Utilization of waterholes by globally threatened species in deciduous dipterocarp forest of the Eastern Plains Landscape of Cambodia

Chanratana Pin, Dusit Ngoprasert, Thomas N.E. Gray, Tommaso Savini
Rachel Crouthers and George A. Gale

Abstract Deciduous dipterocarp forests throughout Asia provide crucial habitat for several globally threatened species. During the dry season water availability in these forests is primarily limited to perennial rivers and waterholes. Such water sources form an essential part of these dry forests and are used by multiple species, including large mammals and birds, but little is known regarding how waterhole characteristics affect wildlife use. We investigated waterhole utilization by six globally threatened dry forest specialists: banteng *Bos javanicus*, Eld's deer *Rucervus eldii*, giant ibis *Thaumatibis gigantea*, green peafowl *Pavo muticus*, lesser adjutant *Leptoptilos javanicus* and Asian woolly-necked stork *Ciconia episcopus*. We camera-trapped 54 waterholes in Srepok Wildlife Sanctuary, eastern Cambodia, during the dry season of December 2015–June 2016. We measured nine waterhole and landscape characteristics, including indicators of human disturbance. Waterhole depth (measured every 2 weeks) and the area of water at the start of the dry season were the main environmental factors influencing waterhole use. Additionally, waterholes further from villages were more frequently used than those nearer. Our study reaffirmed the importance of waterholes in supporting globally threatened species, especially large grazers, which are critical for maintaining these dry forest ecosystems. The results also suggested that artificially enlarging and deepening selected waterholes, particularly those further from human disturbance, could enhance available habitat for a range of species, including grazers. However, this would need to be conducted in coordination with patrolling activities to ensure waterholes are not targets for illegal hunting, which is a problem throughout South-east Asian protected areas.

Keywords Cambodia, camera traps, climate change, grazers, large ungulates, large waterbirds, Srepok Wildlife Sanctuary, waterholes

Chanratana Pin (Corresponding author), Dusit Ngoprasert, Tommaso Savini and George A. Gale King Mongkut's University of Technology Thonburi, Conservation Ecology Program, School of Bioresources and Technology, 49 Thakham, Bangkhuntien, Bangkok 10150, Thailand
E-mail chanratana.pin@gmail.com

Thomas N.E. Gray Wildlife Alliance, Phnom Penh, Cambodia

Rachel Crouthers WWF-Cambodia, Phnom Penh, Cambodia

*Received 15 November 2017. Revision requested 14 December 2017.
Accepted 5 March 2018. First published online 18 December 2018.*

Supplementary material for this article is avaialble at https://doi.org/10.1017/S0030605318000455

Introduction

South-east Asian biodiversity has declined dramatically as a result of habitat loss and degradation and overhunting (Duckworth et al., 2012; Harrison et al., 2016). Within South-east Asia, deciduous dipterocarp forests are of particular concern as they are the most threatened of all tropical forest types (Gillespie et al., 2012; Hansen et al., 2013). Currently, only about 156,000 km^2 of deciduous dipterocarp forest remain in mainland South-east Asia (Wohlfart et al., 2014). However, these forests are crucial for a wide range of globally threatened species (Karanth et al., 2004a; Steinmetz, 2004; McShea et al., 2005, 2011; Gray, 2012).

Deciduous dipterocarp forests are also highly seasonal habitats, experiencing 5–6 months of drought per year (Miles et al., 2006). In such dry tropical habitats, water and food resource availability may be limiting factors for the distributions, movements and home ranges of many species during the dry season (Aung et al., 2001; Redfern et al., 2003), and waterholes are likely to be a substantial component of water surface availability, providing important water resources and foraging habitat for many species (Keo, 2008; Wakefield et al., 2008; Wright et al., 2010; Wright et al., 2012). Utilization of waterholes by wildlife is also likely to be higher during the dry season (Wakefield et al., 2008; Wright et al., 2012). Levels of crucial water availability in South-east Asian deciduous dipterocarp forests are likely to be further impacted by predicted decreases in precipitation and increases in temperature associated with global climate change (Dai, 2013; Trenberth et al., 2014).

The deciduous dipterocarp forests of eastern Cambodia may be particularly vulnerable (Yusuf & Herminia, 2010; Climate Investment Funds, 2014). The Eastern Plains Landscape, a protected area complex covering c. 14,000 km^2 in eastern Cambodia and southern Viet Nam, supports one of the largest extents of deciduous dipterocarp forests remaining in South-east Asia. This landscape is home to several globally threatened species of mammals and birds (Gray et al., 2012a; O'Kelly et al., 2012; Wright et al., 2013b) including the Asian elephant *Elephas maximus*, banteng *Bos javanicus*, Eld's deer *Rucervus eldii*, leopard

Panthera pardus, and globally threatened waterbirds such as the giant ibis *Thaumatibis gigantea*, white-shouldered ibis *Pseudibis davisoni* and green peafowl *Pavo muticus*. During the dry season water availability is mainly limited to perennial rivers and waterholes, which are an essential part of the forest and are used by several of these threatened large species (Keo, 2008; Wright et al., 2012; Gray et al., 2015b). However, little is known about the relationship between wildlife and waterholes in South-east Asian deciduous dipterocarp forests with the exception of two studies on the giant and white-shouldered ibises (Wright et al., 2010, 2012). Although these studies suggested waterholes are important for these two species, it is largely unknown how they impact the other threatened species in this landscape and, for example, how the morphological characteristics of the waterholes affect usage.

We focused on waterhole usage by six dry forest specialists of high conservation concern that utilize waterholes for foraging and/or drinking, including four birds, the giant ibis (categorized as Critically Endangered on the IUCN Red List; Birdlife International, 2017), green peafowl (Endangered), lesser adjutant *Leptoptilos javanicus* (Vulnerable) and Asian woolly-necked stork *Ciconia episcopus* (Vulnerable), and two large herbivorous mammals, banteng (Endangered) and Eld's deer (Endangered) (McShea et al., 2005; Keo, 2008; Wright et al., 2012; Gray et al., 2015b). We hypothesized that (1) water availability in a given waterhole and (2) waterhole characteristics (e.g. size, surrounding vegetation, and availability of adjacent waterholes) will be associated with different levels of use by these target species (especially the giant ibis, lesser adjutant and Asian woolly-necked stork, which feed in the waterholes), and (3) increased human activity at or near waterholes will probably reduce use.

Study area

The study was conducted in the core zone of the 3,729 km^2 Srepok Wildlife Sanctuary, formerly known as the Mondulkiri Protected Forest (Fig. 1). The core zone of the sanctuary (1,292 km^2), previously designated as a Special Ecosystem Zone under a draft Forestry Administration management plan, is also recognized as a possible site for tiger reintroduction (Gray et al., 2017). This is the least disturbed area of the Sanctuary and supports the highest densities of large ungulates in Cambodia (Gray et al., 2012b). Vegetation of the Sanctuary is predominantly deciduous dipterocarp forests dominated by Dipterocarpaceae, including *Shorea siamensis*, *Shorea obtusa*, *Dipterocarpus tuberculatus*, *Dipterocarpus obtusifolius* and *Dipterocarpus intricatus* (McShea et al., 2011; Pin et al., 2013). Srepok also supports the largest population of banteng in Cambodia (Gray et al., 2012c) and is a priority site for leopard *Panthera pardus* in Indochina (Gray & Prum, 2012; Rostro-García et al., 2016). The area is influenced by two distinctive seasons, wet (May–October) and dry (November–April), with a mean total annual rainfall of 1,500–1,800 mm (Bruce, 2013). During the dry season the area experiences frequent forest fires that create an open understory and reduce canopy cover (McShea et al., 2011; Ratnam et al., 2016).

