

Heterogeneous patterns of availability for detection during visual surveys: spatiotemporal variation in sea turtle dive–surfacing behaviour on a feeding ground

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Summary

1. During aerial or boat-based surveys for large-bodied diving taxa (e.g. marine mammals and marine turtles), a proportion of animals present will be missed because they are submerged and out of view, leading to ‘availability bias’ in abundance indices. Information on dive–surfacing patterns can improve corrections for availability bias. However, as dive data are typically limited, availability correction factors are often based on poorly resolved dive and surface times, and diving heterogeneity is not considered.

2. We collected dive records for green turtles *Chelonia mydas*, Linnaeus 1758, and loggerhead turtles *Caretta caretta*, Linnaeus 1758, on a foraging ground in Shark Bay, Western Australia to quantify dive–surfacing patterns and assess potential correlations with easily measured environmental features: habitat depth and water temperature. Bayesian regression models were used to predict dive and surface interval durations across temperature–depth gradients and assess their uncertainty. We used these predictions to quantify variation in availability correction factors, which were multipliers designed, in this case, to adjust surface sightings data to incorporate diving animals.

3. Dive and surface interval durations for both species varied positively with depth and negatively with temperature, consistent with *a priori* expectations, although temperature effects were not always significant. Dive metrics were predictable, although uncertainty increased in deeper habitat with few observed dives.

4. Availability correction factors were highly heterogeneous, with larger corrections necessary in colder, deeper conditions (long-diving, infrequent surfacing behaviour) and smaller corrections required in warmer, shallower conditions (short-diving, frequent-surfacing behaviour).

5. Predictable variation in the diving behaviour of chelonid sea turtles across environmental gradients on a foraging ground reveals that site-specific knowledge of dive–surfacing patterns can be important to mitigate the effects of availability bias during population surveys. Accounting for such trends may improve the reliability of ecological inferences (e.g. spatiotemporal distribution trends) and the efficacy of applications (e.g. conservation planning) based on survey data.

Key-words: abundance estimation, availability bias, detectability, diving, green turtle, loggerhead turtle, sightability, transect sampling

Introduction

When estimating animal abundance and analysing wildlife–habitat relationships using field data, ecologists are often

confronted with the problem of imperfect and heterogeneous detection probability – that is, some proportion of animals present in a surveyed area will be missed and this proportion may vary spatially or temporally (Buckland *et al.* 2004). If not considered during data collection and analysis, imperfect and heterogeneous detection probability can result in biased abundance estimates (e.g. Gu & Swihart 2004), erroneous ecological

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inferences (e.g. Mazerolle, Desrochers & Rochefort 2005) and sub-optimal applications (e.g. Moilanen 2002). As detection probability can be problematic for diverse data collection techniques (e.g. visual and acoustic surveys, mark-recapture methods, Mazerolle *et al.* 2007), accounting for its influence is a pervasive challenge in ecology.

In marine environments, boat-based and aerial transects are often used to survey populations of large-bodied diving taxa (e.g. marine mammals and sea turtles). Detection of animals during these surveys is determined by two factors (Marsh & Sinclair 1989a): first, an animal must be 'available' to observers (i.e. it must be visible given its depth and sighting conditions in the water); second, an available animal must be sighted by observers, which can vary with factors such as observer experience (although even the most experienced observer may miss an available animal, Caughley, Sinclair & Scott-Kemmis 1976). Marsh & Sinclair (1989a) refer to bias in abundance indices arising because of these sources of imperfect detection as availability bias and perception bias, respectively, and specialized methods are required to account for each.

Our focus here is on availability bias, which can be influenced by a combination of survey type (i.e. aerial or boat-based), environmental features (e.g. water turbidity) and the animal's dive-surfacing patterns. For example, in aerial surveys, observers can often see a proportion of submerged animals (e.g. Marsh & Sinclair 1989a,b), and this proportion is contingent upon water turbidity and the proportion of time the animals spend at particular depths (e.g. Pollock *et al.* 2006). In contrast, in many boat-based (e.g. Barlow 1999) and some aerial surveys (e.g. Gómez de Segura *et al.* 2006; Eguchi *et al.* 2007), it is difficult to see into the water and availability comprises the proportion of time animals spend at the surface. Thus, the precise definition of availability bias varies among studies. For our purposes in this case study, we equate animal availability to time spent at the surface (but see Discussion).

Availability bias is a particularly salient issue for long-diving taxa (e.g. marine turtles and deep-diving odontocetes) because these species spend minimal time at the surface (Lutcavage & Lutz 1997; Barlow 1999). Therefore, during a survey, a substantial proportion of animals present will be missed and abundance estimates require large corrections for availability. These availability corrections require data on dive-surfacing patterns, which can be obtained by direct observation or, more commonly, using time-depth recorders (TDR). However, dive data are currently limited in many regions, and correction factors are often based on poorly resolved average dive and surface times. Furthermore, because of inadequate dive data, most studies must make the simplifying assumption that dive-surfacing patterns are uniform across all survey conditions, neglecting potential heterogeneity in dive and surface times (Kasamatsu & Joyce 1995; Barlow 1999; Gómez de Segura *et al.* 2006). If such variation exists and is correlated with features of the environment, abundance estimates derived from survey data may be biased (Laake & Borchers 2004) and spatiotemporal comparisons (e.g. seasonal distribution shifts) confounded.

