Habitat use by two tropical species of waterfowl in central Malaysia

ABDOLLAH SALARI[1,2]*, MOHAMED ZAKARIA[1] & MARK S. BOYCE[2]

[1]Department of Park and Ecotourism, Universiti Putra Malaysia, Serdang, Selangor, Malaysia.
[2]Department of Biological Sciences, University of Alberta, Edmonton, Alberta, Canada.
*Correspondence author. E-mail: abdsalari@gmail.com

Abstract

Two tropical species of waterfowl, the Lesser Whistling-duck (LWD) *Dendrocygna javanica* and Cotton Pygmy-goose (CPG) *Nettapus coromandelianus*, are patchily distributed across Malaysia and little is known about their habitat requirements. We studied patterns of habitat use for LWD and CPG at the Paya Indah Wetlands Reserve, Malaysia (*c.* 3,050 ha), by counting the birds from observation points and using a zero-altered negative binomial model to describe their abundance and distribution at the site. Habitat use by LWD and CPG was highly correlated; for instance both species frequented shallow, nutrient-rich lakes in the study area. Fine-scale measures of vegetation characteristics influenced local distribution, whereas a combination of anthropogenic activities and other habitat features best predicted abundance. Overall, LWD selected the more stable but densely-vegetated marshy shoreline while CPG used vegetated areas near the central deeper portions of the lake. Our habitat-selection models give insight into the ecology of LWD and CPG in Malaysia and can provide a tool for identifying areas for possible habitat restoration and conservation in the region.

Key words: Cotton Pygmy-goose, count data, habitat selection, hurdle models, Lesser Whistling-duck, Paya Indah Wetlands, zero-altered negative binomial.

Patterns of habitat use by animals are likely to be a result of the influence of natural selection on survival and reproduction, which determine the fitness consequences of exploiting different habitats (Morris *et al.* 2008; Gaillard *et al.* 2010). Typically, the extent of habitat use suggests the quality and abundance of resources in those areas, which in turn reflects the fitness consequences of exploiting that habitat (Fretwell 1969), although there are exceptions (Horne 1983). In general, birds (Loegering & Fraser 1995; Bock & Jones 2004) and mammals (McLoughlin *et al.* 2006; McLoughlin *et al.* 2007) aggregate in higher-quality habitats. Availability of adequate food and shelter play a vital role in influencing habitat use by waterfowl (McKinney *et al.* 2006; Guadagnin & Maltchik 2007; Tavares *et al.* 2015), with access to food being influenced by water depth and by the type, structure and density of vegetation in wetland habitats (Baschuk *et al.* 2012). Many waterfowl forage by surface feeding, dabbling through the water and upending, so access to food can also be constrained by their morphology (*e.g.* leg length or bill length), particularly for tactile foragers (Green 1998). Vegetation additionally provides shelter and increases the bird's ability to avoid predators (Forman & Brain 2004), although the specific characteristics of vegetation that affect these decisions are not known. Moreover, disturbance from human activities can cause temporary changes in behaviour and affect temporal and spatial distribution of waterfowl locally (Madsen 1995).

Little is currently known about factors affecting the distribution and abundance of Lesser Whistling-duck (LWD) *Dendrocygna javanica* and Cotton Pygmy-goose (CPG) *Nettapus coromandelianus*. LWDs are medium-size waterfowl native to most areas of south Asia, east Asia and southeast Asia (IUCN 2013). Like all of the whistling ducks *Dendrocygna* sp. they differ from other duck species in having longer legs, a squarish head and an erect goose-like posture when alert (Johnsgard 1976). Although abundant through most of its range in southern and southeast Asia, with population size estimates varying from 100,000 to 1,000,000 birds during the 1980s–1990s (Perennou *et al.* 1994; Rose & Scott 1997; Choudhury 2005), numbers are thought to be in decline (Wetlands International 2015). The CPG distribution is similar to that of the LWD, although it extends to northeast Australia (IUCN 2013). Physically the two species are very different, however, with CPGs having a rounded head, short bill and short legs (Johnsgard 1976). Population size estimates for the CPG are of 100,000 for the South Asian population and up to 1,000,000 for the East/South East Asian population, with population trends classed as "unknown" (Perennou *et al.* 1994; Wetlands International 2015). Both species are mostly gregarious and frequent tropical freshwater wetlands with sufficient aquatic vegetation (Johnsgard 1976 and Fig. 1). They are non-migratory and have a patchy distribution in our study area.

The aim of this study was to describe patterns of habitat use and selection for the two species, based on the premise that abundance and distribution will vary spatially in relation to certain habitat characteristics. Since waterfowl abundance represents a recognised metric for habitat selection, our analyses have a working hypothesis that the models should reveal environmental conditions that are functionally related to both distribution and abundance (Baschuk *et al.* 2012). For instance, marshes with high abundance of vegetation provide suitable environments for breeding, feeding and predatory avoidance for most dabbling ducks (Scheffer & van Nes 2007). A modelling approach has been found by other authors to be useful for investigating waterbird distribution/abundance relative to environmental factors, habitat selection and species-specific requirements and that these models

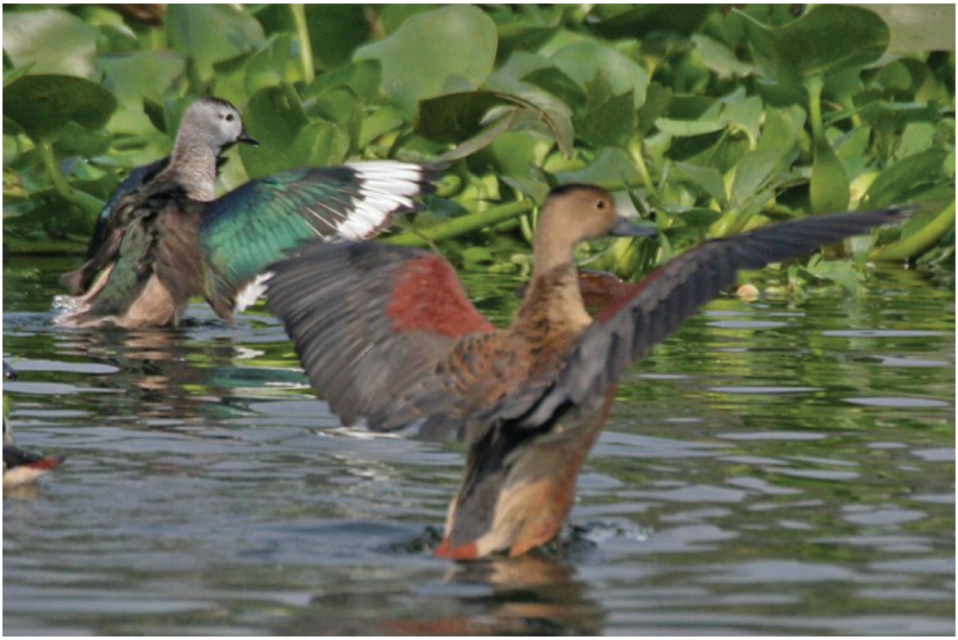

Figure 1. Lesser Whistling-duck (right) and Cotton Pygmy-goose (left) in their shared habitat. (Photograph by J.M. Garg.)

therefore also can provide useful insights for management and conservation (Found *et al.* 2008; Tavares *et al.* 2015).

