and 30 °C) on dive and surface times, although temperature effects were not significant in all cases. The regression equations were used to predict dive and
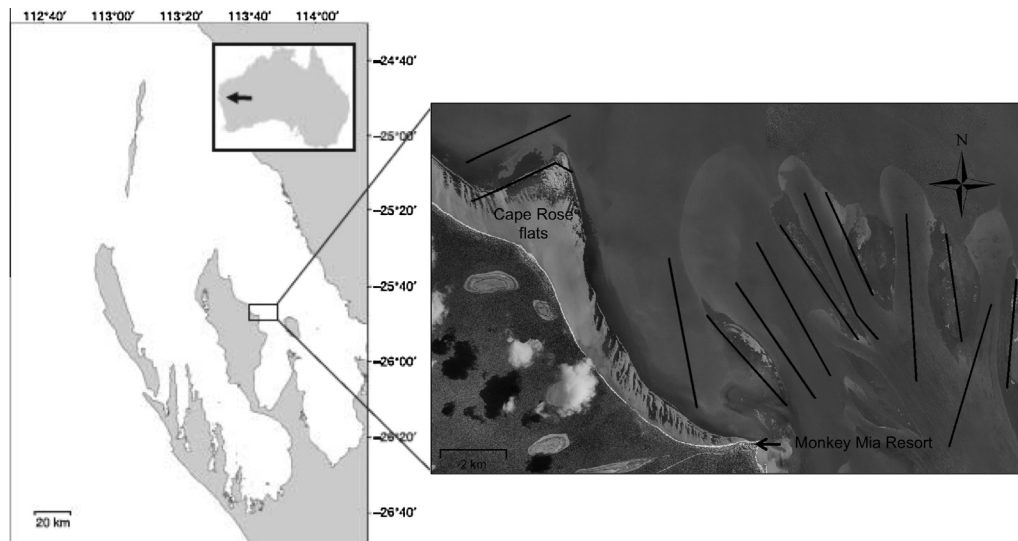
Fig. 1. Map of the study area in the near shore waters of the Eastern Gulf of Shark Bay. Dark lines represent 13 belt transect sites in shallow, seagrass-dominated (n = 6) and deep, sand-dominated (n = 7) habitats. The study area can be divided into two regions: a near shore sand–seagrass flat (Cape Rose flats) and a series of roughly parallel seagrass banks adjacent to the Monkey Mia Resort.

surface times across temperature-depth gradients (by 0.1 °C and 0.1 m, respectively) in the study area. The Bayesian approach allowed us to generate posterior distributions (50,000 iterations) of predicted dive metrics at each temperature-depth combination using a Monte Carlo procedure and calculate posterior medians (medians were used due to positive skew in the distributions) and standard deviations to assess uncertainty in these predictions (see Thomson et al., 2012a, Figs. 2 and 3, Appendices S1 and S2). Median posterior dive and surface times were then used to calculate ACF values following Barlow et al. (1988, see also Appendix A) across the temperature-depth gradients (Thomson et al., 2012a, Fig. 4). In general, larger availability corrections were required in colder, deeper conditions (corresponding to long-diving, infrequent-surfacing behavior) and smaller corrections were required in warmer, shallower conditions (corresponding to short-diving, frequent-surfacing behavior).

Here, we apply the same Monte Carlo procedure to obtain estimates of availability-corrected turtle densities using boat-based transect survey data. For a given turtle surface density in the transect data set, a posterior distribution (50,000 iterations) of availability-corrected density was obtained by multiplying the surface density by an ACF calculated using the regression equations and posterior parameter estimates of Thomson et al. (2012a) along with survey-specific depths and daily temperatures.

The depth of each transect (i.e., average depth of the area within the strip limits) at mean low sea level was obtained from a digital bathymetry map of the study area (Appendix B). For each transect pass, 'survey depth' was determined by adding the tide height at the midpoint of the survey to the site depth in the bathymetry. Since transects bisected either a shallow seagrass bed or deep channel, depths within each transect were relatively homogenous compared with the difference between shallow and deep habitats, and our approach allowed us to account for tidal variation within each transect between different passes (tide range ~1.2 m, Burling et al., 2003). Tide predictions, to the nearest minute, were obtained using the program JTides v. 5.2 (www.arachnoid.com). Daily water temperature data were obtained from a point sampling station near the Monkey Mia Resort (Fig. 1). The waters of Shark Bay are well mixed due to its shallow depth, strong tidal currents and high winds, therefore point sampling should reflect temperatures throughout our relatively small study area (Heithaus, 2001).