Among long-diving taxa, correlations between diving behaviour and environmental features may be particularly common for chelonid (i.e. hard-shelled) marine turtles. Their metabolic rates are linked to ambient water temperature, and as temperature decreases, dive capacity increases because of slower use of stored oxygen (e.g. Hochscheid, Bentivegna & Hays 2005). Additionally, marine reptiles use their lungs as their primary oxygen store leading to buoyancy effects (Graham *et al.* 1987; Minamikawa, Naito & Uchida 1997; Minamikawa *et al.* 2000; Hays, Metcalfe & Walne 2004). In shallow habitat, turtles may dive with less inspired air, leading to shorter dives, than in deeper areas to avoid paying the energetic cost of actively countering buoyancy to remain on or near the seabed (Minamikawa, Naito & Uchida 1997; Houghton, Woolmer & Hays 2000; Hays, Metcalfe & Walne 2004). Thus, broad trends in dive-surfacing behaviour (i.e. average dive and surface times) and the probability of being available for detection during at-sea surveys may exist across temperature and shallow depth gradients.

To assess the potential for, and possible implications of, heterogeneous availability patterns, we studied the diving behaviour of green turtles *Chelonia mydas*, Linnaeus 1758, and loggerhead turtles *Caretta caretta*, Linnaeus 1758, on a foraging ground in Shark Bay, Western Australia. Our goals were: (i) to determine whether dive-surfacing patterns varied with habitat depth and water temperature in accordance with *a priori* expectations; (ii) to assess the extent to which variation in average dive and surface times could be predicted based on these easily measured features of the environment; and (iii) to infer the implications of neglecting nonrandom variation in the probability of being available for detection for analyses of survey data.

Our analyses are not intended as a comprehensive study of factors influencing diving behaviour. Clearly, a diversity of physiological, ecological and environmental variables (e.g. body size, Schreer & Kovacs 1997; prey distribution, Croxall *et al.* 1985; predation risk, Kramer, Manley & Bourgeois 1983; Heithaus & Frid 2003; reproductive status or breeding location, Hays *et al.* 2002) influence dive and surface times. The question here is whether broad, predictable trends in average dive and surface times at the group level exist – with uncertainty around the averages reflecting variation related to other factors – and whether accounting for such trends can improve the reliability of abundance estimates, spatiotemporal comparisons and applications of at-sea survey data.

Methods

STUDY SYSTEM AND SPECIES

Shark Bay, Western Australia (c. 25°45'S, 113°44'E), is a shallow (mostly < 15 m), subtropical bay located c. 800 km north of Perth. Our study area in the bay's Eastern Gulf is characterized by expansive shallow (< 4.5 m) seagrass-dominated habitat separated and surrounded by deeper (> 6.0 m) sand-dominated habitat, with a tidal range of 1.2 m (Burling, Pattiaratchi & Ivey 2003). Sub-adult and adult green and loggerhead turtles use Shark Bay as a feeding ground year round. Green turtles may feed on a variety of seagrasses, algae,

scyphozoan jellyfish and ctenophores (Heithaus *et al.* 2002; Seminoff, Jones & Marshall 2006; Burkholder *et al.* 2011), while loggerhead turtles in neritic foraging areas tend to feed on benthic invertebrates, particularly molluscs and crustaceans (Dodd 1988; Plotkin, Wicksten & Amos 1993; Limpus *et al.* 2001; Lazar *et al.* 2011; J. Thomson *et al.*, unpublished data).

Turtles were captured by hand (Heithaus, Frid & Dill 2002) during haphazard searches and transect surveys of the study area. Curved carapace length (CCL) was measured (± 0.5 cm), and turtles were tagged using titanium flipper tags (Department of Environment and Conservation, Western Australia) applied to a proximal foreflipper scute. Turtles were considered male if the tail length was ≥ 25.0 cm and unclassified, and which would include immature males and all females, if the tail length was < 25.0 cm (Limpus, Couper & Read 1994a,b; Heithaus, Frid & Dill 2002).

We used TDRs (MK9; Wildlife Computers, Redmond, WA, USA) to collect diving data. Tags recorded depth (± 0.5 m) every second and temperature (reported to ± 0.01 °C) every 60 s. TDRs were packaged in high-density foam along with an acoustic pinger (Sonotronics, Tucson, AZ, USA) and a VHF radio transmitter (Telonics, Mesa, AZ, USA) for retrieval. Tag packages were attached using dissolving zinc–magnesium links tethered to a square of nylon mesh glued directly to the turtle's carapace with 5-min epoxy (Devcon, Danvers, MA, USA). Links lasted between 2 and 7 days, and tags were redeployed over the course of the study. The relatively short duration of the deployments was necessary to maximize the probability of tag retrieval and facilitate sampling of a large number of individuals, which is the appropriate sampling unit for this study.

DIVE DATA ANALYSIS

The software Multi Trace Dive (Jensen Software Systems, Laboe, Germany) was used to analyse dive profiles. To smooth profiles, each depth measurement was averaged over thirteen points (centred on itself with six points before and after). Dives were detected, and surface and dive times were measured using vertical velocity and depth thresholds. Dives were analysed if maximum dive depth (i.e. habitat depth) exceeded 1.5 m; at depths < 1.5 m, it was not possible to reliably discern surfacing events. All dives were pooled for analysis, regardless of shape (see Hochscheid *et al.* 1999; Minamikawa *et al.* 2000; Houghton *et al.* 2002; Seminoff, Jones & Marshall 2006) or presumed function, because assessment of turtle behaviour is typically not possible during population surveys (e.g. Marsh & Sinclair 1989b).