Methods

Study area

The Paya Indah Wetlands (PIW) (Malay translation: "beautiful wetland") reserve encompasses 3,050 ha, of which 450 ha are under the administration of the Department of Wildlife and National Parks (DWNP) Peninsular Malaysia. It is adjacent to Malaysia's administrative centre of Putrajaya (at 2.85°–2.88°N, 101.60°–101.63° E), is a part of the Kuala Langat North Forest Reserve (a permanent peat swamp forest), and comprises degraded tin-mining lakes, logged peat swamp forest and large open lakes. Twenty-one lakes are located within the PIW, with heterogeneous ecosystems such as marshes, swamps and open water lakes, and with contrasting hydrochemical and structural attributes in both their spatial and temporal dimensions, but for our study we considered only 17 lakes that were under reserve management (Fig. 2). Two main activities, conducted erratically by local authorities and farmers in the PIW area: (1) sand mining, and (2) construction and maintenance of canals to irrigate oil palm plantations, both cause changes in the hydrochemical, structural, and spatial characteristics of the lakes. Because of its location 50 km south of Kuala Lumpur, 12 km west of Putra Jaya, and

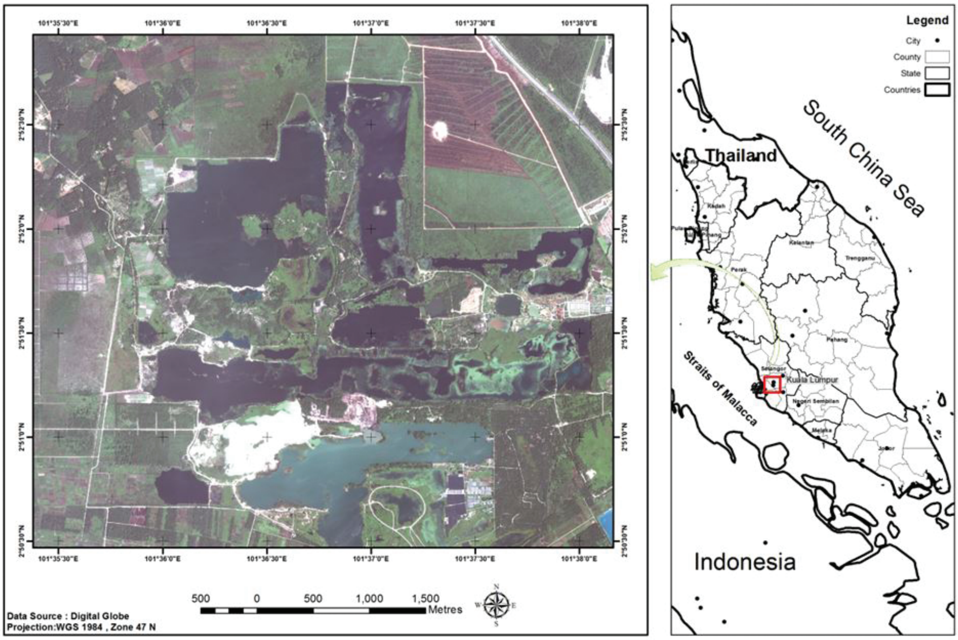

Figure 2. Satellite image (from World View 2) of the of Paya Indah Wetlands, Malaysia. Acquired through http://www.digitalglobe.com in January 2010.

15 km north of Kuala Lumpur International Airport (KLIA), the site is considered to be a "green lung" for the region and also a "super corridor" for migratory species. Rajpar and Zakaria (2010) recorded 13,872 birds from 100 species during a 14-month study at the PIW in 2007–2009, of which 22.3% of individuals and 25% of species were waterbirds, mostly Anatidae.

Species occurrence and abundance data

Two non-migratory waterfowl species – LWD and CPG – were monitored in the PIW. These are the only duck species in the area, both are permanent residents that breed at the site, and they have shared freshwater wetland habitats (Choudhury 2005; Fullagar 2005).

Point-count methods have been used to monitor the abundance of many types of birds (Ralph 1993; Forcey *et al.* 2006; Mordecai *et al.* 2011). We initially chose 288 sampling locations, distributed at random along the shoreline of 17 wetlands but with at least 150 m distance between them to achieve proportional allocation across the site (Fig. 3). Because of time and logistical constraints in undertaking our study, we then marked 48 of the sampling points, again selected at random from within the initial sample. Observations were made within a 150 m fixed radius around each marked sampling point (McKinney & Paton 2009; Leal *et al.* 2011), by the observer scanning in

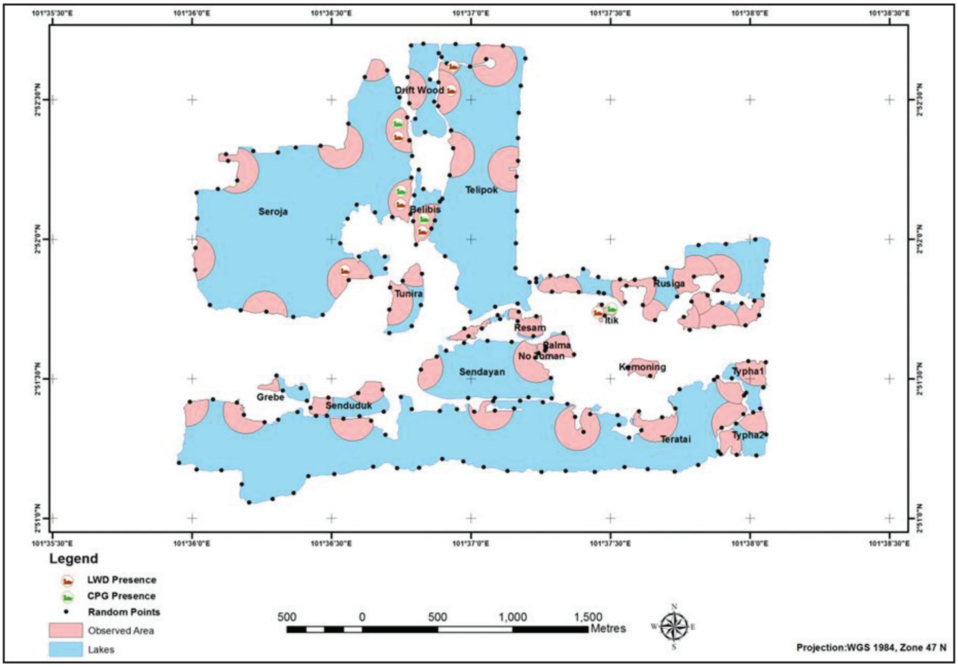

Figure 3. Random available locations (*n* = 288), 150 m radius around fixed observation points (*n* = 48, land excluded) and the names of lakes surveyed in the Paya Indah Wetlands, Malaysia.

a 180° arc to the front during 10-minute visits to each marked point at random times but between 07:00–12:00 h every week. All observations were conducted over two seasons (October–January 2010 and 2012) by the same observer. Variability in observer detection errors therefore could be assumed to be constant, although we believe detection was nearly 100% (Mordecai *et al.* 2011; Farmer *et al.* 2012). All ducks seen from the 48 marked points were recorded except for those in flight. Spatial maps developed from *World View 2* (WV2) satellite imagery (http://www.digitalglobe.com) and from field work were used to extract environmental gradients for covariates used in analysis.