Methods

Waterhole selection and camera-trapping

The coordinates of waterholes used in this study were provided by the Eastern Plains Landscape Project, GIS & Remote Sensing Department, WWF-Cambodia (WWF-Cambodia, 2015, unpubl. data). Fifty-four waterholes were randomly selected from an estimated 350 waterholes in the core zone of the sanctuary using *Hawth's Analysis Tools* (Beyer, 2004) for *ArcGIS 10.1* (ESRI, Redlands, USA). Camera traps (infrared, remote-trip digital camera units Reconyx PC900 HyperFire Professional IR, RECONYX, Holmen, USA) were placed at waterholes during the dry season of December 2015–June 2016 (Fig. 1). Camera traps (one per waterhole) recorded date and time automatically on all photographs, were not baited, and were set to operate 24 h per day with a 1-minute delay between photographs. To maximize encounters of species, camera traps were placed 2–15 m from the water's edge in an area with the highest diversity of wildlife footprints (camera traps were moved to follow the recession of the water level as the dry season progressed). Depending upon topography and location, camera traps were either placed on trees or poles at a suitable location at a height of 50–100 cm, to increase the chance of encountering large ungulates. Maximum trigger distance was checked to make sure cameras could detect animals from a distance of c. 20 m, and all cameras were set to medium sensitivity to minimize false captures associated with moving vegetation.

Data collection

Camera-trapped waterholes were visited every 2 weeks, in a total of 9 visits for the study period. We collected three parameters related to water availability (water depth, pool size, and water volume), three related to physical characteristics of the waterhole and the surrounding landscape (maximum waterhole area, number of waterholes within a 1-km radius, and height of nearest trees adjacent to the target waterhole) and three parameters related to potential human impacts (distance to nearest village, distance to nearest active road/trail, and number of illegal activities within a 1-km radius);

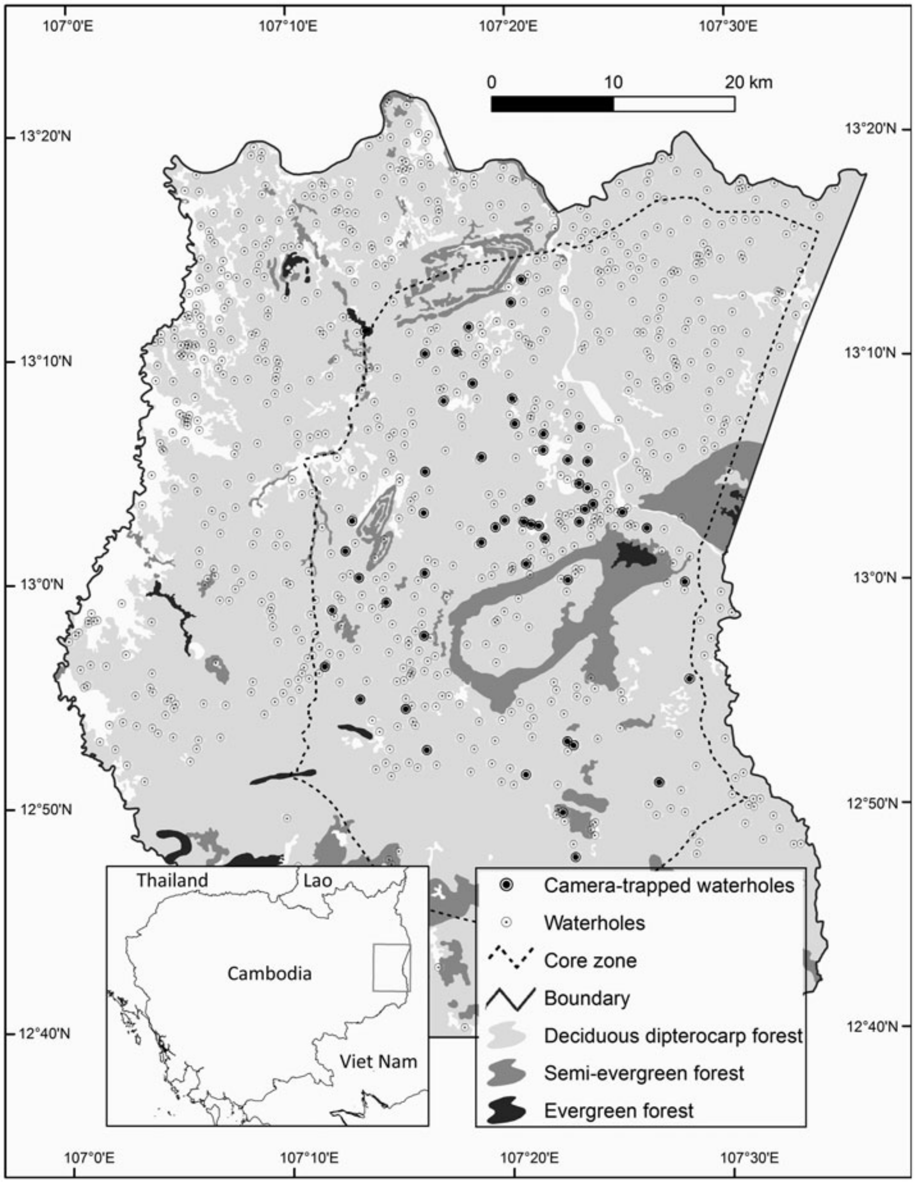

FIG. 1 Srepok Wildlife Sanctuary, Cambodia, showing waterholes and the 54 waterholes that were camera-trapped during the dry season of December 2015–June 2016.

see Table 1 for a description of how these parameters were measured and how often.

Data analysis

Consecutive photographs of the same species taken at an interval of at least 30 minutes, or non-consecutive photographs of the same species at the same station, were defined as notionally independent photographs (O'Brien et al., 2003). Camera-trap photo management and the creation of the database of encountered species was conducted using *camtrap R* (Niedballa et al., 2016) in *R 3.3* (R Core Team, 2016).

We used these photos as an index of the frequency of waterhole use by the target species (but not as an indicator of movement or behaviour at waterholes). Counts of these notionally independent photographs (i.e. one photograph equalling one count regardless of the number of individuals photographed) of focal species were modelled as response variables, with water availability, waterhole characteristics and human disturbance variables as predictor variables. All continuous variables were centred and scaled using *scale* in *R*. We used trap-nights of each camera trap as an offset in fitting the models (Kotze et al., 2012).