2.4. Perception bias

Our strip survey protocol did not allow us to estimate perception bias, but sought to minimize the proportion of available animals missed by observers. Factors that may influence the proportion missed include but are not limited to sea state (Marsh and Saalfeld, 1989) and strip width (Marsh and Sinclair, 1989b). Our approach to minimizing perception bias comprised: (1) a very narrow sightings strip (30 m) on either side of the boat; (2) slow survey speeds (6–9 km h^{-1}); (3) restriction of survey conditions to Beaufort sea states $\leqslant$2; and (4) multiple observers aboard the vessel (mean = 2.91, SD = 1.00). While it is inevitable that some available animals were missed, we are confident that the survey protocol minimized this proportion (but see Section 4.4).

2.5. Analyses of survey data

2.5.1. Seasonal variation in density

We lacked adequate survey data to analyze turtle sightings throughout the whole year. However, we compared monthly, habitat-specific (i.e., 'variable') ACFs, derived using mean monthly temperatures and survey depths, with each species' median (i.e., 'uniform') ACF. For each month in each habitat, we generated 50,000 posterior estimates of the variable ACF and the percent difference between that value and the uniform ACF [(uniform − variable)/variable]∗100. The posterior distribution of the percent difference allowed us to assess the magnitude and direction of bias that would arise in abundance indices, and its uncertainty (95% credible limits of posteriors based on 2.5th and 97.5th percentiles here and in all subsequent sections), if availability were assumed to be uniform between habitats and across the seasonal temperature gradient.

2.5.2. Density and abundance estimates

We estimated the density of turtles in shallow and deep habitats, in warm and cold seasons (February–April and June–August, respectively), using the two availability correction approaches. However, the application of ACFs to estimate density and abundance involved an important practical problem: raw transect data were highly zero-skewed (>85% zeros). The application of ACFs to raw transect data would therefore result in a problematic bi-modal

data distribution with a peak at zero, a large gap, and a second peak for the positive, availability-corrected values. In other words, low turtle densities would be mischaracterized as zeros following availability correction, resulting in underestimation of the mean and overestimation of the variance. To address this, it was necessary to collapse transect data prior to application of ACFs. Sightings were collapsed to a single density for each site within season and year (mean = 9.16 ± 0.26 SE passes per site within season and year). Then, an average density was calculated in each habitat in every year using these site-specific values, along with the mean survey depth and water temperature.

For each season- and habitat-specific surface density for a given year, 50,000 posterior estimates of availability-corrected density were obtained. Posterior distributions for each season-habitat combination were then pooled for all years and the median of each pooled posterior was determined along with the 95% credibility limits. Thus, our availability-corrected density estimates incorporate uncertainty related to dive-surfacing patterns and inter-annual variation in density at the habitat level. The percent difference between posterior medians under the uniform and variable availability approaches was then calculated, as above.

We then estimated the seasonal abundance of each species in the study region, which was 134 km^2 and bounded by the extremes of our transects. For each posterior estimate of availability-corrected density in a season-habitat group for a given year, an estimate of abundance was obtained by multiplying the density by the corresponding area of the habitat type in the whole study area. Posterior estimates of abundance in shallow and deep habitats were summed at each Monte Carlo iteration to obtain a posterior distribution of abundance for the entire study area within season and year. These posteriors were then pooled for all years in cold and warm seasons. The medians and 95% credible limits of the pooled posteriors were obtained. The percent difference between posterior medians under the uniform and variable availability-correction approaches was then calculated, as above.

2.5.3. Habitat use models

We constructed generalized linear mixed effects models to test for the effects of habitat type, season and their interaction on turtle density. These models were not intended as a comprehensive analysis of factors influencing turtle distribution, but as a simple example to evaluate potential effects of unmodeled variation in availability. Prior to modeling, raw transect data were collapsed to a single density per site within season and year (i.e., the first step of data collapse in Section 2.5.2). To retain adequate variation in the response variable for modeling, we did not collapse these data to the habitat level. The resulting data set comprised ~40% zeros, and applying absolute availability correction factors would therefore produce a problematic data and error structure. To overcome this, a relative means of correcting surface counts for availability, similar to that of Marsh and Sinclair (1989a), was used. The depth- and temperature-specific ACF for each data point was divided by the species' median ACF and the observed surface density was multiplied by the resulting value. For example, if the variable ACF was 20% larger than the species' median for a particular data point the surface density would be multiplied by 1.2. The resulting data were surface densities standardized for availability with a distribution amenable to modeling with a Poisson error structure.

Site-level transect data were pooled for all years and site was included as a random effect in the models. Models were run using the software R v. 2.9.2 (R Development Core Team, 2009) and diagnostics were checked using Pearson and deviance residuals following Zuur et al. (2009). We calculated the percent difference between parameter estimates for models run using uncorrected (i.e., uniform availability) and availability-corrected (i.e., variable availability) surface density data for each species.