Dives began when depth exceeded a threshold of 0.75 m, and end of diving was detected when vertical velocity dropped below -0.03 m*s⁻¹ and the turtle returned above 10% of the maximum dive depth. The latter depth threshold was necessary because green and loggerhead turtles often perform gradual ascents making a velocity threshold alone incapable of detecting the end of diving (e.g. Houghton *et al.* 2002). Threshold values were determined by consulting a previous study using Multi Trace Dive to analyse loggerhead turtle dive profiles (Houghton *et al.* 2002) and via preliminary trials with a subset of the dive records from Shark Bay. Following determination of the optimal software settings, each dive was analysed and inspected visually to verify that inflection points indicating the turtle arriving at or leaving the surface were detected consistently. Zero-offset correction was performed manually (see Hagihara *et al.* 2011).

We considered the maximum depth of a dive to reflect habitat depth. This assumption seems reasonable for neritic-stage green and loggerhead turtles in coastal foraging habitat, which engage in most activities (e.g. foraging, resting) on the sea bottom. However, this

method of characterizing habitat depth would not be without error. To attempt to quantify this error, we analysed animal-borne video data linked to dive profiles (see Heithaus *et al.* 2002) for 14 green turtles (mean CCL = 90.0, SD = 12.6, 374 dives) and 18 loggerhead turtles (mean CCL = 94.1 cm, SD = 9.2, 459 dives) in the same study area between April and July in 1999, 2000 and 2003. This data set comprised turtles of similar size to the present study but over a limited range of seasonal conditions. Using all video footage, we determined the proportion of all dives reaching the sea bottom for both species. For dives with both video and depth profile data (76 and 112 dives lacked depth profiles for green and loggerhead turtles, respectively), we classified dive types following published visual criteria (summarized in Seminoff, Jones & Marshall 2006) and determined which dive types would most likely cause habitat classification errors. This information was then applied to reduce error in the stand-alone TDR data set (see Results).

To allow for postrelease stress, the first 4 h of each deployment were excluded from analysis. This cut-off was determined by visual inspection of dive profiles, which revealed a trend toward higher dive frequency during this period for some individuals, similar to a 6-h period of elevated dive frequency in green turtles observed by Hazel, Lawler & Hamann (2009). In a study of green turtle behaviour in the Gulf of California (Seminoff, Jones & Marshall 2006), animal-borne video loggers revealed typical behaviours immediately following release, suggesting minimal capture stress effects. However, given that our TDR deployments spanned multiple days, we opted for the more conservative approach. To coincide with the timing of population surveys, only daytime dives (between 08:00 and 18:00 h local time) were analysed.

STATISTICAL ANALYSIS

Statistical analyses were conducted using R (R Foundation for Statistical Computing, Vienna, Austria) and WinBUGS (Imperial College & MRC, UK). For several reasons, we took a Bayesian multi-level regression approach to this problem (Bryk & Raudenbush 1992; Gelman & Hill 2006). First, a hierarchical approach allowed us to use individual dives or surface intervals as data points while accounting for the repeated measures nature of the data via random effects for each turtle. Second, we wanted to include independent variables at different levels in the models. Habitat depth, for instance, should have explanatory power at the level of an individual dive but would be less meaningful as a daily average because turtles can move across the range of depths in the study area within a day. While temperature data were collected frequently by the TDRs (every 60 s), we wanted to assess the influence of temperature at a scale that would be transferable to abundance surveys lacking fine-scale data. Therefore, we collapsed temperatures to daily means. The Bayesian paradigm allowed us to assess uncertainty in estimates of dive and surface interval duration and availability correction factors using posterior distributions.

MULTI-LEVEL REGRESSION MODEL

We constructed identical models for dive and surface interval durations (log-transformed to eliminate heteroscedasticity) for each species. Initially, the models included dive depth, daily temperature and their interaction as fixed effects. Preliminary examination of the residuals from these models revealed evidence of nonlinearity between depth and duration; therefore, we also included a quadratic depth term in each model. A variance parameter was estimated for each turtle because TDR deployments were short and of variable

duration. The generalized hierarchical regression equation for our models was:

$$Y_{ijk} = \beta_{0j} + \beta_{1j}X_{ijk} + \beta_{2j}X_{ijk}^2 + \gamma_{0j}W_{jk} + \gamma_{1j}W_{jk}X_{ijk} + \varepsilon_{ijk} \quad \text{eqn 1}$$

where Y_{ijk} is the duration of dive or surface interval i performed by turtle j on day k , β_{0j} is the turtle-specific intercept, β_{1j} is the coefficient for dive depth (X_{ijk}), β_{2j} is the coefficient for depth² (X_{ijk}^2), γ_{0j} is the coefficient for daily temperature (W_{jk}), γ_{1j} is the coefficient for the temperature*depth interaction ($W_{jk}X_{ijk}$), and ε_{ijk} is the residual error, which we assumed to be normally distributed with a mean of zero and variance σ_j^2 . The random effects were assumed to be normally distributed with means and variances:

$$\beta_{0j} \sim N(\beta_0, \sigma_{\beta_0}^2),$$

$$\beta_{1j} \sim N(\beta_1, \sigma_{\beta_1}^2),$$

$$\beta_{2j} \sim N(\beta_2, \sigma_{\beta_2}^2),$$

$$\gamma_{0j} \sim N(\gamma_0, \sigma_{\gamma_0}^2),$$

$$\gamma_{1j} \sim N(\gamma_1, \sigma_{\gamma_1}^2).$$

To reduce error in the estimation of the intercept caused by the large gap between minimum temperature (*c.* 16 °C) and zero, we centred temperature and depth data by subtracting the mean from each observation. Five Monte Carlo Markov Chains were run for each model with 2 050 000 iterations thinned every 200 and a burn-in period of 5000 iterations (prior to thinning). Model diagnostics including chain convergence, within-chain autocorrelation and posterior parameter distributions were evaluated using the 'Coda' package in R. WinBUGS model sample code can be found in Appendix S1 (Supporting Information).