R package *glmmADMB* (Fournier et al., 2012) was used to fit Poisson or negative binomial models in a generalized linear mixed models (GLMMs) framework for banteng, Eld's deer, giant ibis, lesser adjutant and Asian woolly-necked stork. Because of the large number of zero counts in the green peafowl dataset, we used *pscl* (Achim et al., 2008) to fit zero-inflated regression models, allowing us to model the excess zeros and the count values independently (Zuur & Ieno, 2016).

Prior to analysis we checked the data for outliers, overdispersion and correlations among predictor variables (Zuur

TABLE 1 Variables, and method of measurement, used to describe 54 waterholes in the Srepok Wildlife Sanctuary (Fig. 1) during the dry season of December 2015–June 2016.

Variables	Measurement
Water availability	
Pool size	Walked with GPS at edge of waterline to estimate surface area of water (m^2) (measured on each visit)
Waterhole depth	Measuring tape/stick used to measure depth at centre of waterhole (cm) (measured on each visit)
Water volume	Pool surface area × depth (m^3) (calculated on each visit)
Waterhole characteristic	
Max. waterhole area	Walked with GPS at point where water reached its max. perimeter (m^2) (measured once at the beginning of the study period)
Waterholes within 1-km radius	*ArcGIS* used to calculate number of waterholes within 1-km radius of each focal waterhole (count)
Tree height	Rangefinder used to calculate mean tree height in the four cardinal directions (m) (measured while standing in the centre of the waterhole)
Anthropogenic factors	
Distance to road	*ArcGIS* used to calculate straight-line distance to nearest active road (km)
Distance to village	*ArcGIS* used to calculate straight-line distance to nearest village (km)
Illegal activities within 1-km radius	*ArcGIS* used to calculate number of sightings/signs of illegal activities (number of snares, logging sites, illegal camping sites) within 1-km radius, derived from the SMART database of ranger patrolling information (WWF-Cambodia, 2015, unpubl. data), supplemented with sightings/signs encountered during this study (counts; see Methods)

et al., 2009; Zuur & Ieno, 2016). Variables with correlations > 0.5 were not included in the same model. There were no strong correlations among predictor variables except between water volume and pool size ($r = 0.93$). We fitted predictor variables into models to determine the effect of each on the species count data; we also tested additive models of a combination of selected predictor variables. In addition, we tested models that included both waterhole characteristics and human disturbance variables.

Model selection was based on AIC (Akaike Information Criterion) and AIC weights (Burnham & Anderson, 2003). However, when there was uncertainty based on these criteria, we employed model averaging to compute average estimates of beta coefficients of candidate models. We conducted model averaging of the most supported candidate models where $\Delta AIC \leq 2.00$. We used *MuMIn* (Barton, 2018) for model averaging.

Results

A total of 49 waterholes of the 54 camera-trapped dried out by April 2016. However, eight refilled with water following rains during the first week of May 2016. Camera traps operated on average 138 trap-nights per waterhole (range 44–182 trap-nights). A total of 6,444 trap-nights captured > 4,700 notionally independent photographs of at least 29 species (Supplementary Table 1). Among the target species, lesser adjutant and banteng were the most frequently encountered (Supplementary Table 1). Camera traps captured the six target species utilizing waterholes in several ways, but there appeared to be general patterns of use. Banteng and Eld's deer were recorded drinking and grazing at waterholes, lesser adjutant and Asian woolly-necked stork foraged in the deeper areas of the pools, and giant ibis and green peafowl foraged in dry and/or saturated substrates at the edges of the waterholes (Plate 1).

Models (both GLMMs and zero-inflated regression models) that had AIC weights ≥ 0.01, as well as all null models, describing the relationship between counts of notionally independent photos of target species utilizing waterholes and predictor variables are shown in Table 2 (all models are shown in Supplementary Table 2). The most supported model had an AIC weight > 0.85 for Eld's deer and green peafowl, two top candidate models ($\Delta AIC \leq 2.00$ and $w_i > 0.85$) were selected for banteng and Asian woolly-necked stork, three top candidate models ($\Delta AIC \leq 2.00$ and $w_i = 0.81$) were selected for lesser adjutant. Four top candidate models ($\Delta AIC \leq 2.00$ and $w_i = 0.91$) were selected for giant ibis (Table 2).

Estimated beta coefficients from the top models and model averaging across the most supported candidate models for banteng, Eld's deer, lesser adjutant, Asian woolly-necked stork, giant ibis and green peafowl are shown in Table 3. The direction of the impacts of waterhole characteristics on the utilization by the target species are shown in Table 4. Overall, deeper and/or larger waterholes were preferred by all species except banteng. However, lesser adjutant and Asian woolly-necked stork had a curvilinear relationship with water depth, reflecting a preference up to a threshold depth of 30–40 cm and then declining usage at greater depth (Fig. 2). Banteng showed a negative relationship with water volume and preferred waterholes surrounded by tall trees. The Critically Endangered giant

Plate 1 Photographs of (a) banteng *Bos javanicus*, (b) Eld's deer *Rucervus eldii*, (c) giant ibis *Thaumatibis gigantea*, (d) green peafowl *Pavo muticus*, (e) lesser adjutant *Leptoptilos javanicus* and (f) Asian woolly-necked stork *Ciconia episcopus* drinking and/or foraging at waterholes during the dry season of December 2015–June 2016.

ibis was the only species that was also associated with the abundance of neighbouring waterholes. All species except green peafowl were more likely to occur at waterholes further from villages.

Discussion

We provide the first detailed study of the variables influencing utilization of waterholes by wildlife in a dry dipterocarp forest. As predicted, our results suggested that water availability (water depth and pool size) played a major role in the utilization of waterholes by six globally threatened target species. In addition, waterhole characteristics and associated landscape characteristics including maximum waterhole area, proximity to other waterholes in the surrounding landscape, height of trees adjacent to waterholes, and human disturbance, particularly distance to the nearest village, also influenced waterhole use by these species (Table 4).

Importance of waterholes for large herbivores

Deeper waterholes retained water for longer than shallower ones, and the deeper waterholes probably provide critical drinking water for ungulates. Most large herbivores need to access drinking water to complement forage consumption during the dry season when food and water are scarce (Western, 1975; Manser & Brotherton, 1995; Gedir et al., 2016). In addition, some will forage as well as drink at waterholes (Valeix et al., 2008), and our photographs appear to support this (Plate 1). Thus, the availability of water probably influences movement and home ranges during the dry season, although our data was unable to address movement of individual animals (Aung et al., 2001; Redfern et al., 2003; Smit et al., 2007). Our results show a positive relationship between maximum waterhole area and depth for Eld's deer, but a negative relationship between water volume and use of waterholes by banteng. The reason for the latter is unclear but banteng were recorded at 78% (42) of the 54 waterholes, suggesting they were widely distributed in the study

Table 2 Summary of all GLMMs and zero-inflated regression models that had AIC weights ≥ 0.01, used to explain the number of notionally independent photographs of six target species at 54 waterholes. For definitions of predictor variables see Table 1.