Weekly counts were summed to provide monthly counts to reduce temporal autocorrelation. A resource unit (extending over a 150 m radius, excluding land, from 48 observation points) was considered to have been used when LWD or CPG were recorded in the unit during either the first or second sampling season. The same protocol was applied for abundance values, where abundance was taken to be the total number of birds counted in the used resource units. Available resource units for all distribution and abundance analyses were defined as being the entire set of 288 possible resource units (following Johnson *et al.* 2006), which included the subset of 48 observation units from which counts were made.

Environmental explanatory variables

Remotely sensed data has proven to be a powerful way to describe environmental conditions for ecological purposes (Pettorelli *et al.* 2011). WV2-derived Normalized Difference Vegetation Index (NDVI) gives an index of primary productivity that can be linked to ecological mechanisms (Pettorelli *et al.* 2005; Williams & Peterson 2009).

Variation in water depth influences the species composition and abundance of emergent and submersed vegetation in wetlands (Robel 1961; Anderson 1978; van der Valk *et al.* 1999; van der Valk & Murkin 2002). Vegetation, in turn, influences the amount of available food, nesting sites and cover for marsh birds and waterfowl (Murkin *et al.* 1997; Tavares *et al.* 2015). In addition, water depth affects available food resources because it limits access by some avian species (Pöysä 1983; Lantz *et al.* 2011; Lunardi *et al.* 2012). Water depth can also influence invertebrate populations that are important food for waterfowl (Cox *et al.* 1998). Furthermore, waterfowl are known to select lakes based on water quality (Hansson *et al.* 2010). Anthropogenic disturbance has been shown to negatively affect activities and behaviour of most waterfowl (Dahlgren & Korschgen 1992; Fox & Madsen 1997; Väänäanen 2001; Pease *et al.* 2005).

To identify those environmental characteristics that were predictive of the distribution and abundance of LWD and CPG in PIW, several variables were measured, using fieldwork, satellite-image analysis, and spatial statistics. Identification of the dominant emergent vegetation was determined from a coarse-scale aquatic vegetation map of wetlands in combination with numerous field visits for validation. NDVI values, extracted based on Red and Near Infra-Red 2 bands, were inspected and used with visually interpreted data to create a map of land-use/land-cover for the PIW area, and inside wetlands polygons were grouped into two classes: "open water" and "vegetated". Annual mean water-quality index (WQI) of lakes and lake-level fluctuation data for 2010 were obtained from PIW reserve management. The WQI was derived using measurements of dissolved oxygen (DO), biological oxygen demand (BOD), chemical oxygen demand (COD), ammonical nitrogen (AN), suspended solids (SS) and pH. Numerous depth samples from all 17 lakes were obtained by field surveys during the first season of data collection. ArcGIS 10 spatial analysis tools were used to estimate aquatic vegetation percentage covers, interpolation, and distance and density measurements.

Procedures for estimating the fine-grain explanatory variables used in this study from World View 2 satellite imagery are described in greater detail in Salari *et al.* (2014). Additionally, regional climate data permits analysis of relationships between climate variables and habitat selection (Huston 1999). For instance, nest-site selection in waterfowl is largely influenced by microclimate conditions such as temperature and humidity (Gloutney & Clark 1997). Furthermore, in those Anatids with female-only incubation, maternal behaviour is influenced by these environmental factors which in turn might affect population growth rate and abundance (Hepp *et al.* 2006). Hence, monthly climate data were obtained from KLIA International Airport for each of the observation periods to explore the possible effect of local weather conditions on habitat use by our study species.

Data analysis

We developed models for two levels: distribution and abundance, using count data for LWD and CPG collected over the 8-month study period. To do this, we applied a negative binomial model using the hurdle function (Potts & Elith 2006) available in the PCSL-contributed package (Zeileis *et al.* 2007) for R software. This zero-altered negative binomial (ZANB) model assumes that a binary process determines whether a count model should be > 0 (binomial GLM) and then a count process independently generates the positive values. If the count value exceeds unity, the presence threshold is fulfilled and the conditional distribution of the positive values is governed by a zero-truncated negative binomial model. The explanatory covariates for the two components are not constrained to be the same in ZANB models, although here we have used same covariates for both components. We tested for over-dispersion of LWD and CPG data by calculating a variance-to-mean ratio, where ratios of > 1 are considered to indicate over-dispersion (Zorn 1996). We also plotted the overall distribution of abundance data to ensure that they approximated a negative binomial distribution. Over-dispersion is additionally considered likely when the residual deviance of a model is significantly higher than the residual degrees of freedom (Crawley 2012).

Strong correlations between explanatory variables can cause problems in model fitting and interpretation (Graham 2003; Heikkinen *et al.* 2006). We began with a pre-selection of covariates that were most ecologically relevant to the species. After that, we used a variance inflation factor (VIF) to test for collinearity; collinear variables with VIF values larger than 3 can cause estimation problems (Zuur 2007). We chose a subset of 23 variables among environmental factors believed to be causal for habitat use by the two species at the scale of our study using covariates that determine the quality and quantity of habitats for most waterfowl (Hansson *et al.* 2010; Kreakie *et al.* 2012). After those data-screening procedures and based on our ecological knowledge of the species, 13 non-collinear candidate explanatory variables were chosen to model habitat use by LWD and CPG in the PIW (Table 1).

We ranked eight biologically plausible *a priori* models for LWD and four for CPG to evaluate those relationships (Tables 2 & 3) using information-theoretic methods. Given the lack of earlier studies of how these species select their habitats, we chose covariates included in these models on the basis of our field observations and literature on similar taxa, and as such appreciate that these analyses are exploratory. We began our comparison by calculating the null model, which was a model incorporating a constant but with no explanatory variable serving as a reference point or null model to evaluate the

Table 1. Candidate explanatory variables used for modelling distribution and abundance of Lesser Whistling-ducks and Cotton Pygmy-geese in the Paya Indah Wetlands, Malaysia.