3. Results

3.1. Seasonal variation in density

Habitat-specific trends were observed in the percent difference between uniform and variable ACFs across the year-round temperature gradient (Fig. 2). For both species, the assumption of uniform availability would lead to overestimates of abundance in shallow habitats, particularly at warmer times of year (December–March). Conversely, the assumption of uniform availability would lead to underestimates of abundance in deep habitats in most cases, particularly during the coldest months (June–August).

3.2. Density and abundance estimates

Density estimates in season-habitat groups varied substantially between the uniform and variable availability correction approaches (Table 1). For example, density in deep habitat during the cold season (June–August) was underestimated by 45% for green turtles and 21% for loggerhead turtles under the assumption of uniform availability. Densities in shallow habitats during the warm season (February–April) were overestimated by 128% for green turtles and 51% for loggerhead turtles. The absolute percent difference between density estimates under the two availability-correction approaches was <20% in only two season-habitat groups, both for loggerhead turtles.
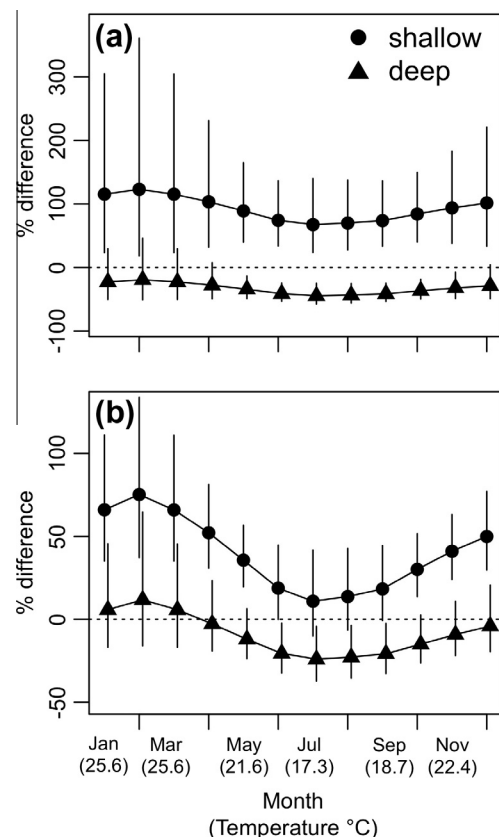
Fig. 2. The percent difference between variable ACFs in shallow and deep habitats across a seasonal temperature gradient and the species median for green turtles (a) and loggerhead turtles (b). The points and error bars represent the median and 95% credible limits of each percent difference posterior distribution.

Table 1
Estimated densities (turtles km^{-2}) of green and loggerhead turtles in season-habitat groups under uniform and variable availability-correction approaches. Statistics presented are the medians and 95% credibility limits of the posterior distributions.

Species	Season	Habitat	Uniform availability	Variable availability	% Difference in medians
Green	Cold	Deep	2.49 (0.66, 4.09)	4.51 (0.96, 8.53)	−44.8
		Shallow	3.75 (1.08, 8.77)	2.08 (0.51, 6.50)	80.3
	Warm	Deep	11.66 (7.17, 15.38)	15.24 (7.06, 28.18)	−23.5
		Shallow	13.39 (1.48, 29.68)	5.88 (0.55, 19.01)	127.7
Loggerhead	Cold	Deep	9.05 (5.68, 13.91)	11.47 (6.58, 20.52)	−21.1
		Shallow	3.95 (0.00, 9.26)	3.41 (0.00, 9.74)	15.8
	Warm	Deep	28.15 (22.74, 32.16)	27.58 (18.05, 37.06)	2.1
		Shallow	8.31 (5.89, 12.37)	5.52 (3.36, 8.99)	50.5

Table 2
Abundance estimates for green and loggerhead turtles in each season under uniform and variable availability correction approaches. Statistics presented are the medians and 95% credibility limits of the posterior distributions.

Species	Season	Uniform availability	Variable availability	% Difference in medians
Green	Cold	348 (77, 933)	336 (78, 1009)	3.6
	Warm	1330 (362, 3435)	1210 (378, 3002)	9.9
Loggerhead	Cold	735 (347, 1766)	843 (405, 2160)	−12.8
	Warm	2062 (1299, 3202)	1801 (1016, 3210)	14.5

When turtle densities in season-habitat groups were extrapolated to the full study area to estimate seasonal abundance, the magnitude of availability-related bias was generally low (<15%, Table 2). For example, during the warm season green turtle abundance was overestimated by 10% while loggerhead turtle abundance was overestimated by 15% under the assumption of uniform availability.