Model	K[1]	AIC[2]	ΔAIC	w_i[3]
Banteng *Bos javanicus*[4]				
Water volume + Tree height	5	676.64	0.00	0.51
Water volume + Tree height + Distance to village	6	677.49	0.85	0.34
Tree height	4	681.18	4.54	0.05
Water volume	4	682.15	5.51	0.03
Distance to village	4	682.83	6.19	0.02
Pool size	4	684.07	7.43	0.01
Water depth	4	685.35	8.71	0.01
Number of illegal activities	4	685.41	8.77	0.01
Null model	3	691.02	14.38	0.00
Eld's deer *Rucervus eldii*[4]				
Water depth + Max waterhole area + Distance to village	5	208.72	0.00	0.91
Water depth + Distance to village	4	213.39	4.67	0.09
Null model	2	259.04	50.32	0.00
Lesser adjutant *Leptoptilos javanicus*[4]				
Water depth + *Water depth^2 + Max waterhole area + Distance to village	7	655.84	0.00	0.39
Water depth + *Water depth^2 + Max waterhole area	6	657.03	1.19	0.22
Water depth + *Water depth^2	5	657.16	1.32	0.20
Water depth + *Water depth^2 + Waterholes 1-km	6	658.45	2.61	0.11
Water depth + *Water depth^2 + Tree height	6	659.15	3.31	0.07
Null model	3	700.41	44.57	0.00
Asian woolly-necked stork *Ciconia episcopus*[4]				
Water depth + *Water depth^2 + Distance to village	6	339.17	0.00	0.67
Water depth + *Water depth^2	5	340.60	1.43	0.33
Null model	3	359.12	19.96	0.00
Giant ibis *Thaumatibis gigantea*[4]				
Water depth + Waterholes 1-km + Distance to village	4	126.71	0.00	0.39
Water depth + Distance to village	3	127.81	1.10	0.23
Water depth + Waterholes 1-km	3	128.65	1.95	0.15
Water depth + Max waterhole area + Distance to village	4	128.67	1.96	0.14
Water depth	2	131.03	4.32	0.04
Water depth + Max waterhole area	3	131.29	4.58	0.04
Null model	1	155.90	29.19	0.00
Green peafowl *Pavo muticus*[5]				
Pool size | Max waterhole area	4	75.49	0.00	0.85
Water depth | Max waterhole area	4	80.15	4.66	0.08
Tree height | Max waterhole area	4	83.42	7.92	0.02
Distance to road | Max waterhole area	4	83.80	8.31	0.01
Max waterhole area | Max waterhole area	4	83.93	8.43	0.01
Null model	2	94.21	18.72	0.00

[1]Number of parameters.
[2]Akaike Information Criterion.
[3]AIC weights.
[4]GLMMs.
[5]Zero-inflated regression models.
*Quadratic polynomial of water depth.

area compared to Eld's deer, which were recorded at only six waterholes. Tree height adjacent to waterholes also had a positive effect on utilization of waterholes by banteng. Tall deciduous dipterocarp trees may provide understory vegetation that is particularly suitable for wild cattle during the dry season (Steinmetz, 2004; Gray, 2012). Although large herbivores play an essential role as the primary prey for large carnivores (Karanth et al., 2004b; Hayward et al., 2006, 2012, 2014; Wolf & Ripple, 2016), little is known about the role these herbivores have in maintaining and structuring these Asian savannah ecosystems (Ratnam et al., 2016). Nevertheless, the role of waterholes in sustaining large herbivores is likely to be vital in the deciduous dipterocarp forests of the region. Natural salt licks are also a key resource for large mammals (Matsubayashi et al., 2007; Lameed & Jenyo-Oni, 2012; Matsuda et al., 2015) but the extent to

TABLE 3 Estimated coefficients, 85% CI and SE for regression models predicting the number of notionally independent photos of six target species at 54 waterholes. For definitions of variables see Supplementary Table 1.

Parameters	Coefficient	85% CI	SE
Banteng *javanicus* [1]			
Intercept	−3.34	−3.57–−3.10	0.16
Water volume	−0.43	−0.69–−0.17	0.18
Tree height	0.28	0.11–0.44	0.12
Distance to village	0.05	−0.04–0.30	0.09
Eld's deer *Rucervus eldii*			
Intercept	−7.96	−9.82–−6.09	1.29
Water depth	1.28	0.86–1.71	0.29
Max waterhole area	0.46	0.21–0.71	0.17
Distance to village	1.31	0.71–1.90	0.41
Lesser adjutant *Leptoptilos javanicus* [1]			
Intercept	−3.08	−3.40–−2.75	0.22
Water depth	1.57	1.20–1.94	0.25
*Water depth^2	−0.37	−0.47–−0.26	0.07
Max waterhole area	0.13	−0.01–0.36	0.14
Distance to village	0.12	0.05–0.49	0.17
Asian woolly-necked stork *Ciconia episcopus* [1]			
Intercept	−2.87	−3.26–−2.49	0.27
Water depth	1.19	0.76–1.62	0.30
*Water depth^2	−0.68	−0.98–−0.38	0.21
Distance to village	0.18	0.06–0.48	0.17
Giant ibis *Thaumatibis gigantea* [1]			
Intercept	−5.46	−5.79–−5.12	0.23
Water depth	0.59	0.40–0.77	0.13
Waterholes 1-km	0.18	0.07–0.55	0.20
Distance to village	0.35	0.12–0.73	0.25
Max waterhole area	0.02	−0.05–0.38	0.08
Green peafowl *Pavo muticus* [2]			
Count model			
Intercept	−5.07	−5.49–−4.65	0.29
Pool size	0.94	0.50–1.37	0.30
Zero model			
Intercept	1.11	−0.01–2.23	0.78
Max. waterhole area	3.93	1.08–6.78	1.98

[1]GLMM averaging.
[2]Zero-inflated function models.
*Quadratic polynomial of water depth.