Variables abbreviation	Description	Source	Units	Value Ranges
Dep_cv	Mean coefficient of variation of water depth in a 150 m radius around each available point	Field(GIS)	–	0.52–1.22
Dep	Mean water depth in a 150 m radius around each available point	Field(GIS)	M	0.20–7.85
Dis_rd	Distance from available points to nearest road	WV2&Field(GIS)	M	14.35–116
Dis_hum	Distance from units to nearest human development	Field(GIS)	M	89.22–779.80
Hum_den	Density of human linear development in a 150 m radius around each unit	Field(GIS)	km/km^{-2}	0.00–16.71
Rd_den	Density of roads in a 150 m radius each unit	WW2&Field(GIS)	km/km^{-2}	0.00–0.008
NDVI	Mean NDVI of each unit	VW2(GIS)	–	0.14–0.76
Spik1	Percent cover of Spike Rush in each unit	WW2&Field(GIS)	%	0–100
Mix1_15	Percent cover of mixture of Spike Rush and Water Lily in each unit	WW2&Field(GIS)	%	0–99
WQI	Mean water quality index (.5m) of each unit	PIWM(GIS)	–	50.26–89.90
LLF	Mean of water level fluctuation of each unit	PIWM(GIS)	M	6.00–7.75
Temp	Monthly mean daily temperature in the PIW	Sepang(KLIA) Weather station	C	26–28
Humidity	Monthly mean daily relative humidity in the PIW	Sepang(KLIA) Weather station	%	80–87

Land-use/ land-cover features were extracted from World View 2 Imagery (WV2) with 10 m resolution. Procedures for estimating fine-grain explanatory variables by using World View 2 satellite imagery are described in greater detail in Salari *et al.* (2014). Units = 150 m radius around observation and random points (terrestrial areas excluded). PIWM = Paya Indah Wetland Management data. KLIA = Kuala Lumur International Airport weather station, Sepang, Malaysia. WQI = Malaysian Water Quality Index, accessible at http://www.doe.gov.my.

Table 2. Ranking of *a priori* candidate zero-altered negative binomial (hurdle, ZANB) models for Lesser Whistling-duck in the Paya Indah wetlands, Malaysia.

Model No.	Model structure	K	AIC_c	Δ_i	w_i	LL
8	Spik1+Mix1_15+NDVI+Dis_hum+WQI+ LLF+Temp+Humidity	19	750.68	0.00	1.00	–356.3
2	Spik1+Mix1_15+Dep_cv+LLF+WQI+ Temp+Humidity	17	767.55	16.30	0.00	–366.8
7	Spik1+Mix1_15+NDVI+Dis_hum+WQI+ Temp+Humidity	17	786.44	35.19	0.00	–376.0
5	Spik1+Mix1_15+NDVI+Dis_hum+ Temp+Humidity	15	807.71	55.96	0.00	–388.0
6	Spik1+Mix1_15+NDVI+Rd_den+ Temp+Humdity	15	897.01	145.26	0.00	–433.5
4	Spik1+Mix1_15+Rd_den+Hum_den+ Temp+Humidity	15	919.82	168.07	0.00	–449.9
1	Spik1+Mix1_15+NDVI+Temp+ Humdity	13	924.36	172.17	0.00	–449.2
3	Spik1+Mix1_15+Rd_den+Temp+ Humidity	13	933.42	181.23	0.00	–453.7

Abbreviations for variables listed in the model structure are provided in Table 1. K = total parameters count for binary and zero truncated negative binomial parts of ZANB including intercepts plus θ. Δi = differences among AICc scores of model i and best fitting model. w_i = AICc weights. LL = log likelihood scores.

performance of other candidate models. In the final stage, Akaike's information criterion corrected for small sample sizes (AICc), was used to select the most parsimonious of the candidate ZANB models (Burnham & Anderson 2002; Johnson & Omland 2004). To adjust for variation in resource unit size, we applied log area of resource units as an offset term.

Results

Species-distribution models

A total of 1,262 LWD and 1,526 CPG were detected during the first field season, in 2010/11, decreasing to 931 LWD and 1,417 CPG recorded in 2011/12. The two species were detected at relatively few of the observation points during the study (LWD = 7/48, CPG = 4/48; Fig. 3).

Table 3. Ranking of *a priori* candidate zero-altered negative binomial (hurdle, ZANB) models for Cotton Pygmy-geese in the Paya Indah wetlands, Malaysia.

Model No.	Model structure	K	AIC_c	Δ_i	w_i	LL
3	Spik1+Mix1_15+NDVI+Temp+Humdity	13	558.72	0.00	1.00	–265.9
1	Spik1+Mix1_15+Temp+Humdity	11	567.14	8.41	0.00	–272.1
4	Spik1+Mix1_15+Rd_den+Temp+Humdity	13	568.34	9.61	0.00	–270.5
2	NDVI+Temp+Humdity	9	657.35	98.62	0.00	–319.4

Abbreviations for variables listed in the model structure are provided in Table 1. K = total parameters count for binary and zero truncated negative binomial parts of ZANB including intercepts plus θ. Δ*i* = differences among AICc scores of model i and best fitting model. w_i = AICc weights. LL = log likelihood scores.

In general, the variables with the most support for species presence in the ZANB modelling were the same for both species at the PIW site. The number of explanatory variables in ZANB models for CPG presence/absence in each of the 48 observed resource units is smaller than for the LWD models because larger models caused convergence errors on attempting to fit the ZANB model (Harrell 2001). LWD and CPG were absent from many resource units and so the probability of their being present was small. As the GLM produces a response deviance on the same scale for all nested models, we can compare results of models with different link transformations. This allows for flexibility in exploring which link function is most appropriate. We compared results of both logit link and complementary log-log link models and chose the former one for the binomial part of ZANB, not only because it is better understood but also because the AICc comparison of these models did not show an improved fit on using a clog-log link function.

Caution must be observed in interpretation of results in binary part of ZANB because a zero outcome is the prediction. The signs of the coefficients have precisely the opposite interpretation from that of a normal binomial model. In other words, a positive coefficient indicates that the variable increases the probability of zeros and a negative coefficient indicates that the variable decreases the probability of zeros.

Based on the lowest AICc values, LWD distribution is inversely related to the percent cover of a mixture of Spikerush *Eleocharis dulcis* and Water Lily *Nympheae lotus*, water level fluctuation and, interestingly, the water quality in each unit and the distance to the nearest human development (Table 4).

Table 4. Estimated coefficients and standard errors for zero-altered negative binomial (hurdle, ZANB) models for the top AICc-selected model for the Lesser Whistling-duck habitat use in the Paya Indah wetlands, Malaysia.