3.3. Habitat use models

Correction of surface densities for availability altered parameter estimates, and affected parameter significance marginally in one case (Table 3). For green turtles, the effect of season was overestimated by 20% under uniform availability, although this parameter was significant in both models. Habitat type had a positive but non-significant effect on green turtle density in the uniform model, and a negative but non-significant effect in the variable model. The interaction term for green turtles differed by 43% between the two models but was non-significant in both cases. The effect of season on loggerhead turtle density was overestimated by 36% under uniform availability, although this parameter was significant in both models. The effect of habitat on loggerhead turtle density was underestimated by 35% in the uniform availability model, and the effect became marginally significant following correction for availability (P-value changed from 0.196 in the uniform model to 0.054 in the variable model). The interaction term was not affected by availability correction in the loggerhead models.

4. Discussion and conclusions

4.1. Availability bias for chelonid sea turtles

In general, the effects of variable availability of turtles in Shark Bay were intuitive based on trends in their diving behavior (i.e., short-diving, frequent-surfacing behavior in warmer, shallower conditions and long-diving, infrequent-surfacing behavior in colder, deeper conditions). For example, the application of a single ACF across all survey conditions led to heavily biased abundance indices in season- and habitat-specific subsets of survey data. Density tended to be underestimated in deeper areas, particularly during the cold season, and overestimated in shallower areas, particularly during the warm season. This suggests that survey-specific estimates of availability may be required to reliably quantify the distribution of turtles within or among heterogeneous study areas. However, the effect of variation in availability patterns was less marked when estimating total abundance in the study area.

The effects of availability correction in habitat use models were also generally consistent with expectations based on turtles' diving trends. For example, the uniform availability model indicated that loggerhead density was significantly higher in the warm relative to the cold season. However, since turtles are more likely to be available for detection during the warm season, correction of surface densities for availability should reduce the seasonal effect, which was indeed observed in the variable availability model (36% difference in parameter estimates). Furthermore, in the uniform model, loggerhead density was lower, though not significantly, in shallow relative to deep habitat. Since turtles are more likely to be available in shallow habitat, correction for availability in the variable model should increase the magnitude of the habitat effect, which was also observed.

The general conclusion that can be drawn from these results is that variation in surface sightings of turtles in Shark Bay can be confounded, to some extent, by predictable variation in availability resulting from diving behavior. Therefore, reliable inferences about turtle distribution from survey data require the ability to tease apart the effects of abundance and availability on near-surface sightings. The potential for this effect has been noted previously for chelonid sea turtles. For example, Shoop and Kenney (1992) collected surface sightings data for loggerhead turtles in the eastern United States and used these to infer seasonal distribution shifts. However, they also acknowledged that decreased surface sightings during winter could result from migratory patterns and/or reduced availability due to turtles hibernating on the seabed. In such cases, depth use and satellite tracking data are valuable because they can be used to test the validity of interpretations of survey data.

Chelonid sea turtles present an interesting case study for this problem because a degree of predictable variation between dive and surface times and environmental or habitat variables appears to exist across species, life stages and regions. For example, a

Table 3

Results of habitat use models for green and loggerhead turtles under uniform (left) and variable (right) availability-correction approaches. The level of each categorical variable being compared to the reference level is indicated in parentheses.

Species	Parameter	Uniform-availability model			Variable-availability model			% Difference in estimates
		Estimate	SE	P-value	Estimate	SE	P-value	
Green	Season (warm)	1.819	0.467	<0.001	1.518	0.362	<0.001	19.8
	Habitat (shallow)	0.911	0.630	0.148	−0.168	0.619	0.786	−642.3
	Habitat*Season	−0.885	0.576	0.125	−0.619	0.571	0.279	43.0
Loggerhead	Season (warm)	1.003	0.257	<0.001	0.737	0.235	0.002	36.1
	Habitat (shallow)	−0.678	0.524	0.196	−1.047	0.543	0.054	−35.2
	Habitat*Season	−0.306	0.507	0.547	−0.298	0.545	0.585	2.7

negative relationship between temperature and dive duration has been documented for several species in multiple locations (e.g. Bentivegna et al., 2003; Southwood et al., 2003; Hochscheid et al., 2005, 2007; Storch et al., 2005; Thomson et al., 2012a). Furthermore, in shallow coastal habitat a positive relationship may be found between habitat depth and dive duration. This is because lung buoyancy can lead to shorter dives, on average, in very shallow relative to deeper areas where turtles can achieve negative buoyancy with full lungs (Minamikawa et al., 1997, 2000; Hochscheid et al., 2003; Hays et al., 2004). Therefore, variation in availability linked to depth and temperature may be a relatively common source of detection heterogeneity for chelonids in seasonal environments and shallow coastal habitat.