MODEL CHECKING

At the individual dive or surface interval level, we calculated a pseudo- R^2 value (correlation between the logs of predicted and actual values) for each model. However, we were most interested in each model's ability to predict average dive and surface interval durations at the population level under particular depth and temperature conditions. We, therefore, summarized dive and surface interval durations in 2-m by 2 °C bins, used the regression equations to predict average dive and surface times in each bin and calculated pseudo- R^2 values. We then calculated mean absolute prediction errors across all bins for each model. Standard deviations of the posterior distributions provided a measure of the precision of model predictions.

To illustrate depth- and temperature-related variation in diving behaviour, we calculated posterior median dive and surface interval durations, and their uncertainty, over all possible combinations of depth and temperature in the observed range (by 0.1 m and 0.1 °C) for each species. Medians were used because of positive skew in the posterior samples resulting from long-duration dives presumably related to resting.

AVAILABILITY CORRECTION FACTORS

Abundance in a surveyed area can be estimated by dividing the observed count by detection probability, which is the probability of being available times the probability of perception. Thus, the inverse

of the probability of being available (p_a) can be considered an availability correction factor – a multiplier that adjusts abundance indices to incorporate animals missed because they were not visible (Marsh & Sinclair 1989a). Here, we present depth- and temperature-related heterogeneity in this multiplier, calculating p_a following Barlow *et al.* (1988):

$$p_a = \frac{s+t}{s+d} \quad \text{eqn 2}$$

where s is the predicted surface interval duration (s), d is the predicted dive duration (s), and t is a 'sampling window', which represents the length of time (s) for which an animal would be within visible range of a passing observer. The t variable accounts for the fact that sampling is not instantaneous and an animal's availability status can change while within detectable range (e.g. an animal that was submerged when first within range could surface). Here, we specified $t = 30$ s, which corresponds to the average speed and the sightings distance limit for turtles during boat-based strip surveys conducted by the authors in Shark Bay. Note that if $d < t$, p_a could be > 1 as calculated above. In such cases, p_a can be restricted to 1, and duplicate sightings of an animal subsequent to the initial surfacing can be excluded. In the current data set, however, predicted d was always $> t$.

We used posterior samples of dive and surface interval durations to calculate availability correction factors, and their uncertainty, across all possible combinations of temperature and depth in the observed data sets. These survey-specific correction factors are intended as an illustrative example of the potential for, and implications of, nonrandom variation in availability patterns.

Results

Between 2005 and 2008, TDRs were successfully deployed on 29 green (8 male, 21 unclassified, 3692 daytime dives) and 46 loggerhead turtles (18 male, 24 unclassified, 3591 daytime dives). Four loggerhead turtles were captured twice and have two dive records in the data set, but only a single turtle identity. Green turtles ranged in size (CCL) from 81.0 to 118.0 cm (mean = 96.9, SD = 9.1), while loggerhead turtles ranged from 74.0 to 104.5 cm (mean = 94.0, SD = 7.7). Mean daytime water temperature, averaged over the course of a TDR deployment, ranged between ca. 16 and 30 °C for both species, which corresponds to seasonal variation in water temperature within the study area (Heithaus 2001). Diving by both species, and particularly loggerhead turtles, was concentrated in habitats < 8 m deep; the relative density of observed dives across temperature and depth gradients is shown in Fig. 1.

CLASSIFYING HABITAT DEPTH FROM DIVE PROFILES

In the video data set, *c.* 70% of all dives by green and loggerhead turtles reached the sea floor. In the stand-alone TDR records, turtles often performed short V-shaped (Type 2) or parabolic (Type 5) dives just beneath the surface during sequences of much longer, deeper dives to a consistent depth (e.g. bouts of square-bottom U-shaped, or Type 1, dives often associated with benthic resting or activity, Hochscheid *et al.* 1999; Houghton *et al.* 2002). Taking the maximum depth of the short 'near-surface' dives to represent habitat depth would

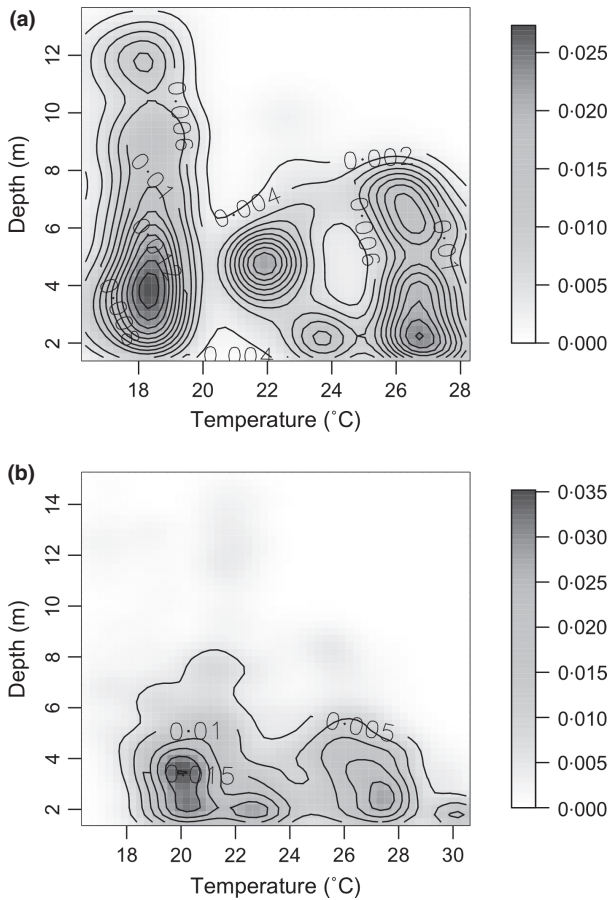


Fig. 1. The distribution of dives by green (a) and loggerhead turtles (b) across the full range of depth and temperature in each data set. Scale bars, shading and contour lines reflect the proportion of the data set (by number of dives) at each temperature–depth combination.