Variable (codes)[a]	Group A (zeros)[b]		Group ~A (counts)	
	Coefficient	s.e.	Coefficient	s.e.
Intercept	–3.37E+01	1.68E+01	3.20	8.42
Spik1	–1.71E+00	1.05E+00	0.73	0.33
Mix1_15	6.36E+00	8.17E–01	0.41	0.42
NDVI	–1.86E+01	3.46E+00	6.01	1.10
Dis_hum	9.23E–03	1.98E–03	2×10^{-3}	8×10^{-4}
WQI	6.31E–02	2.38E–02	4×10^{-3}	1×10^{-2}
LLF	3.29E+00	7.27E–01	–2.82	0.76
Temp	8.84E–04	4.04E–01	0.05	0.12
Humidity	2.48E–02	9.00E–02	0.07	0.03

[a] Code definitions for variables are provided in Table 1. [b] Group A estimates relate to the process of being zero/non-zero in binary part of the ZANB model. Since a zero outcome is the prediction in this part, the signs of the coefficients have precisely the opposite interpretation from that of a logit model. In other words, a positive coefficient indicates that the variable increases the probability of zeros and a negative coefficient indicates that the variable decreases the probability of zeros. Group ~A estimates relate to the abundance (intensity of use) part of ZANB model of Lesser Whistling-duck in Paya Indah wetlands, Malaysia.

The mean NDVI (productivity) of each unit and proportion of Spikerush in each unit has a positive effect on LWD distribution (Table 4). The lowest AICc model for CPG showed that distribution was inversely related to the percent cover of a mixture of Spikerush and Water Lily in each unit. As for LWD, CPG distribution had a positive relationship to the mean NDVI of each unit (Table 5). Overall, it seems that LWD selected more stable densely vegetated marshy edge areas while CPG frequented vegetated areas near the central, deeper parts of the lake.

Species abundance models

LWD and CPG were present in few resource units, not even reaching that expected from a standard Poisson distribution which is sometimes used as the basis for count data modelling (residual deviance = 13,809, d.f. = 2,298 for the

Table 5. Estimated coefficients and standard errors for zero-altered negative binomial (hurdle, ZANB) models for the top AICc selected model for Cotton Pygmy-goose habitat use in the Paya Indah Wetlands, Malaysia. [a] See footnote to Table 4.

Variable (codes)	Group A (zeros)[a]		Group ~A (counts)	
	Coef.	s.e.	Coef.	s.e.
Intercept	–3.03E+00	1.80E+01	–14.41	5.16
Spik1	1.62E+00	6.21E–01	3.67	0.43
Mix1_15	4.91E+00	4.96E–01	3.52	0.36
NDVI	–6.18E+00	2.00E+00	–3.26	2.61
Temp	–3.74E–11	4.62E–01	0.08	0.13
Humidity	–1.17E–10	1.02E–01	0.06	0.02

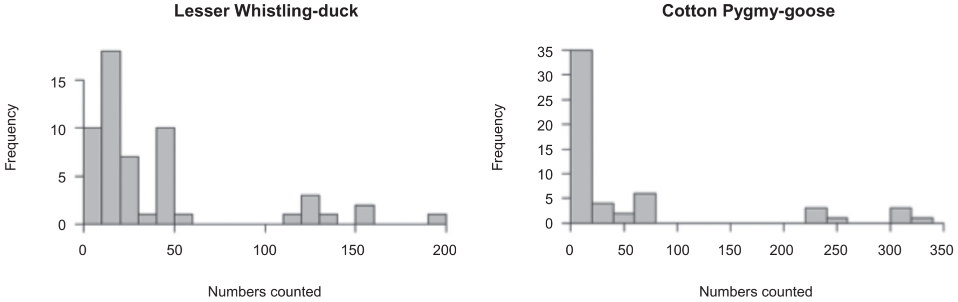

Figure 4. Lesser Whistling–duck and Cotton Pygmy–goose abundance within a 150 m fixed radius around observation points (Fig. 2) in the Paya Indah Wetlands, Malaysia, during October–January 2010, 2012.

Poisson model). Also, visual examination of the count data (Fig. 4) combined with a variance-to-mean ratio test showed over-dispersion of zero-count data (variance-to-mean ratio = 91), indicating that abundance data would be best fitted using a negative binomial model. In contrast with the distribution model (zero hurdle), results of abundance (count data) analysis from the ZANB regression models can be interpreted in a regular manner. These indicated that LWD abundance was positively related to the percent cover of Spikerush, mean NDVI of each unit, and the distance between the sampling unit and human activities. In addition, LWD abundance was related to monthly mean relative humidity and inversely related to water level fluctuations. The abundance model results for CPG were similar to those for LWD in showing that the percentage of Spikerush cover and also the mixed Spikerush and Water Lily cover were positively associated with bird abundance in a unit (Tables 4 & 5).

Discussion

Anatidae are ecologically dependent on wetland habitat for at least part of their annual cycle. Conservation of these waterfowl largely depends on the recognition of key factors affecting their site selection. Wetlands International has published an *Atlas of Key Sites for Anatidae in the East Asian Flyway* (Miyabayashi & Mundkur 1999), which reviewed the distribution of Anatidae species in the region, defined population boundaries and identified important areas for these species. Key sites for Lesser Whistling-duck in Thailand and Myanmar were listed in this document, with none reported for Malaysia, albeit information on breeding areas for birds in the East Asian Flyway is incomplete. Although our study provides a preliminary assessment of the ecology for two little known waterfowl species, it therefore should be noted that there may be conditions at other sites not present at our study site that make other sites more attractive to these birds.

In this paper we estimated model parameters to identify factors contributing to the distribution and intensity of use by the Lesser Whistling-duck and Cotton Pygmy-goose at Paya Indah Wetlands. While data accessibility and collection were limited, we believe that our study will not only help to inform conservation measures by revealing which environmental variables best explain species distribution and abundance but also encourage further research to flesh out those species' ecology and life history. LWD prefer freshwater wetlands where there is sufficient aquatic vegetation in which to hide, and they forage mostly on aquatic plants, nibbling on their seeds and shoots. They also feed on insects and aquatic invertebrates. They are gregarious and consume aquatic vegetation by dabbling in shallow water areas (Johnsgard 1976). CPG also preferred habitats that are freshwater wetlands where there is sufficient aquatic vegetation to forage. They are gregarious and foraging is undertaken by dabbling and picking at the water surface or by stripping seeds and flowers from aquatic plants (Johnsgard 1976). Most of the results from our species/habitat analysis correspond with our observations of the species' biology and habitat preferences in the field. Water level fluctuations, water quality and anthropogenic disturbance play a vital role in determining the quality and quantity of habitat for waterfowl in general (Perry & Deller 1996; Madsen 1998; Hansson *et al.* 2010; Tavares *et al.* 2015). We evaluated the effects of those variables on LWD and CPG distribution and abundance in the PIW. Our results showed that water level fluctuation has a different effect on distribution than on abundance. Although highly variable, the water-level at resource units provided more resources for both species by different mechanisms (Hansson *et al.* 2010; Kreakie *et al.* 2012), with fluctuations causing shallow water habitat to shift away from the shoreline when water levels recede and back towards the shorelines as water levels rise. Although this shift in habitat location may increase waterfowl energetic costs, it also likely increases available food and habitat by maintaining emergent parts of the wetlands (Murkin *et al.* 1997).