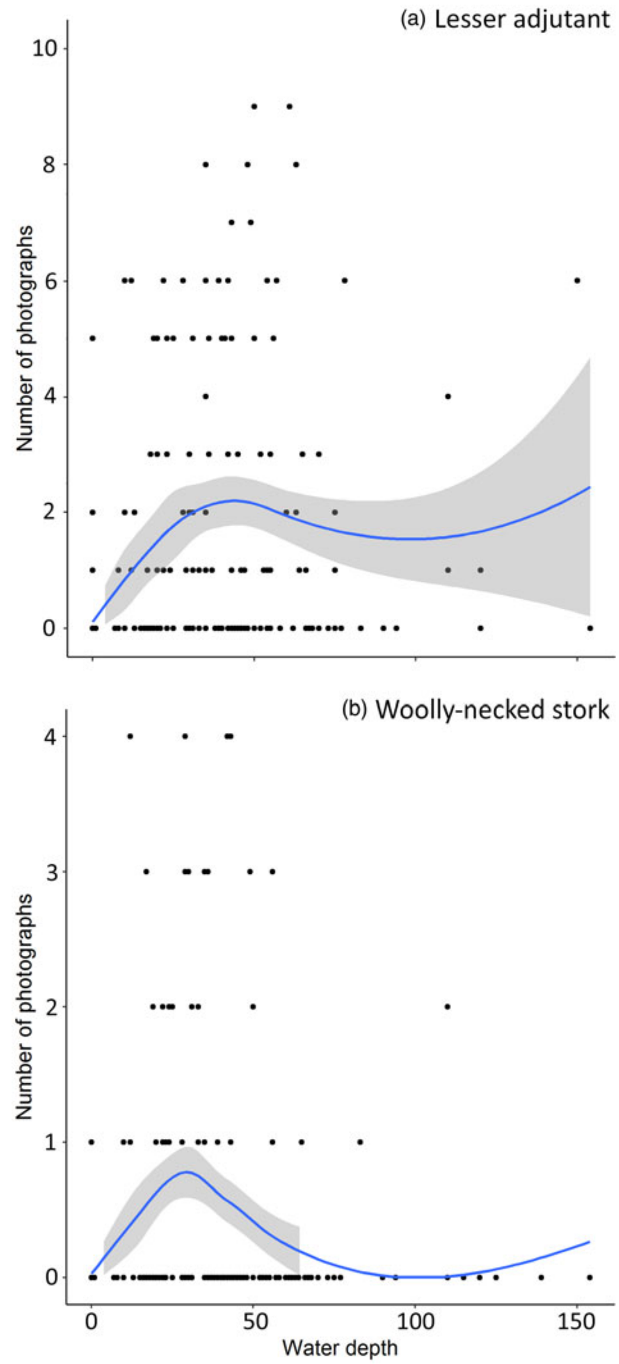

FIG. 2 Curvilinear relationship of notionally independent photographs of (a) lesser adjutant *Leptoptilos javanicus* and (b) Asian woolly-necked stork *Ciconia episcopus* with waterhole depth (measured at the centre of each waterhole). The curve was fitted using loess smoothing.

which ungulates in Cambodian deciduous dipterocarp forests obtain minerals from waterholes is unclear and merits further research.

Importance of waterholes for large birds

Three of the four bird species studied, giant ibis, lesser adjutant and Asian woolly-necked stork, preferred deeper waterholes, whereas green peafowl had a preference for larger pool areas (Tables 3 & 4). Numerous studies have demonstrated that water depth influences foraging habitat of waterbirds (e.g. Colwell & Taft, 2000; Ma et al., 2010). In particular, fluctuation in water depth determines the accessibility of foraging habitat, which in turn provides a greater diversity of foraging habitats, thus supporting a greater diversity of waterbirds (Collazo et al., 2002; Stapanian & Waite, 2003). Additionally, the density of waterholes within a 1-km radius around waterholes positively influenced utilization by giant ibis (Table 4). Giant ibis is a dry forest specialist, has the smallest global range of our target species and is restricted to deciduous dipterocarp forests (BirdLife

TABLE 4 Summary of the relationships (positive, negative, or no effect) between measured predictor variables and the number of notionally independent photos of six target species at waterholes. Distance to roads and number of illegal activities detected around waterholes did not show an effect.

Species	Pool size	Water depth	Water volume	Max. waterhole area	No. of waterholes within 1-km radius	Tree height	Distance to village
Banteng			–			+	+
Eld's deer		+		+			+
Giant ibis		+		+	+		+
Green peafowl	+			+			
Lesser adjutant		+		+			+
Asian woolly-necked stork		+					+

International, 2017). The model for this species contained the most waterhole variables, suggesting a strong and specific association with waterholes during the dry season. Giant ibis is the only waterbird in our study that nests in deciduous dipterocarp forest during the wet season and this could be a factor in explaining its strong association with waterholes. However, wet season monitoring would be needed to assess any year-round dependence on waterholes. Waterhole utilization by green peafowl was related to pool size and waterhole size. Keo (2008), noted that as water levels fluctuate, pool size may play a major role in providing foraging habitat for large birds as well as grazers, particularly when resources are scarce during the dry season.

Waterhole size

Waterhole size (i.e. maximum area) positively influenced waterhole utilization by giant ibis, lesser adjutant, green peafowl and Eld's deer (Tables 3 & 4). Camera-trap photos (Plate 1) show these species foraging in a relatively wide area beyond the open water of the waterholes. Some species do not regularly drink from waterholes but will opportunistically forage at waterholes if available. We suggest larger waterholes may offer more foraging habitat, and also contain important microhabitats, including short grass, as well as both dry and saturated substrates. Furthermore, these microhabitats may provide primary food resources, including frogs, crabs and crickets, especially for giant ibis (Keo, 2008; Wright et al., 2012; Wright et al., 2013a). As such, large waterholes are likely to be particularly significant for conservation in Cambodian deciduous dipterocarp forests; declines in large herbivore numbers, which probably play an important role in keeping waterhole areas open, could have significant knock-on effects on other biodiversity, including foraging waterbirds.

Anthropogenic factors

As predicted, most of the target species were more likely to frequent waterholes located further from human activity, in this case, villages (Table 4), possibly related to food availability as waterholes closer to villages are more likely to be harvested for fish (including eels) and frogs by local people (Keo, 2008). This is supported by earlier studies that suggested the giant ibis foraged at waterholes further from human settlements because of the species' sensitivity to disturbance (Keo, 2008; Wright et al., 2012). However, further research is needed to determine whether the cause is human depletion of forage availability, persecution or other direct disturbance. The distribution and habitat use of banteng are also thought to be significantly affected by human disturbance (Pedrono et al., 2009; Gray & Phan, 2011; Gardner et al., 2016). Eld's deer, however, is known to occur in areas with relatively high levels of human disturbance locally (e.g. Ang Trapeang Thmor, Cambodia, and Savannakhet Eld's deer sanctuary, Laos; Gray et al., 2015a). However, both sites are small and have been the target of conservation outreach focused on Eld's deer. We suggest that these areas may be exceptional and that, more widely across the species' range, Eld's deer will have been extirpated from many locations close to villages. The species' small fragmented population in Srepok Wildlife Sanctuary is predominantly concentrated in the inner core of the protected area, perhaps a result of past hunting across most of the landscape (Loucks et al., 2009). Our data did not show any relationship between green peafowl and distance to villages, but other studies have reported that green peafowl prefer to forage in areas further from human settlements (Brickle, 2002; Liu et al., 2008; Sukumal et al., 2015). It is possible that green peafowl in our study area were less affected by human disturbance compared to neighbouring Viet Nam, and less affected by resource competition at waterholes than other target species. However, peafowl are probably impacted by hunting, including egg harvesting, and capture for the pet trade (Goes, 2009).

Management implications

Dogs and cattle were recorded at 24 of the 54 camera-trapped waterholes, accompanying people collecting water and fishing, and utilized the same resources used by our target species. Resource competition between local people and wildlife may therefore be of concern. Illegal hunting also poses a significant threat to these globally threatened species: we found illegal hunting gear (including snares) at waterholes. Snaring continues to be a major threat in South-east Asia's protected areas (O'Kelly, 2013; Harrison et al., 2016; Gray et al., 2018). The number of illegal activities detected around waterholes did not feature in any of the most supported models for any of our study species, but accurately recording levels of illegal activity within protected areas is difficult and it is likely that data from the Spatial Monitoring and Reporting System Tool, as used in our study, is biased in a number of unpredictable ways (Gavin et al., 2009). In addition, there was an inadequate number of rangers (only 40–50 rangers working in the protected area of $> 3{,}700$ km^2) and patrolling was probably not conducted at all the waterholes. However, our study provides baseline data for conservation and protected area management in this sanctuary.