lead to depth misclassification because we could be confident that these dives did not represent brief movements to shallow habitat. This assertion was supported by the video data with linked dive profiles, which revealed that Type 2 and Type 5 dives by loggerhead turtles and Type 5 dives by green turtles were less likely to reach the sea bottom than other dive types frequently observed in that study. Therefore, to reduce habitat misclassification, we adjusted the habitat depth of the ‘near-surface’ dives to the average of the maximum depths of the two neighbouring long dives if the near-surface dive depth was less

than half of that value. The habitat-adjusted dives comprised 6.4% (238/3692) and 3.4% (121/3591) of the green and loggerhead TDR data sets, respectively.

Another source of habitat misclassification may be sequences of Type 5 dives that reflect movement along the sea bottom (maximum dive depth would be a reliable proxy for habitat depth) or in the water column (maximum dive depth would not be a reliable proxy for habitat depth). We could not account for this source of error because these sequences were not noted during analysis of TDR records and, if they had been, it would still not be possible to distinguish between those that were benthic versus mid-water. Moving forward, data loggers with GPS capability, which provide location data that can be compared with bathymetry, can eliminate this source of error.

REGRESSION MODEL RESULTS

We found a significant (i.e. 95% credible intervals did not contain zero) positive effect of habitat depth on duration in all regression models (Tables 1 and 2). A significant, negative effect of temperature on dive and surface interval duration was found for loggerhead turtles, while a negative but nonsignificant trend with temperature was found for green turtles. The quadratic term for depth was significant in some cases but not others while the interaction term was nonsignificant in all cases (Tables 1 and 2). Final regression equations with parameter coefficients and the depth and temperature values used to centre data are included as Appendix S2 (Supporting Information).

MODEL CHECKING

At the individual dive cycle level, pseudo- R^2 values for dive and surface interval models were 0.33 and 0.28, respectively, for green turtles and 0.36 and 0.42 for loggerhead turtles. When comparing predictions of the regression equations with average observed durations in 2-m by 2 °C bins, pseudo- R^2 values for dive and surface interval models were 0.73 and 0.51, respectively, for green turtles and 0.47 and 0.65 for loggerhead turtles. However, for both species, large prediction errors occurred primarily in bins with relatively few dives. If, for instance, bins with fewer than 30 dives were excluded and prediction errors re-examined, pseudo- R^2 values for dive and surface interval models were 0.77 and 0.67, respectively, for green turtles and 0.76 and 0.90 for loggerhead turtles.

Table 1. Descriptive statistics of the posterior distributions of model parameters for green turtles. LCL and UCL represent lower and upper 95% credible limits of posterior distributions. Asterisks denote parameters whose credible limits do not include zero

Parameter	Dives				Surface intervals			
	Mean	SD	LCL	UCL	Mean	SD	LCL	UCL
β_0 (Intercept)	1.831*	0.103	1.623	2.031	2.002*	0.143	1.724	2.287
β_1 (Depth)	0.222*	0.042	0.141	0.309	0.108*	0.042	0.027	0.193
β_2 (Depth ²)	-0.001	0.011	-0.023	0.020	0.027*	0.009	0.009	0.046
γ_0 (Temperature)	-0.043	0.032	-0.105	0.022	-0.045	0.043	-0.134	0.037
γ_1 (Depth*Temperature)	0.001	0.015	-0.029	0.031	0.016	0.015	-0.013	0.045

Table 2. Descriptive statistics of the posterior distributions of model parameters for loggerhead turtles. LCL and UCL represent lower and upper 95% credible limits of posterior distributions. Asterisks denote parameters whose credible limits do not include zero

Parameter	Dives				Surface intervals			
	Mean	SD	LCL	UCL	Mean	SD	LCL	UCL
β_0 (Intercept)	2.683*	0.096	2.492	2.869	3.627*	0.115	3.398	3.853
β_1 (Depth)	0.319*	0.037	0.245	0.392	0.331*	0.037	0.257	0.405
β_2 (Depth ²)	-0.044*	0.013	-0.071	-0.019	-0.035*	0.013	-0.061	-0.012
γ_0 (Temperature)	-0.087*	0.031	-0.149	-0.027	-0.071*	0.034	-0.137	-0.003
γ_1 (Depth*Temperature)	-0.009	0.014	-0.036	0.017	-0.011	0.013	-0.036	0.015

Furthermore, for green turtles, prediction errors became exceedingly high (but with no directional bias) toward 'extreme' depths of the data set (> 10 m), which comprised 7.1% of observed dives (Fig. 1a). For loggerhead turtles, prediction errors in depths > 10 m were large and consistently negative, and these dives comprised 4.7% of the data set (Fig. 1b). For both species, these predictions were considered unreliable, and we proceeded with a predicted data set truncated at 10 m. Mean absolute prediction errors for dives and surface intervals in all bins < 10 m, including those with < 30 dives, were 2.1 min and 2.8 s, respectively, for green turtles and 5.5 min and 18.0 s for loggerhead turtles. Observed dive data summarized in 2-m by 2 °C bins (means with 95% confidence limits) are provided in Appendix S3 (Supporting Information).