Both waterfowl species were more abundant in stable habitats with low water level variation. Moderate water depth in each unit supported presence of both species in our study. Baschuk *et al.* (2012) observed that shallow waters make it easier for dabbling ducks to access submerged aquatic vegetation for feeding. Furthermore, emergent vegetation, especially Spikerush, was particularly important for both species in our study area, which may influence the amount of available food and cover. In addition, such environments might act as more suitable habitats to breeding, feeding and predatory avoidance (Murkin *et al.* 1997; Frid & Dill 2002).

NDVI selection coefficient values near zero or positive values indicated that non-vegetated water bodies such as open water were not preferred. Our results show that high mean NDVI of each unit was positively related to abundance of LWD. Growing nutritious vegetation has low red-light reflectance and high near-infrared reflectance and thus yields high NDVI values. High values of NDVI are also related to higher photosynthetic activity and, consequently, primary productivity (Nicholson *et al.* 1998; Vicente-Serrano & Heredia-Laclaustra 2004). Higher primary productivity can, in turn, increase food abundance in higher trophic levels, such as arthropods, which constitutes a nutritious food source for most waterfowl (Gordo 2007). Furthermore, high NDVI values are related to improved ecological conditions for waterfowl niche exploitation (Dalby *et al.* 2014); therefore, this could be related to increased habitat preference and abundance of LWD in our units.

Several studies have sought to identify how human activities affect waterbirds (Klein *et al.* 1995; Frid & Dill 2002; Fox *et al.* 2014). Most studies show that anthropogenic activities decrease habitat preferences by waterfowl (Dahlgren & Korschgen 1992; Fox & Madsen 1997; Väänänen 2001; Pease *et al.* 2005). But they may still select disturbed habitats if alternative habitats are too distant or of low quality (Frid & Dill 2002; Gill 2007). Anthropogenic activities play different roles in shaping distribution and abundance patterns on our study area. Surprisingly, distance to human activities around each observation point had inverse effects on distribution of LWD, but positive effects on LWD abundance. Most human developments are around the shoreline in the PIW, which our data revealed is the LWD preferred habitat, yet the ducks were more abundant in marshy edges when far from anthropogenic activities.

Habitat selection often requires trade-offs between habitat availability and exposure to potentially detrimental factors (Dussault *et al.* 2006; Bastille Rousseau *et al.* 2010). Our results highlight the importance of major factors, and their potential interactions, in determining LWD and CPG distribution and abundance. We had insufficient sampling to include seasonal factors in our analysis, which will undoubtedly exert a significant effect on

LWD and CPG presence and abundance through time. Future studies should incorporate time-series remote-sensing imagery to understand changes through the habitat and seasonal dietary analysis (Elmberg *et al.* 2003) to better document seasonal variation in LWD and CPG diets, as well as spatial and temporal distributions in relation to landscape change and food/shelter availability.

We believe that our best models reflect the ecological processes affecting habitat use by waterfowl in PIW. The majority of the explanation provided by our binary model was a description of how LWD and CPG selected habitats determining patterns of distribution. Given that waterfowl were absent from the majority of sectors, explanation of ecological processes that determined variation in abundance was of interest, examined using truncated negative binomial in zero-altered models. We found evidence that both LWD and CPG preferred shallow, nutrient-rich "marshy" lakes which many studies have shown to be important for waterfowl (Murphy *et al.* 1984; Bayley & Prather 2003). In addition, our distribution model indicated medium to low sensitivity to human disturbance by LWD. However, the abundance model indicated that counts were low in areas close to anthropogenic activities, reflecting the restricted availability of suitable habitats in the PIW. In general, distribution models might enlighten management, but abundance models provide more information, better our understanding of processes, and ultimately can contribute to better management and conservation. In particular, management should focus on establishing screened buffer zones around important waterfowl roosting and feeding areas as well as manipulating vegetation composition and configuration through effective water level management strategies, to ensure future abundance of both LWD and CPG in the PIW.

Acknowledgements

The authors are grateful to the Malaysian governmental agencies NAHRIM and DWNP for providing data and allowing us to conduct this research. We thank Paya Indah Wetlands Reserve guards and staff for their help during field surveys. We also thank Department of Biological Sciences, University of Alberta and Faculty of Forestry, Universiti Putra Malaysia staff and students for their support.

References

Anderson, M.G. 1978. Distribution and production of Sago Pondweed (*Potamogeton pectinatus L*) on a Northern Prairie Marsh. *Ecology* 59: 154–160.

Baschuk, M.S., Koper, N., Wrubleski, D.A. & Goldsborough, G. 2012. Effects of water depth, cover and food resources on habitat use of marsh birds and waterfowl in boreal wetlands of Manitoba, Canada. *Waterbirds* 35: 44–55.

Bastille Rousseau, G., Fortin, D. & Dussault, C. 2010. Inference from habitat selection analysis depends on foraging strategies. *Journal of Animal Ecology* 79: 1157–1163.

Bayley, S.E. & Prather, C.M. 2003. Do wetland lakes exhibit alternative stable states? Submersed aquatic vegetation and chlorophyll in western boreal shallow lakes. *Limnology and Oceanography* 48: 2335–2345.

Bock, C.E. & Jones, Z.F. 2004. Avian habitat evaluation: should counting birds count?

Frontiers in Ecology and the Environment 2: 403–410.

Burnham, K.P. & Anderson, D.R. 2002. *Model Selection and Multimodel Inference: a Practical Information-Theoretic Approach*. Springer, New York, USA.

Choudhury, A. 2005. Lesser Whistling-duck *Dendrocygna javanica*. *In* J. Kear (ed.), *Ducks, Geese and Swans, Volume 1*, pp. 207–209. Oxford University Press, Oxford, UK.

Cox, R.R., Hanson, M.A., Roy, C.C., Euliss, N.H., Johnson, D.H. & Butler, M.G. 1998. Mallard duckling growth and survival in relation to aquatic invertebrates. *Journal of Wildlife Management* 62: 124–133.

Crawley, M.J. 2012. *The R Book*. John Wiley & Sons, New York, USA.

Dahlgren, R. & Korschgen, C.E. 1992. Human disturbances of waterfowl: An annotated bibliography. No. 188. U.S. Dept. of the Interior, Fish and Wildlife Service, Washington D.C., USA.

Dalby, L., McGill, B.J., Fox, A.D. & Svenning, J.C. 2014. Seasonality drives global scale diversity patterns in waterfowl (*Anseriformes*) via temporal niche exploitation. *Global Ecology and Biogeography* 23: 550–562.

Dussault, C., Courtois, A. & Ouellet, J.P. 2006. A habitat suitability index model to assess moose habitat selection at multiple spatial scales. *Canadian Journal of Forest Research* 36: 1097–1107.