Understanding the utilization of waterholes by globally threatened species is critical for wildlife conservation and protected area management given that the deciduous dipterocarp forests of eastern Cambodia are predicted to be impacted by anthropogenic climate change (Yusuf & Herminia, 2010). Modelling the impacts of drought on ungulate populations suggested that water stress could have negative impacts on sedentary and grazer species (Duncan et al., 2012), and maintaining sufficient water resources is a guideline for protected area management in such dry habitats (Bolduc & Afton, 2004). Manipulation of waterholes, and rehabilitation of other water sources to retain rainwater, to improve habitat for wildlife during the dry period, are management tools that should be investigated for Cambodian deciduous dipterocarp forests (Kumar & Sahi, 2009; Gray et al., 2015b). However, prior to any large-scale manipulation, modification of waterholes should be in the form of a small- to medium-scale experiment, to test our theories about the benefits of manipulation. Provision of artificial waterholes can also mitigate negative human–wildlife interactions by preventing wildlife moving out of protected areas and exploiting water resources within villages or settlements (Dave, 2010). Although deepening and enlarging of selected natural waterholes in suitable locations (such as those further from villages) could significantly enhance remaining dry forest habitat (Gray et al., 2015b), this would have to be accompanied by additional law enforcement, as hunting remains the biggest driver of population declines of large mammals throughout Indochina (Harrison et al., 2016).

Acknowledgements This research project was conducted as part of a master's degree that was financially supported by a WWF-EFN, Russell E. Train Fellowship, The Rufford Foundation, and USAID and Humanscale through WWF-Cambodia. We thank USAID and IDEA WILD for the provision of research equipment, including camera traps, WWF-Cambodia and Mondulkiri Provincial Department of Environment for logistical and fieldwork support, the Eastern Plains Landscape Project, WWF-Cambodia, which coordinated with Provincial Department of Environment, and the Srepok Wildlife Sanctuary manager for providing supporting documentation. Our research was conducted in the Srepok Wildlife Sanctuary with permission granted by the Mondulkiri Provincial Department of Environment under a MoU between the Ministry of Environment and WWF-Cambodia.

Author contributions Project development: CP assisted by DN, TG, TS, RC and GG; data collection and analysis: CP with the assistance of DN; writing: CP assisted by DN, TG, TS, RC and GG.

Conflicts of interest None.

Ethical standards Our research was carried out following the legal standards of Cambodia's Natural Protected Area law, and under the permission of the Ministry of Environment, Provincial Department of Environment, and with the necessary approvals from King Mongkut's University of Technology Thonburi.

References

Achim, Z., Christian, K. & Simon, J. (2008) Regression models for count data in *R. Journal of Statistical Software*, 27, 1–25.

Aung, M., McShea, W.J., Htung, S., Than, A., Soe, T.M., Monfort, S. & Wemmer, C. (2001) Ecology and social organization of a tropical deer (*Cervus eldi thamin*). *Journal of Mammalogy*, 82, 836–847.

Barton, K. (2018) *MuMIn: Multi-model inference*. Https://CRAN.R-project.org/package=MuMIn [accessed 15 January 2018].

Beyer, H.L. (2004) *Hawth's analysis tools for ArcGIS. Spatial Ecology*. Http://www.spatialecology.com/htools [accessed 11 February 2018].

BirdLife International (2017) *Thaumatibis gigantea* (amended version of 2016 assessment). In *The IUCN Red List of Threatened Species 2017*. Http://www.iucnredlist.org/details/22697536/0 [accessed 14 February 2018].

Bolduc, F. & Afton, A.D. (2004) Relationships between wintering waterbirds and invertebrates, sediments and hydrology of coastal marsh ponds. *Waterbirds*, 27, 333–341.

Brickle, N.W. (2002) Habitat use, predicted distribution and conservation of green peafowl (*Pavo muticus*) in Dak Lak province, Vietnam. *Biological Conservation*, 105, 189–197.

Bruce, C. (2013) Creating options for long-term resource use and conservation in the eastern plains dry forest landscape of Cambodia. In *Evidence-based Conservation: Lessons From the Lower Mekong. Earthscan From Routledge* (eds T.C.H. Sunderland, J. Sayer, & M.-H. Hoang), pp. 145–156. Routledge, Abingdon, UK.

Burnham, K.P. & Anderson, D.R. (2003) *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach*. Springer, New York, USA.

Climate Investment Funds (2014) *Supplementary Appendix M—CAM GMS BCC-PPCR, Climate Change Impact Modeling and Vulnerability Assessments for Koh Kong and Mondulkiri Provinces in Cambodia. Promoting Climate-Resilient Agriculture in Koh Kong and Mondulkiri Provinces as Part of the Greater Mekong Subregion Biodiversity Conservation Corridors Project*. Climate Investment Fund, Washington, DC, USA.

Collazo, J.A., O'Harra, D.A. & Kelly, C.A. (2002) Accessible habitat for shorebirds: factors influencing its availability and conservation implications. *Waterbirds*, 25, 13–24.