The predicted duration of green turtle dives increased toward the colder, deeper extreme of the data set and decreased toward the warmer, shallower extreme (Fig. 2a). Predicted surface intervals were shortest at the warmer, shallower extreme and increased as temperature decreased at shallower depths. At depths > c. 7 m, surface interval duration increased with depth consistently across all temperature conditions (Fig. 2c). Uncertainty in green turtle dive and surface interval predictions increased at greater depths, particularly toward the warmer, deeper extreme (Fig. 2b,d). Trends in loggerhead turtle dive and surface interval predictions were similar to each other, with the longest durations toward the colder, deeper extreme and the shortest durations toward the warmer, shallower extreme (Fig. 3a,c). Uncertainty in these estimates increased with depth, particularly toward the colder, deeper extreme (Fig. 3b,d).

Availability correction factors were highly heterogeneous for both species and increased toward colder, deeper conditions (although correction factors for loggerhead turtles decreased slightly above ca. 8 m at the colder extreme) and decreased toward warmer, shallower conditions (Fig. 4a,c). Standard deviations of availability correction factor estimates for both species were quite low but increased toward the warmer and colder extremes in deeper habitat (Fig. 4b,d).

Discussion

Both perception and availability biases should be addressed when estimating abundance and conducting spatiotemporal comparisons of survey data for diving taxa (Marsh & Sinclair

1989a). A variety of techniques have been developed to correct for perception bias (e.g. distance sampling and related methods, see Buckland *et al.* 1993, 2004) while comparatively little research has focused on availability bias, particularly for elusive long-diving taxa (but see Barlow 1999; Okamura 2003; Okamura, Minamikawa & Kitakado 2006). In sea turtle studies, surface densities have often been analysed without accounting for availability (e.g. Shoop & Kenney 1992), or methods of standardizing sightings across turbidity gradients (Marsh & Sinclair 1989a) have been employed (e.g. Preen *et al.* 1997). These methods provide estimates of minimum abundance only and spatiotemporal comparisons rest on the tenuous assumption that dive-surfacing patterns are uniform within a study area.

While dive records have been used to account for unavailability of turtles because of diving in more recent studies, dive data are still often limited (e.g. Gómez de Segura *et al.* 2003, 2006; Eguchi *et al.* 2007) and larger data sets are required to better resolve correction factors. In Shark Bay, a large number of dive records for green and loggerhead turtles revealed highly heterogeneous, but predictable, availability patterns – assuming availability comprises time at the surface – across two common environmental gradients: seasonal water temperature and habitat depth. Our results indicate that variation in dive and surface times, if not accounted for, may lead to biased abundance indices and confounded spatiotemporal comparisons, highlighting the value of diving studies to survey-based research.

Consider, for example, depth-related changes in green turtle diving at 18 °C. At this temperature, median dive duration in water 9 m deep was predicted to be 15.6 min (SD = 4.2) with a 15.7-s surface interval (SD = 4.3), resulting in an availability correction factor of 20.8 (SD = 3.5). At the same temperature but in water 3 m deep, median dive duration was predicted to be 4.2 min (SD = 0.7), surface interval duration to be 8.1 s (SD = 1.7) and the correction factor would be 6.8 (SD = 0.9). If we were to ignore diving heterogeneity and use a single correction factor (10.3, SD = 0.8) based on the species' average dive and surface times (the current approach), we would underestimate abundance by a factor of 10.5 in the 9-m habitat and overestimate by a factor of 3.5 in the 3-m habitat. Thus, quantifying the spatial distribution of turtles in our study area requires knowledge of depth-related variation in dive-surfacing patterns. Elsewhere, because of lack of dive data, surface densities have been used to examine