4.2. Relevance to other taxa

Our results have important implications for surveys and the management of several taxonomic groups in diverse ecosystems. For example, variation in leatherback turtle (*Dermochelys coriacea*) dive and surface times has also been noted in relation to availability for detection during aerial surveys. Specifically James et al. (2006) provided the first availability estimates for leatherbacks and showed that availability varied between periods spent in high-latitude foraging areas and during migrations to lower-latitude breeding areas. They concluded that fine-scale spatial and temporal analyses of leatherback activities, which may be inferred using dive profiles, are needed to refine availability corrections and abundance estimates derived from aerial surveys.

Many long-diving marine mammals including deep-diving cetaceans (e.g., beaked whales) are surveyed by boat or plane, and abundance estimates for these species rely heavily on availability corrections. However, dive records for these species are limited owing to their elusive nature (Barlow, 1999; Baird et al., 2006). Additional dive records, and analyses of variation in dive and surface times related to environmental, habitat or individual variables, are required to improve the reliability of availability corrections for this group (Kasamatsu and Joyce, 1995; Barlow, 1999), especially considering the paucity of abundance data for many species (IUCN, 2012).

Several non-air-breathing marine vertebrates, including some large sharks (e.g. Williams et al., 2006; Rowat et al., 2009), are surveyed by boat or plane. Since these species may spend varying amounts of time near the surface where they are visible, and at depths where they are not, depth use records are necessary to account for diving-related availability bias. For example, variation in the proportion of time basking sharks (*Cetorhinus maximus*) spend feeding in near-surface waters, possibly related to variation in ocean mixing, has been suggested as a source of regional detection bias during aerial surveys in the British Isles (Southall et al., 2005). Therefore, diving and depth use studies are valuable for the conservation and management of this and other shark species.

Finally, while we have focused primarily on long-diving taxa, availability bias can also be high for short-diving species, especially in turbid water (e.g., sirenians Pollock et al., 2006; Edwards et al., 2007). Therefore, experimental work seeking to estimate availability and perception biases for diving taxa in general is needed to generate reliable data for conservation assessments and planning.

4.3. Conservation implications

Population status assessments, monitoring and effective conservation strategies depend on the availability of reliable abundance and distribution data. In the marine environment, such information is often unavailable owing to difficulties in collecting and analyzing survey data. As a result, status assessments are often not possible (e.g., among beaked whales, family Ziphiidae, 17 of 18 red-listed species are considered data deficient, IUCN, 2012) and the strength of inferences that can be made from survey data regarding animal movements is often limited by caveats related to detection probability. For example, McDaniel et al. (2000) used aerial survey data to evaluate potential overlap between marine turtle distribution and a shrimp fishery in the Gulf of Mexico. However, an important caveat in this survey was that the waters of the western region of the Gulf were very turbid, restricting sightings to turtles at the surface, whereas in the eastern region of the Gulf the water was clearer, possibly allowing submerged turtles to be counted. Given the large and variable proportion of time marine turtles may spend submerged (Lutcavage and Lutz, 1997; Thomson et al., 2012a), and considering our results here, such potential detection heterogeneity may have a substantial impact on the analysis and application of survey data. Thus, diving and depth use studies, along with innovative experimental methods of modeling overall detection probability (e.g. Pollock et al., 2006), are highly valuable to the assessment and conservation of a variety of marine taxa. Indeed, many of the taxonomic groups referred to here include species of conservation concern, and reliable abundance and distribution data are therefore badly needed.

4.4. Assumptions

We made two assumptions that require evaluation to improve future applications of our methods. First, we assumed that our survey protocol minimized perception bias – the proportion of available turtles missed by observers. Due to the large size of the turtles relative to the narrow strip width, the slow survey speeds, the number of observers on board and the sea state restrictions for our surveys, we feel that this assumption is reasonable. However, perception bias can be high even for relatively large and conspicuous animals (e.g., dugongs Pollock et al., 2006) so future work should test this assumption using independent observers to quantify perception bias in conjunction with dive-based availability corrections.