Elmberg, J., Nummi, P., Pöysä, H. & Sjöberg, K. 2003. Breeding success of sympatric dabbling ducks in relation to population density and food resources. *Oikos* 100: 333–341.

Farmer, R.G., Leonard, M.L. & Horn, A.G. 2012. Observer effects and avian-call-count survey quality: rare-species biased and overconfidence. *Auk* 129: 76–86.

Forcey, G.M., Anderson, J.T., Ammer, F.K. & Whitmore, R.C. 2006. Comparison of two double-observer point-count approaches for estimating breeding bird abundance. *Journal of Wildlife Management* 70: 1674–1681.

Forman, D. & Brain, P. 2004. Reproductive strategies used by moorhens (*Gallinula chloropus*) colonizing an artificial wetland habitat in south Wales. *Journal of Natural History* 38: 389–401.

Found, C., Webb, S.M. & Boyce, M.S. 2008. Selection of lake habitats by waterbirds in the boreal transition zone of northeastern Alberta. *Canadian Journal of Zoology* 86: 277–285.

Fox, A. & Madsen, J. 1997. Behavioural and distributional effects of hunting disturbance on waterbirds in Europe: implications for refuge design. *Journal of Applied Ecology* 34: 1–13.

Fox, A.D., Flint, P.L., Hohman, W.L. & Savard, J.P.L. 2014. Waterfowl habitat use and selection during the remigial moult period in the northern hemisphere. *Wildfowl* (Special Issue No. 4): 131–168.

Fretwell, S. 1969. On territorial behavior and other factors influencing habitat distribution in birds. *Acta Biotheoretica* 19: 45–52.

Frid, A. & Dill, L.M. 2002. Human-caused disturbance stimuli as a form of predation risk. *Conservation Ecology* 6: 11.

Fullagar, P. 2005. Cotton Teal (Cotton Pygmy-goose) *Netttapus coromandelianus*. *In* J. Kear (ed.), *Ducks, Geese and Swans, Volume 2*, pp. 475–477. Oxford University Press, Oxford, UK.

Gaillard, J.-M., Hebblewhite, M., Loison, A., Fuller, M., Powell, R., Basille, M. & Van Moorter, B. 2010. Habitat–performance relationships: finding the right metric at a given spatial scale. *Philosophical Transactions of the Royal Society B: Biological Sciences* 365: 2255–2265.

Gill, J.A. 2007. Approaches to measuring the effects of human disturbance on birds. *Ibis* 149: 9–14.

Gloutney, M.L. & Clark, R.G. 1997. Nest-Site Selection by Mallards and Blue-Winged Teal in Relation to Microclimate. *The Auk 114*: 381–395.

Gordo, O. 2007. Why are bird migration dates shifting? A review of weather and climate effects on avian migratory phenology. *Climate Research* 35: 37–58.

Graham, M.H. 2003. Confronting multicollinearity in ecological multiple regression. *Ecology* 84: 2809–2815.

Green, A.J. 1998. Comparative feeding behaviour and niche organization in a Mediterranean duck community. *Canadian Journal of Zoology* 76: 500–507.

Guadagnin, D. & Maltchik, L. 2007. Habitat and landscape factors associated with neotropical waterbird occurrence and richness in wetland fragments. *Biodiversity and Conservation* 16: 1231–1244.

Hansson, L.A., Nicolle, A., Bronmark, C., Hargeby, A., Lindstrom, A. & Andersson, G. 2010. Waterfowl, macrophytes, and the clear water state of shallow lakes. *Hydrobiologia* 646: 101–109.

Harrell, F.E. 2001. Regression modeling strategies: with applications to linear models, logistic regression, and survival analysis. Springer.

Heikkinen, R.K., Luoto, M., Araujo, M.B., Virkkala, R., Thuiller, W. & Sykes, M.T. 2006. Methods and uncertainties in bioclimatic envelope modelling under climate change. *Progress in Physical Geography* 30: 751–777.

Hepp, G.R., Kennamer, R.A. & Johnson, M.H. 2006. Maternal effects in wood ducks: incubation temperature influences incubation period and neonate phenotype. *Functional Ecology* 20: 308–314.

Horne, B.V. 1983. Density as a misleading indicator of habitat quality. *Journal of Wildlife Management* 47: 893–901.

Huston, M.A. 1999. Local processes and regional patterns: appropriate scales for understanding variation in the diversity of plants and animals. *Oikos* 86: 393–401.

IUCN. 2013. IUCN Red List for birds. BirdLife International, Cambridge, UK.

Johnsgard, P.A. 1976. Handbook of waterfowl behaviour Cornell University Press, USA.

Johnson, J.B., & Omland, K.S. 2004. Model selection in ecology and evolution. *Trends in Ecology & Evolution* 19: 101–108.

Johnson, C.J., Nielsen, S.E., Merrill, E.H., McDonald, T.L. & Boyce, M.S. 2006. Resource selection functions based on use-availablity data: theoretical motivation and evaluation methods. *Journal of Wildlife Management* 70: 347–357.

Klein, M.L., Humphrey, S.R. & Percival, H.F. 1995. Effects of ecotourism on distribution of waterbirds in a wildlife refuge. *Conservation Biology* 9: 1454–1465.

Kreakie, B.J., Fan, Y. & Keitt, T.H. 2012. Enhanced migratory waterfowl distribution modeling by inclusion of depth to water table data. *Plos One* 7: e30142.

Lantz, S.M., Gawlik, D.E. & Cook, M.I. 2011. The effects of water depth and emergent vegetation on foraging success and habitat selection of wading birds in the Everglades. *Waterbirds* 34: 439–447.

Leal, A.I., Martins, R.C. Palmeirim, J.M. & Granadeiro, J.P. 2011. Influence of habitat fragments on bird assemblages in Cork Oak woodlands. *Bird Study* 58: 309–320.

Lele, S.R., Merrill, E.H., Keim, J. & Boyce, M.S. 2013. Selection, use, choice, and occupancy: clarifying concepts in resource selection studies. *Journal of Animal Ecology* 82: 1183–1191.

Loegering, J.P. & Fraser, J.D. 1995. Factors affecting Piping Plover chick survival in different brood-rearing habitats. *Journal of Wildlife Management* 59: 646–655.

Lunardi, V.O., Macedo, R.H., Granadeiro, J.P. & Palmeirim, J.M.. 2012. Migratory flows and foraging habitat selection by shorebirds along the northeastern coast of Brazil: the case of Baía de Todos os Santos. *Estuarine, Coastal and Shelf Science* 96: 179–187.

Madsen, J. 1995. Impacts of disturbance on migratory waterfowl. *Ibis* 137: S67–S74.

Madsen, J. 1998. Experimental refuges for migratory waterfowl in Danish wetlands. I. Baseline assessment of the disturbance effects of recreational activities. *Journal of Applied Ecology* 35: 386–397.

McKinney, R.A., McWilliams, S.R. & Charpentier, M.A. 2006. Waterfowl–habitat associations during winter in an urban North Atlantic estuary. *Biological Conservation* 132: 239–249.