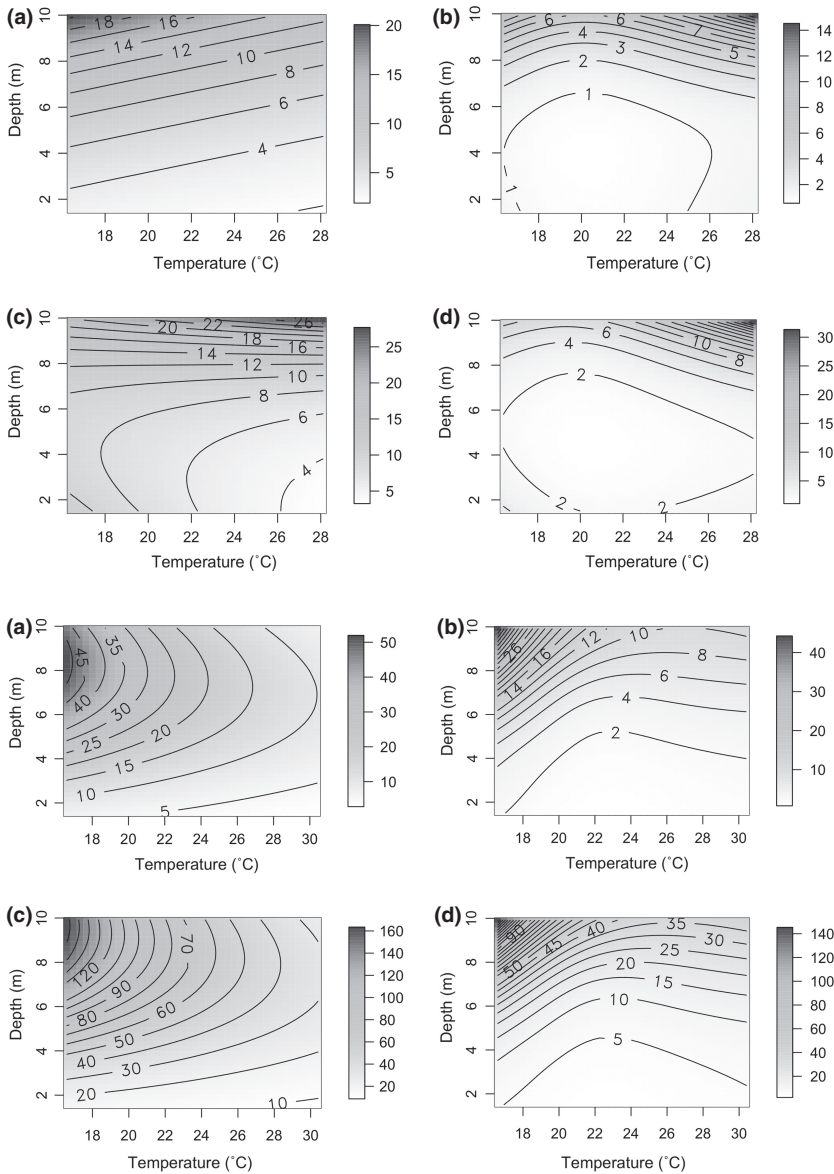


Fig. 2. For green turtles, contour plots of predicted median dive duration (min) and corresponding standard deviations (a and b, respectively) and median surface interval duration (s) and corresponding standard deviations (c and d, respectively) across temperature and depth combinations.

Fig. 3. For loggerhead turtles, contour plots of predicted median dive duration (min) and corresponding standard deviations (a and b, respectively) and median surface interval duration (s) and corresponding standard deviations (c and d, respectively) across temperature and depth combinations.

spatiotemporal variation in turtle distribution patterns (e.g. Shoop & Kenney 1992; Gómez de Segura *et al.* 2006) and address applied questions (e.g. potential spatial overlap with fisheries, McDaniel, Crowder & Priddy 2000). Consideration of diving behaviour may alter our interpretation of spatiotemporal trends in surface density data and increase confidence in biological inferences (e.g. Shoop & Kenney 1992) or management decisions.

Temperature-duration and depth-duration relationships appear to have considerable generality across chelonid species, locations and life stages. For example, Hochscheid *et al.* (2007) found a strong correlation between seasonal water temperature and dive duration by loggerhead turtles in the Mediterranean. Dives routinely lasted > 180 min for loggerheads experiencing winter temperatures as low as *c.* 13 °C and variation in temperature explained 56% of the variation in dive duration. Captive juvenile Mediterranean loggerheads, subjected to natural seasonal fluctuations in water temperature, showed a shift toward longer dives in the winter period

(Bentivegna, Hochscheid & Minucci 2003). A positive relationship between dive depth and duration was found for three dive types commonly performed by green turtles in relatively shallow (< 20 m) habitat around Cyprus (Hochscheid *et al.* 1999). Because chelonids are often distributed across depth gradients in coastal areas (e.g. Marsh & Saalfeld 1989; Shoop & Kenney 1992) and frequently occur in seasonal environments (e.g. Renaud & Carpenter 1994; Preen *et al.* 1997; Southwood *et al.* 2003; Hochscheid, Bentivegna & Hays 2005), it seems reasonable to suggest that depth- and temperature-related diving trends may be pervasive sources of detection heterogeneity for these taxa.

While our regression models were able to predict median dive and surface times with a reasonably high level of accuracy and precision, several limitations are worth noting. For both species, predictions were imprecise and inaccurate in water > 10 m deep, and prediction errors were largest in temperature-depth conditions with few observed dives. More data (i.e. longer deployments) should result in increasingly reliable

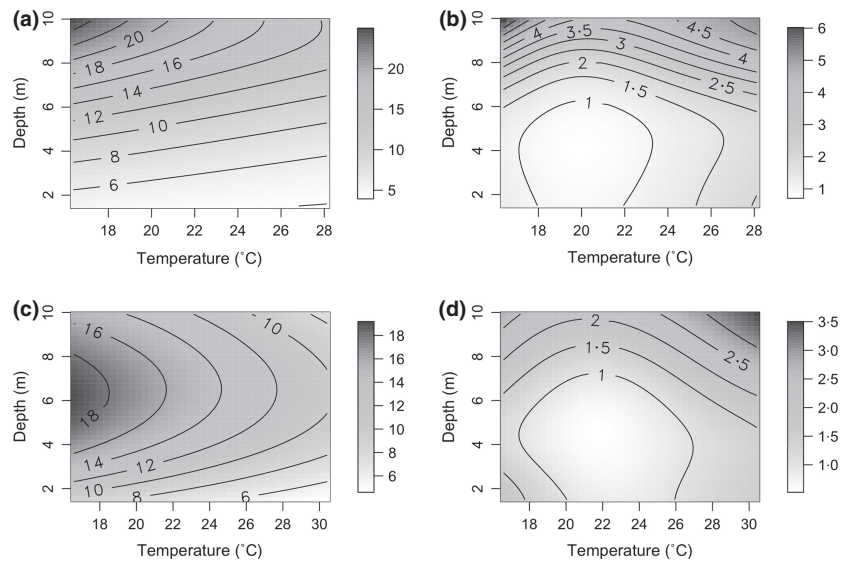


Fig. 4. Contour plots of the median availability correction factors and corresponding standard deviations for green turtles (a and b, respectively) and loggerhead turtles (c and d, respectively) across all temperature and depth combinations.