We also assumed that surface times detected by the dive analysis software used by Thomson et al. (2012a) perfectly corresponded to times when turtles would be at the surface and

available for detection. This may not always be the case due to errors in dive profile analysis, particularly in very shallow areas where it can be challenging for analysis software to distinguish time at the surface from near-surface movements (Hagihara et al., 2011). However, the TDRs used in this study sampled depth every second to ±0.5 m, and a 13-s rolling average was used to smooth dive profiles prior to analysis. Since the mean depth of our shallow sites averaged across all passes within each season and year was 2.6 m ±0.1 (SE), mischaracterizations of surface time in shallow habitat resulting from sensor error should have been minimal. Zero-offset correction to account for sensor drift, which was performed manually in our study, may have resulted in some near-surface movements being mischaracterized as surfacing events or vice versa. We do not expect that such errors would bias our analyses or alter our conclusions regarding the influence of predictable spatiotemporal variation in availability on analyses of survey data. However, to minimize error arising from dive analysis parameterization and maximize the accuracy of abundance estimates in future applications, it would be useful to compare dive profile analyses with direct observations of surfacing behavior (Hagihara et al., 2011).

4.5. Recommendations

The implications of our findings for survey-based research depend on the particular aims of a project. For example, if the goal of a survey is to estimate total abundance, an accurate estimate of average or median dive and surface times within the study area should be sufficient to account for availability bias. If, however, spatiotemporal analyses within or among survey areas are intended, the availability issue may be more challenging, requiring additional data and more detailed analyses. Therefore, we recommend that researchers consider the potential effects of availability bias relative to their goals *a priori* and prioritize diving studies as necessary. Furthermore, the ability to test for and incorporate variable availability patterns into analyses of survey data will depend in part on the feasibility of collecting dive data over appropriate spatial scales. If diving data cannot be collected over appropriate scales, it may be advisable to integrate transect surveys with other data types to validate their interpretation. For example Southall et al. (2005) compared aerial survey data for basking sharks with satellite tracks, which revealed that tagged sharks spent considerable time in areas where survey sightings were low. Regional variation in depth use (i.e., near-surface feeding behavior) was the suspected source of detection bias in the surveys. Therefore, in addition to diving studies, integrating surveys with tracking information can be a useful means of evaluating detection bias in surveys.

4.6. Conclusions

Our work with marine turtles in Shark Bay supports the contention of others that a greater understanding of dive-surfacing patterns is needed to reduce the effects of availability bias on abundance estimates and spatiotemporal analyses of survey data for long-diving marine vertebrates (Kasamatsu and Joyce, 1995; Barlow, 1999; James et al., 2006). This includes non-air-breathing species such as large sharks that spend varying amounts of time at or near the surface. We have shown that failing to account for spatiotemporal variation in availability patterns can lead to confounded analyses, which may result in sub-optimal applications of survey data. However, we have also demonstrated analytical methods by which dive data can be applied to overcome this challenge. Considering the conservation status and ecological importance of many large-bodied diving taxa, diving studies are badly needed to generate the data required for effective management of these groups.

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.biocon.2013.06.005.

References

Baird, R.W., Webster, D.L., McSweeney, D.J., Ligon, A.D., Schorr, G.S., Barlow, J., 2006. Diving behaviour of Cuvier's (*Ziphius cavirostris*) and Blainville's (*Mesoplodon densirostris*) beaked whales in Hawai'i. Can. J. Zool. 84, 1120–1128.

Barlow, J., 1999. Trackline detection probability for long-diving whales. In: Garner, G.W., Laake, J.L., Robertson, D.G. (Eds.), Marine Mammal Survey and Assessment Methods. A.A Balkema, Rotterdam, pp. 209–221.

Barlow, J., Oliver, C.W., Jackson, T.D., Taylor, B.L., 1988. Harbor porpoise, *Phocoena phocoena*, abundance estimation for California, Oregon, and Washington: II. Aerial surveys. Fish. Bull. 86, 433–444.

Bentivegna, F., Hochscheid, S., Minucci, C., 2003. Seasonal variability in voluntary dive duration of the Mediterranean loggerhead turtle, *Caretta caretta*. Sci. Mar. 67, 371–375.

Buckland, S.T., Anderson, D.R., Burnham, K.P., Laake, J.L., Borchers, D.L., Thomas, L., 2004. Advanced Distance Sampling. Oxford University Press, Oxford, UK.

Burkholder, D.A., Heithaus, M.R., Thomson, J.A., Fourqurean, J., 2011. Diversity in trophic interactions of green sea turtles *Chelonia mydas* on a relatively pristine coastal foraging ground. Mar. Ecol. Prog. Ser. 439, 277–293.

Burling, M.C., Pattiaratchi, C.B., Ivey, G.N., 2003. The tidal regime of Shark Bay, Western Australia. Estuar., Coast. Shelf Sci. 57, 725–735.