Colwell, M. & Taft, O. (2000) Waterbird communities in managed wetlands of varying water depth. *Waterbirds*, 23, 45–55.
Dai, A. (2013) Increasing drought under global warming in observations and models. *Nature Climate Change*, 3, 52–58.
Dave, C. (2010) *Understanding Conflicts and Conservation of Indian Wild Ass Around Little Rann of Kachchh, Gujarat*. India. Final technical report submitted to Rufford Small Grant Programme, London, UK.
Duckworth, J., Batters, G., Belant, J., Bennett, E., Brunner, J., Burton, J. et al. (2012) Why South-east Asia should be the world's priority for averting imminent species extinctions, and a call to join a developing cross-institutional programme to tackle this urgent issue. *Surveys and Perspectives Integrating Environment and Society*, 5, 77–95.
Duncan, C., Chauvenet, A.L., McRae, L.M. & Pettorelli, N. (2012) Predicting the future impact of droughts on ungulate populations in arid and semi-arid environments. *PLoS ONE*, 7, e51490.
Fournier, D.A., Skaug, H.J., Ancheta, J., Ianelli, J., Magnusson, A., Maunder, M.N. et al. (2012) AD model builder: using automatic differentiation for statistical inference of highly parameterized complex nonlinear models. *Optimization Methods and Software*, 27, 233–249.
Gardner, P., Hedges, S., Pudyatmoko, S., Gray, T.N.E. & Timmins, R.J. (2016) *Bos javanicus*. In *The IUCN Red List of Threatened Species 2016*. Http://dx.doi.org/10.2305/IUCN.UK.2016-2.RLTS.T2888A46362970.en [accessed 13 November 2017].
Gavin, M.C., Solomon, J.N. & Blank, S.G. (2009) Measuring and monitoring illegal use of natural resources. *Conservation Biology*, 24, 89–100.
Gedir, J.V., Cain III, J.W., Krausman, P.R., Allen, J.D., Duff, G.C. & Morgart, J.R. (2016) Potential foraging decisions by a desert ungulate to balance water and nutrient intake in a water-stressed environment. *PLoS ONE*, 11, e0148795.
Gillespie, T.W., Lipkin, B., Sullivan, L., Benowitz, D.R., Pau, S. & Keppel, G. (2012) The rarest and least protected forests in biodiversity hotspots. *Biodiversity and Conservation*, 21, 3597–3611.
Goes, F. (2009) The status and distribution of green peafowl *Pavo muticus* in Cambodia. *Cambodian Journal of Natural History*, 2009, 7–15.
Gray, T.N.E. (2012) Studying large mammals with imperfect detection: status and habitat preferences of wild cattle and large carnivores in eastern Cambodia. *Biotropica*, 44, 531–536.
Gray, T.N.E., Brook, S.M., McShea, W.J., Mahood, S., Ranjitsingh, M.K., Miyunt, A. et al. (2015a) *Rucervus eldii*. In *The IUCN Red List of Threatened Species 2015*. Http://dx.doi.org/10.2305/IUCN.UK.2015-2.RLTS.T4265A22166803.en [accessed 11 November 2017].
Gray, T.N.E., Crouthers, R., Ramesh, K., Vattakaven, J., Borah, J., Pasha, M.K.S. et al. (2017) A framework for assessing readiness for tiger *Panthera tigris* reintroduction: a case study from eastern Cambodia. *Biodiversity and Conservation*, 26, 2383–2399.
Gray, T.N.E., Hughes, A.C., Laurance, W.F., Long, B., Lynam, A.J., O'Kelly, H. et al. (2018) The wildlife snaring crisis: an insidious and pervasive threat to biodiversity in Southeast Asia. *Biodiversity and Conservation*, 27, 1031–1037.
Gray, T.N.E., McShea, W.J., Koehncke, A., Sovanna, P. & Wright, M. (2015b) Artificial deepening of seasonal waterholes in eastern Cambodia: impact on water retention and use by large ungulates and waterbirds. *Journal of Threatened Taxa*, 7, 7189–7195.
Gray, T.N.E., Ou, R., Huy, K., Pin, C. & Maxwell, A. (2012a) The status of large mammals in eastern Cambodia: a review of camera trapping data 1999–2007. *Cambodian Journal of Natural History*, 2012, 42–55.
Gray, T.N.E. & Phan, C. (2011) Habitat preferences and activity patterns of the larger mammal community in Phnom Prich wildlife sanctuary, Cambodia. *The Raffles Bulletin of Zoology*, 59, 311–318.
Gray, T.N.E., Phan, C., Pin, Gray, T.N.E. & Prum, S. (2012) Leopard density in post-conflict landscape, Cambodia: evidence from spatially explicit capture-recapture. *The Journal of Wildlife Management*, 76, 163–169.
Gray, T.N.E., Phan, C., Pin, C. & Prum, S. (2012b) Establishing a monitoring baseline for threatened large ungulates in eastern Cambodia. *Wildlife Biology*, 18, 406–413.
Gray, T.N.E., Prum, S., Pin, C. & Phan, C. (2012c) Distance sampling reveals Cambodia's eastern plains landscape supports the largest global population of the endangered banteng *Bos javanicus*. *Oryx*, 46, 563–566.
Gray, T.N.E., Hughes, A.C., Laurance, W.F., Long, B., Lynam, A.J., O'Kelly, H. et al. (2018) The wildlife snaring crisis: an insidious and pervasive threat to biodiversity in Southeast Asia. *Biodiversity and Conservation*, 27, 1031–1037.
Hansen, M.C., Potapov, P.V., Moore, R., Hancher, M., Turubanova, S., Tyukavina, A. et al. (2013) High-resolution global maps of 21st-century forest cover change. *Science*, 342, 850–853.
Harrison, R.D., Sreekar, R., Brodie, J.F., Brook, S., Luskin, M., O'kelly, H. et al. (2016) Impacts of hunting on tropical forests in Southeast Asia. *Conservation Biology*, 30, 972–981.
Hayward, M., Henschel, P., O'brien, J., Hofmeyr, M., Balme, G. & Kerley, G. (2006) Prey preferences of the leopard (*Panthera pardus*). *Journal of Zoology*, 270, 298–313.
Hayward, M., Jędrzejewski, W. & Jedrzejewska, B. (2012) Prey preferences of the tiger *Panthera tigris*. *Journal of Zoology*, 286, 221–231.
Hayward, M.W., Lyngdoh, S. & Habib, B. (2014) Diet and prey preferences of dholes (*Cuon alpinus*): dietary competition within Asia's apex predator guild. *Journal of Zoology*, 294, 255–266.
Karanth, K.U., Chundawat, R.S., Nichols, J.D. & Kumar, N.S. (2004a) Estimation of tiger densities in the tropical dry forests of panna, central India, using photographic capture–recapture sampling. *Animal Conservation*, 7, 285–290.
Karanth, K.U., Nichols, J.D., Kumar, N.S., Link, W.A. & Hines, J.E. (2004b) Tigers and their prey: predicting carnivore densities from prey abundance. *Proceedings of the National Academy of Sciences of the United States of America*, 101, 4854–4858.
Keo, O. (2008) *Ecology and conservation of giant ibis in Cambodia*. PhD thesis. University of East Anglia, Norwich, UK.
Kotze, D.J., O'Hara, R.B. & Lehvävirta, S. (2012) Dealing with varying detection probability, unequal sample sizes and clumped distributions in count data. *PLOS ONE*, 7, e40923.
Kumar, S. & Sahi, D.N. (2009) Mammalian diversity and management plan for Jasrota Wildlife Sanctuary, Kathua (J&K). *Tigerpaper*, 36, 18–23.
Lameed, A.G. & Jenyo-Oni, A. (2012) Species-Diversity utilization of salt lick sites at borgu sector of kainji lake national park, Nigeria. In *Biodiversity Enrichment in a Diverse World* (ed. A.G. Lameed), pp. 35–62. InTech, Rijeka, Croatia.
Liu, Z., Zhou, W., Zhang, R., Xie, Y., Huang, Q. & Wen, Y. (2008) Foraging sites selection of green peafowl (*Pavo muticus imperator*) in different seasons in Shiyangjiang valley of upper Yuanjiang drainage, Yunnan. *Biodiversity Science*, 16, 539–546.
Loucks, C., Mascia, M.B., Maxwell, A., Huy, K., Duong, K., Chea, N. et al. (2009) Wildlife decline in Cambodia, 1953–2005: exploring the legacy of armed conflict. *Conservation Letters*, 2, 82–92.
Ma, Z., Cai, Y., Li, B. & Chen, J. (2010) Managing wetland habitats for waterbirds: an international perspective. *Wetlands*, 30, 15–27.

Manser, M.B. & Brotherton, P.N.M. (1995) Environmental constraints on the foraging behaviour of a dwarf antelope (*Madoqua kirkii*). *Oecologia*, 102, 404–412.