McKinney, R.A. & Paton, P.W.C. 2009. Breeding birds associated with seasonal pools in the northeastern United States. *Journal of Field Ornithology* 80: 380–386.

McLoughlin, P.D., Boyce, M.S., Coulson, T. & Clutton-Brock, T. 2006. Lifetime reproductive success and density-dependent, multi-variable resource selection. *Proceedings of the Royal Society B-Biological Sciences* 273: 1449–1454.

McLoughlin, P.D., Gaillard, J.M., Boyce, M.S., Bonenfant, C., Messier, F., Duncan, P., Delorme, D., Van Moorter, B., Said, S. & Klein, F. 2007. Lifetime reproductive success and composition of the home range in a large herbivore. *Ecology* 88: 3192–3201.

Miyabayashi, Y. & Mundkur, T. 1999. *Atlas of Key Sites for Anatidae in the East Asian Flyway.* Wetlands International – Japan, Tokyo, Japan and Wetlands International – Asia Pacific, Kuala Lumpur, Malaysia.

Mordecai, R.S., Mattsson, B.J., Tzilkowski, C.J. & Cooper, R.J. 2011. Addressing challenges when studying mobile or episodic species: hierarchical Bayes estimation of occupancy and use. *Journal of Applied Ecology* 48: 56–66.

Morris, D.W., Clark, R.G. & Boyce, M.S. 2008. Habitat and habitat selection: theory, tests, and implications. *Israel Journal of Ecology and Evolution* 54: 287–294.

Murkin, H.R., Murkin, E.J. & Ball, J.P. 1997. Avian habitat selection and prairie wetland dynamics: A 10-year experiment. *Ecological Applications* 7: 1144–1159.

Murphy, S.M., Kessel, B. & Vining, L.J. 1984. Waterfowl populations and limnologic characteristics of taiga ponds. *Journal of Wildlife Management* 48: 1156–1163.

Nicholson, S.E., Tucker, C.J. & Ba, M. 1998. Desertification, drought, and surface vegetation: An example from the West African Sahel. *Bulletin of the American Meteorological Society* 79: 815–829.

Pease, M.L., Rose, R.K. & Butler, M.J. 2005. Effects of human disturbances on the behavior of wintering ducks. *Wildlife Society Bulletin* 33: 103–112.

Perennou, P.C., Mundkur, T. & Scott, D.A. 1994. *The Asian Waterfowl Census 1987–1991: Distribution and Status of Asian waterfowl.* AWB Publication No. 86 and IWRB Publication No. 24. Asian Wetlands Bureau, Kuala Lumpur, Malaysia and IWRB, Slimbridge, UK.

Perry, M.C. & Deller, A.S. 1996. Review of factors affecting the distribution and abundance of waterfowl in shallow-water habitats of Chesapeake Bay. *Estuaries* 19: 272–278.

Pettorelli, N., Ryan, S., Mueller, T., Bunnefeld, N., Jedrzejewska, B., Lima, M. & Kausrud, K. 2011. The Normalized Difference Vegetation Index (NDVI): unforeseen successes in animal ecology. *Climate Research* 46: 15–27.

Pettorelli, N., Vik, J.O., Mysterud, A., Gaillard, J.M., Tucker, C.J. & Stenseth, N.C. 2005. Using the satellite-derived NDVI to assess ecological responses to environmental change. *Trends in Ecology & Evolution* 20: 503–510.

Potts, J.M. & Elith, J. 2006. Comparing species abundance models. *Ecological Modelling* 199: 153–163.

Pöysä, H. 1983. Morphology-Mediated niche organization in a guild of dabbling ducks. *Ornis Scandinavica* 14: 317–326.

Rajpar, M. & Zakaria, M. 2010. Density and diversity of waterbirds and terrestrial birds at Paya Indah Wetland reserve, Selangor Peninsular Malaysia. *Journal of Biological Sciences* 10: 658–666.

Ralph, C.J. 1993. Designing and implementing a monitoring program and the standards for conducting point counts. *Status and Management of Neotropical Migratory Birds* 229: 204–207.

Robel, R.J. 1961. Water depth and turbidity in relation to growth of sago pondweed. *Journal of Wildlife Management* 25: 436–438.

Rose, P.M. & Scott, D.A. 1997. *Waterfowl Population Estimates. Second Edition*. Wetlands International Publication No. 44. Wetlands International, Wageningen, The Netherlands.

Salari, A., Zakaria, M., Nielson, C. & Boyce, M.S. 2014. Quantifying tropical wetlands using field surveys, spatial statistics and remote Sensing. *Wetlands* doi: 10.1007/s13157-014-0524-3.

Scheffer, M. & van Nes, E.H. 2007. Shallow lakes theory revisited: various alternative regimes driven by climate, nutrients, depth and lake size. *Hydrobiologia* 584: 455–466.

Tavares, D.C., Guadagnin, D.L., de Moura, J.F., Siciliano, S. & Merico, A. 2015. Environmental and anthropogenic factors structuring waterbird habitats of tropical coastal lagoons: Implications for management. *Biological Conservation* 186: 12–21.

Väänänen, V.-M. 2001. Hunting disturbance and the timing of autumn migration in Anas species. *Wildlife Biology* 7: 3–9.

van der Valk, A.G., Bremholm, T.L. & Gordon, E. 1999. The restoration of sedge meadows: Seed viability, seed germination requirements, and seedling growth of Carex species. *Wetlands* 19: 756–764.

van der Valk, A.G. & Murkin, H.R. 2002. Changes in nutrient pools during an experimentally simulated wet-dry cycle in the Delta Marsh, Manitoba, Canada. *International Association of Theoretical and Applied Limnology* 27: 3444–3451.

Vicente-Serrano, S.M. & Heredia-Laclaustra, A. 2004. NAO influence on NDVI trends in the Iberian Peninsula (1982–2000). *International Journal of Remote Sensing* 25: 2871–2879.

Wetlands International. 2015. *Waterbird Population Estimates No. 5*. Wetlands International, Wageningen, The Netherlands. Accessible online at wpe.wetlands.org (last accessed 5 November 2015).

Williams, R.A.J. & Peterson, A.T. 2009. Ecology and geography of avian influenza (HPAI H5N1) transmission in the Middle East and northeastern Africa. *International Journal of Health Geographics* 8: 47.

Zeileis, A., Kleiber, C. & Jackman, S. 2007. Regression models for count data in R. Research Report Series / Department of Statistics and Mathematics, 53. Department of Statistics and Mathematics, WU Vienna University of Economics and Business, Vienna, Austria.

Zorn, C.J. 1996. Evaluating zero-inflated and hurdle Poisson specifications. *Midwest Political Science Association* 18: 1–16.

Zuur, A.F., Leno, W.N. & Smith, G.M. 2007. *Analysing Ecological Data*. Springer, New York, USA.