Dodd, C.K., 1988. Synopsis of the biological data on the loggerhead sea turtle *Caretta caretta* (Linnaeus 1758). U.S. fish and wildlife service. Biol. Rep. 88, 1–110.

Edwards, H.H., Pollock, K.H., Ackerman, B.B., Reyholds III, J.E., Powell, J.A., 2007. Estimation of detection probability in manatee aerial survey at a winter aggregation site. J. Wildlife Manage. 71, 2052–2060.

Eguchi, T., Gerrodette, T., Pitman, R.L., Seminoff, J.A., Dutton, P.H., 2007. At-sea density and abundance estimates of the olive ridley turtle *Lepidochelys olivacea* in the eastern tropical Pacific. Endangered Species Res. 3, 191–203.

Gómez de Segura, A., Tomás, J., Pedraza, S.N., Crespo, E.A., Raga, J.A., 2006. Abundance and distribution of the endangered loggerhead turtle in Spanish Mediterranean waters and the conservation implications. Anim. Conserv. 9, 199–206.

Gu, W., Swihart, R.K., 2004. Absent or undetected? Effects of non-detection of species occurrence on wildlife-habitat models. Biol. Conserv. 116, 195–203.

Hagihara, R, Jones, R.E., Sheppard, J.K., Hodgson, A.J., Marsh, H., 2011. Minimizing errors in the analysis of dive recordings from shallow-diving animals. J. Exp. Mar. Biol. Ecol. 399, 173–181.

Hays, G.C., Metcalfe, J.D., Walne, A.W., 2004. The implications of lung-regulated buoyancy control for dive depth and duration. Ecology 85, 1137–1145.

Heithaus, M.R., 2001. The biology of tiger sharks, *Galeocerdo cuvier*, in Shark Bay, Western Australia: sex ratio, size distribution, and seasonal changes in catch rates. Environ. Biol. Fish. 61, 25–36.

Heithaus, M.R., Dill, L.M., 2002. Food availability and tiger shark predation risk influence bottlenose dolphin habitat use. Ecology 83, 480–491.

Heithaus, M.R., McLash, J.J., Frid, A., Dill, L.M., Marshall, G.J., 2002. Novel insights into green sea turtle behavior using animal-borne video cameras. J. Mar. Biol. Assoc. U.K. 82, 1049–1050.

Hochscheid, S., Bentivegna, F., Speakman, J.R., 2003. The dual function of the lung in chelonian sea turtles: buoyancy control and oxygen storage. J. Exp. Mar. Biol. Ecol. 297, 123–140.

Hochscheid, S., Bentivegna, F., Hays, G.C., 2005. First records of dive durations for a hibernating sea turtle. Biol. Lett. 1, 82–86.

Hochscheid, S., Bentivegna, F., Bradai, M.N., Hays, G.C., 2007. Overwintering behaviour in sea turtles: dormancy is optional. Mar. Ecol. Prog. Ser. 340, 287–298.

IUCN, 2012. IUCN Red List of Threatened Species. Version 2012.1. <www.iucnredlist.org>.

James, M.C., Ottensmeyer, C.A., Eckert, S.A., Myers, R.A., 2006. Changes in diel diving patterns accompany shifts between northern foraging and southward migration in leatherback turtles. Can. J. Zool. 84, 754–765.

Kasamatsu, F., Joyce, G.G., 1995. Current status of odontocetes in the Antarctic. Antarct. Sci. 7, 365–379.

Laake, J.L., Calambokidis, J., Osmek, S.D., Rugh, D.J., 1997. Probability of detecting harbor porpoise from aerial surveys: estimating g(0). J. Wildlife Manage. 61, 63–75.

Limpus, C.J., de Villiers, D.L., de Villiers, M.A., Limpus, D.J., Read, M.A., 2001. The loggerhead turtle, Caretta caretta, in Queensland: feeding ecology in warm temperate waters. Mem. Queensland Mus. 46, 631–645.

Lutcavage, M.E., Lutz, P.L., 1997. Diving physiology. In: Lutz, P.L., Musick, J.A. (Eds.), The Biology of Sea Turtles. CRC Press, Boca Raton, pp. 277–296.

Marsh, H., Saalfeld, W.K., 1989. Distribution and abundance of dugongs in the northern Great Barrier Reef marine park. Aust. Wildlife Res. 16, 429–440.

Marsh, H., Sinclair, D.F., 1989a. Correcting for visibility bias in strip transect aerial surveys of aquatic fauna. J. Wildlife Manage. 53, 1017–1024.

Marsh, H., Sinclair, D.F., 1989b. An experimental evaluation of dugong and sea turtle aerial survey techniques. Aust. Wildlife Res. 16, 639–650.