Matsubayashi, H., Lagan, P., Majalap, N., Tangah, J., Sukor, J.R.A. & Kitayama, K. (2007) Importance of natural licks for the mammals in Bornean inland tropical rain forests. *Ecological Research*, 22, 742–748.

Matsuda, I., Ancrenaz, M., Akiyama, Y., Tuuga, A., Majalap, N. & Bernard, H. (2015) Natural licks are required for large terrestrial mammals in a degraded riparian forest, Sabah, Borneo, Malaysia. *Ecological Research*, 30, 191–195.

McShea, W.J., Davies, S.J. & Bhumpakphan, N. (2011) *The Ecology and Conservation of Seasonally Dry Forests in Asia*. Smithsonian Institution Scholarly Press, Washington, DC, USA.

McShea, W.J., Koy, K., Clements, T., Johnson, A., Vongkhamheng, C. & Aung, M. (2005) Finding a needle in the haystack: regional analysis of suitable Eld's deer (*Cervus eldi*) forest in Southeast Asia. *Biological Conservation*, 125, 101–111.

Miles, L., Newton, A.C., DeFries, R.S., Ravilious, C., May, I., Blyth, S. et al. (2006) A global overview of the conservation status of tropical dry forests. *Journal of Biogeography*, 33, 491–505.

Niedballa, J., Sollmann, R., Courtiol, A. & Wilting, A. (2016) *camtrapR* : an *R* package for efficient camera trap data management. *Methods in Ecology and Evolution*, 7, 1457–1462.

O'Brien, T.G., Kinnaird, M.F. & Wibisono, H.T. (2003) Crouching tigers, hidden prey: Sumatran tiger and prey populations in a tropical forest landscape. *Animal Conservation*, 6, 131–139.

O'Kelly, H.J. (2013) *Monitoring conservation threats, interventions, and impacts on wildlife in a Cambodian tropical forest*. Phd thesis. Imperial College, London, UK.

O'Kelly, H.J., Evans, T.D., Stokes, E.J., Clements, T.J., Dara, A., Gately, M. et al. (2012) Identifying conservation successes, failures and future opportunities; assessing recovery potential of wild ungulates and tigers in eastern Cambodia. *PLOS ONE*, 7, e40482.

Pedrono, M., Tuan, H.M., Chouteau, P. & Vallejo, F. (2009) Status and distribution of the endangered banteng *Bos javanicus birmanicus* in Vietnam: a conservation tragedy. *Oryx*, 43, 618–625.

Pin, C., Phan, C., Prum, S. & Gray, T.N.E. (2013) Structure and composition of deciduous dipterocarp forest in the Eastern Plains Landscape, Cambodia. *Cambodian Journal of Natural History*, 2013, 27–34.

R Core Team (2016) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria. Https://www.R-project.org [accessed 3 October 2017].

Ratnam, J., Tomlinson, K.W., Rasquinha, D.N. & Sankaran, M. (2016) Savannahs of Asia: antiquity, biogeography, and an uncertain future. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 371, 20150305.

Redfern, J.V., Grant, R., Biggs, H. & Getz, W.M. (2003) Surface-water constraints on herbivore foraging in the Kruger national park, South Africa. *Ecology*, 84, 2092–2107.

Rostro-García, S., Kamler, J., Ash, E., Clements, G., Gibson, L., Lynam, A. et al. (2016) Endangered leopards: range collapse of the Indochinese leopard (*Panthera pardus delacouri*) in Southeast Asia. *Biological Conservation*, 201, 293–300.

Smit, I.P., Grant, C.C. & Devereux, B.J. (2007) Do artificial waterholes influence the way herbivores use the landscape? Herbivore distribution patterns around rivers and artificial surface water sources in a large African savanna park. *Biological Conservation*, 136, 85–99.

Stapanian, M.A. & Waite, T.A. (2003) Species density of waterbirds in offshore habitats in western lake Erie. *Journal of Field Ornithology*, 74, 381–393.

Steinmetz, R. (2004) Gaur (*Bos gaurus*) and banteng (*B. javanicus*) in the lowland forest mosaic of Xe Pian Protected Area, Lao PDR: abundance, habitat use, and conservation. *Mammalia*, 68, 141–157.

Sukumal, N., McGowan, P.J. & Savini, T. (2015) Change in status of green peafowl *Pavo muticus* (family Phasianidae) in Southcentral Vietnam: a comparison over 15 years. *Global Ecology and Conservation*, 3, 11–19.

Trenberth, K.E., Dai, A., van der Schrier, G., Jones, P.D., Barichivich, J., Briffa, K.R. & Sheffield, J. (2014) Global warming and changes in drought. *Nature Climate Change*, 4, 17–22.

Valeix, M., Fritz, H., Matsika, R., Matsvimbo, F. & Madzikanda, H. (2008) The role of water abundance, thermoregulation, perceived predation risk and interference competition in water access by African herbivores. *African Journal of Ecology*, 46, 402–410.

Wakefield, S., Attum, O., Robinson, E.R. & Sandoka, M.A. (2008) Seasonal use of a waterhole by Nubian ibex *Capra nubiana* (Artiodactyla: Bovidae). *Mammalia*, 72, 123–125.

Western, D. (1975) Water availability and its influence on the structure and dynamics of a savannah large mammal community. *African Journal of Ecology*, 13, 265–286.

Wohlfart, C., Wegmann, M. & Leimgruber, P. (2014) Mapping threatened dry deciduous dipterocarp forest in South-east Asia for conservation management. *Tropical Conservation Science*, 7, 597–613.

Wolf, C. & Ripple, W.J. (2016) Prey depletion as a threat to the world's large carnivores. *Royal Society Open Science*, 3, 160252.

Wright, H.L., Buckingham, D.L. & Dolman, P.M. (2010) Dry season habitat use by Critically Endangered white-shouldered ibis in northern Cambodia. *Animal Conservation*, 13, 71–79.

Wright, H.L., Collar, N., Lake, I., Vorsak, B. & Dolman, P. (2012) Foraging ecology of sympatric white-shouldered ibis *Pseudibis davisoni* and giant ibis *Thaumatibis gigantea* in northern Cambodia. *Forktail*, 28, 93–100.

Wright, H.L., Collar, N.J., Lake, I.R. & Dolman, P.M. (2013a) Amphibian concentrations in desiccating mud may determine the breeding season of the white-shouldered ibis (*Pseudibis davisoni*). *The Auk*, 130, 774–783.

Wright, H.L., Ko, S., Norin, N. & Phearun, S. (2013b) White-shouldered ibis *Pseudibis davisoni* population size and the impending threat of habitat conversion. *Forktail*, 29, 162–165.

Yusuf, A.A. & Francisco, H. (2010) *Hotspots! Mapping Climate Change Vulnerability in Southeast Asia*. Economy and Environment Program for Southeast Asia, Singapore. Http://www.eepsea.net/pub/book/Coffee_Book_Final_29Sep10.pdf [accessed 3 November 2017].

Zuur, A.F. & Ieno, E.N. (2016) *Beginner's Guide to Zero-Inflated Models with R*. Highland Statistics Limited, Newburgh, UK.

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, USA.