predictions, particularly in deeper areas. However, additional variation in dive and surface times may exist in deeper areas that the models were simply not able to capture. Furthermore, the extent to which the relationships found here would hold in conditions outside the range in Shark Bay is unclear. The habitat depth–duration relationship, for example, may apply in gradients from a few metres to the minimum at which turtles can achieve negative buoyancy with full lung volume – estimated by Hays *et al.* (2000) to be 19 m for adult green turtles – beyond which diving may be less predictable by habitat depth. Finally, predictable variation in dive durations may be more common than surface interval durations. For example, Hochscheid *et al.* (2007) documented a de-coupling of covariation between loggerhead turtle dives and surface intervals at extremely long dive durations ($> c.$ 210 min) performed in cold temperatures. Differences in the ability to predict the two metrics would lead to greater uncertainty in availability corrections.

APPLICATION: POSSIBILITIES AND LIMITATIONS

Availability corrections can be applied in conjunction with methods of correcting for perception bias. For example, Pollock *et al.* (2006) used dive records and experimental surveys to adjust aerial dugong *Dugong dugon*, Müller 1776, counts for availability bias and multiple independent observers to correct for perception bias. Gómez de Segura *et al.* (2006) used distance sampling with multiple independent observers to account for perception bias in aerial surveys of loggerhead turtles and dive records to adjust counts for animals missed because of diving (although spatiotemporal comparisons were conducted assuming uniform diving behaviour because of inadequate dive data). Therefore, our results principally highlight the need for more detailed information on dive–surfacing patterns, which can be incorporated into existing survey and analytical techniques.

Heterogeneous availability patterns can be accommodated if a survey region can be subdivided such that availability may

vary among, but remain relatively uniform within, survey units. In the context of the temperature and depth relationships shown here, if survey units are oriented roughly parallel to depth contours, correction factors for diving can be determined separately for different depth strata. If surveys are repeated over seasonal gradients, separate correction factors can be applied at different times of year. While straightforward in theory, in practice, the scale at which variable availability patterns can be accounted for will depend on the spatial extent of the survey and the feasibility of collecting dive data. Fine-scale corrections may not be realistic in many cases. However, even a relatively coarse approach (e.g. separate correction factors for discrete seasons or broad depth categories into which survey units can be aggregated) would be a substantial improvement on current methods and enable greater ecological insight from sightings data.

FUTURE RESEARCH

Our results logically lead one to question what consequences neglecting diving variability may have for common analyses of chelonid survey data. Therefore, integrating diving variation into these analyses and comparing the results with the traditional approach (i.e. using a single correction factor across all survey conditions) are an important research goal. Furthermore, the statistical models developed here provide a foundation that may be improved upon. For example, we have not tested for temporal autocorrelation among model residuals or explicitly considered the correlation between dive and surface interval durations. While the models did predict dive and surface times remarkably well, suggesting suitability for this purpose, these additional elements may improve model fit. Statistical preference may be given to Bayesian and simulation methods (e.g. Pollock *et al.* 2006) moving forward owing to their ability to account for multiple sources of uncertainty.

We have assumed that the probability of turtles being available is determined by the proportion of time spent at the

surface. However, in some surveys, particularly aerial surveys, a proportion of submerged animals may also be visible (e.g. Marsh & Sinclair 1989b; Preen *et al.* 1997). In this more complex scenario, availability bias will depend on both the animals' dive–surfacing behaviour and water turbidity or other sea conditions influencing visibility (e.g. sea state). In a study of dugongs, Pollock *et al.* (2006) combined dive records with experimental surveys using submerged dugong models to estimate corrections for availability bias in heterogeneous turbid conditions. Such an approach could also be applied to marine turtles. However, a key challenge for turtles is that species identification can be difficult (e.g. Preen *et al.* 1997), especially if they are submerged. As dive–surfacing patterns can vary strongly among species, a trade-off exists between sightings frequency (i.e. including or excluding uncertain species identifications, many of which would be submerged turtles) and the reliability of corrections for the diving component of availability bias.

Comparative studies testing the generality of the trends found in Shark Bay in other foraging areas, or examining other sources of variation among sites, would also be valuable. For example, the activities and diving behaviour of chelonids may vary markedly between different breeding areas owing to the availability or lack of resources (Hays *et al.* 2002). Such differences may need to be considered if survey data are used to estimate abundance or assess habitat use patterns. Furthermore, we have not tested for the effects of factors such as turtle size or sex here, opting instead to approach the problem from the perspective of a population survey in which these variables cannot be assessed. This necessitates the assumption that the turtles captured for TDR deployment are representative of the population that would be the focus of the survey. However, more detailed, individual-level diving models are of biological interest and may be relevant to this application (e.g. if survey data are to be compared among regions with different size distributions or sex ratios). Time-of-day effects may also be important if surveys are conducted at different times.

Finally, while predictable diving variation may be particularly common for chelonid sea turtles (especially in seasonal, coastal environments), seasonal variation in diving, for example, has also been found in large marine mammals surveyed by boat or plane (e.g. sperm whales *Physeter macrocephalus*, Linnaeus 1758, Jaquet, Dawson & Slooten 2000; minke whales *Balaenoptera acutorostrata*, Lacépède 1804, Stockin *et al.* 2001). The prevalence and applicability of such heterogeneity to population surveys may warrant further investigation.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. WinBUGS sample code for one Bayesian regression model.

Appendix S2. Final regression equations for dive and surface interval models.

Appendix S3. Dive data summarized in depth and temperature bins.

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