Mazerolle, M.J., Desrochers, A., Rochefort, L., 2005. Landscape characteristics influence pond occupancy by frogs after accounting for detectability. Ecol. Appl. 15, 824–834.

McDaniel, C.J., Crowder, L.B., Priddy, J.A., 2000. Spatial dynamics of sea turtle abundance and shrimping intensity in the U.S. Gulf of Mexico. Cons. Ecol. 4, 15. http://www.consecol.org/vol4/iss1/art15.

Minamikawa, S., Naito, Y., Uchida, I., 1997. Buoyancy control in diving behavior of the Loggerhead Turtle, Caretta caretta. J. Ethol. 15, 109–118.

Minamikawa, S., Naito, Y., Sato, K., Matsuzawa, Y., Bando, T., Sakamoto, W., 2000. Maintenance of neutral buoyancy by depth selection in the loggerhead turtle Caretta caretta. J. Exp. Biol. 203, 2967–2975.

Moilanen, A., 2002. Implications of empirical data quality to metapopulation model parameter estimation and application. Oikos 96, 516–530.

Okamura, H., Minamikawa, S., Kitakado, T., 2006. Effect of surfacing patterns on abundance estimates of long-diving animals. Fish. Sci. 72, 631–638.

Pollock, K.H., Marsh, H.D., Lawler, I.R., Alldredge, M.W., 2006. Estimating animal abundance in heterogeneous environments: an application to aerial surveys for dugongs. J. Wildlife Manage. 70, 255–262.

Preen, A.R., Marsh, H., Lawler, I.R., Prince, R.I.T., Shepherd, R., 1997. Distribution and bundance of dugongs, turtles, dolphins and other megafauna in Shark Bay, Ningaloo Reef and Exmouth Gulf, Western Australia. Wildlife Res. 24, 185–208.

R Development Core Team, 2009. R: A language and environment for statistical computing. R Foundation for Statistical Computing (Ed.), Vienna, Austria.

Rowat, D., Gore, M., Meekan, M.G., Lawler, I.R., Bradshaw, C.J.A., 2009. Aerial survey as a tool to estimate whale shark abundance trends. J. Exp. Mar. Biol. Ecol. 368, 1–8.

Seminoff, J.A., Jones, T.T., Marshall, G.J., 2006. Underwater behaviour of green turtles monitored with video-time-depth recorders: what's missing from dive profiles? Mar. Ecol. Prog. Ser. 322, 269–280.

Shoop, C.R., Kenney, R.D., 1992. Seasonal distributions and abundances of loggerhead and leatherback sea turtles in waters of the northeastern United States. Herpetol. Monogr. 6, 43–67.

Southall, E.J., Sims, D.W., Metcalfe, J.D., Doyle, J.I., Fanshawe, S., Lacey, C., Shrimpton, J., Solandt, J.-L., Speedie, C.D., 2005. Spatial distribution patterns of basking sharks on the European shelf: preliminary comparison of satellite-tag geolocation, survey and public sightings data. J. Mar. Biol. Assoc. U.K. 85, 1083–1088.

Southwood, A.L., Reina, R.D., Jones, V.S., Jones, D.R., 2003. Seasonal diving patterns and body temperatures of juvenile green turtles at Heron Island, Australia. Can. J. Zool. 81, 1014–1024.

Storch, S., Wilson, R., Hillis-Starr, Z.-M., Adelung, D., 2005. Cold-blooded divers: temperature-dependent dive performance in the wild hawksbill turtle Eretmochelys imbricata. Mar. Ecol. Prog. Ser. 293, 263–271.

Thomson, J.A., Cooper, A.B., Burkholder, D.A., Heithaus, M.R., Dill, L.M., 2012a. Heterogeneous patterns of availability for detection during visual surveys: spatiotemporal variation in sea turtle dive-surfacing behaviour on a feeding ground. Methods Ecol. Evol. 3, 378–387.

Thomson, J.A., Heithaus, M.R., Burkholder, D.A., Vaudo, J.J., Wirsing, A.J., Dill, L.M., 2012b. Site specialists, diet generalists? Isotopic variation, site fidelity and foraging by loggerhead turtles in Shark Bay, Western Australia. Mar. Ecol. Prog. Ser. 453, 213–226.

Williams, R., Okey, T.A., Wallace, S.S., Gallucci, V.F., 2006. Shark aggregation in coastal waters of British Columbia. Mar. Ecol. Prog. Ser. 414, 249–256.

Zuur, A.F., Ieno, E.N., Walker, N.J., Saveliev, A.A., Smith, G.M., 2009. Mixed Effects Models and Extensions in Ecology with R. Springer, New York.