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Modelling wetland habitat preferences of Lewin's Rail *Lewinia pectoralis pectoralis* near Melbourne in southern Victoria

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Abstract. Comparatively little is known of the habitat requirements of the Vulnerable Eastern Australian Lewin's Rail *Lewinia pectoralis pectoralis* and, currently, urban planning possibly overlooks the presence of this, and other, cryptic species of marsh bird. We used logistic regression analysis to identify the preferred habitat attributes of Lewin's Rail, and developed a simple predictive model to assess the suitability of wetland habitats for this species. The 31 sites selected included wetlands where Lewin's Rail was known to have occurred and other wetlands where the species was seemingly absent. We measured landscape variables and fine-scale habitat attributes at each of these wetland sites. We used the information-theoretic approach to model the data and ranked the models based on the second order Akaike's Information Criterion, corrected for small sample size (AIC_c). In general, the best-fit models indicate that low, dense vegetation and the abundance of shrubs in adjoining vegetation are the most useful baseline indicators of the presence of Lewin's Rail. Results suggest that even apparently degraded wetlands in urbanised landscapes can provide habitat for this species. The model provides a means of assessing the likelihood of occurrence of Lewin's Rail at any wetland, and will allow assessment of habitat suitability and potential impacts of disturbance to be made with increased confidence by conservation and urban planners through the identification of specific areas where detailed on-ground survey is warranted.

Introduction

Lewin's Rail *Lewinia pectoralis* is a cryptic species of marsh bird that is widely distributed across Australia, New Guinea, and Flores, Indonesia (BirdLife International 2016). Three subspecies are recognised in Australia: the Western Australian subspecies *L. p. clelandi*, which is regarded as extinct; the Tasmanian subspecies *L. p. brachypus*; and the eastern subspecies *L. p. pectoralis* (Garnett & Crowley 2000; BirdLife Australia 2017). The distribution of the eastern subspecies extends patchily across coastal areas from northern Queensland to south-eastern South Australia, including Kangaroo Island. In Victoria, Lewin's Rail occurs mainly in the south of the state, primarily in central Victoria, from Western Port Bay to western Port Phillip Bay, but also around the Gippsland Lakes and Latrobe Valley in the east and the Otway Ranges and Portland in the west (Marchant & Higgins 1993; Barrett *et al*. 2003).

The eastern subspecies of Lewin's Rail is described as having declined over at least half of its known range in recent decades, and was classified as Near Threatened under *The Action Plan for Australian Birds 2000* (Garnett & Crowley 2000). More recently, knowledge suggested that its range was sufficiently large, and any population decline too slow, to meet threat-assessment criteria, although information on declines was inconsistent (Garnett *et al.* 2011). However, in Victoria, Lewin's Rail is classified as Vulnerable (DSE 2013), and is also listed as threatened under the Victorian *Flora and Fauna Guarantee Act 1988.* Despite its secretive nature, it is probably genuinely rare in Victoria, particularly when compared with the Tasmanian subspecies, which is frequently heard calling (Garnett & Crowley 2000).

The Action Plan for Australian Birds 2000 listed the primary threat to Lewin's Rail as the contraction of habitat through the loss and modification of wetlands and diversion of rivers. Grazing and trampling of wetland vegetation as well as inappropriate burning regimes, and depredation by Red Foxes *Vulpes vulpes* and Cats *Felis catus* were listed as additional threats, which make it prone to localised extinctions. Lewin's Rail is possibly particularly vulnerable during times of drought, when it may be confined to only a few wetland refugia. The extinction of the western subspecies suggests that Lewin's Rail may be more sensitive to changes in habitat than other waterbird species (Garnett & Crowley 2000).

With a human population concentrated in coastal regions, Lewin's Rail is under increasing threat from human pressures in south-eastern Australia. In the Port Phillip and Western Port region, where Victorian records of Lewin's Rail are concentrated (e.g. Emison *et al*. 1987), wetlands are increasingly exposed to pressures from development and other impacts of human disturbance (e.g. Antos *et al*. 2007). In this densely populated region, nearly two-thirds of wetlands have been drained, filled or significantly modified following European settlement (PPWCMA 2004). Considering this loss, it is important that remaining wetland habitats in the region are managed appropriately for the conservation of wetland species.

Understanding the habitat requirements of a species is essential to addressing the threats of habitat loss and modification. Lewin's Rail typically avoids exposure by skulking in dense aquatic or fringing vegetation of wetlands or watercourses, including long, tussocky grasses, reeds, rushes, sedges or shrub thickets (e.g. paperbarks *Melaleuca* spp.). Individuals forage close to cover on soft, exposed mud or in very shallow water, probing for molluscs, worms, crustaceans and insects, and quickly retreat to cover when disturbed (Emison *et al*. 1987; Marchant & Higgins 1993; Garnett & Crowley 2000).

The range of habitats reported for Lewin's Rail is broad, ranging from swamp forest to coastal lagoons and coastal saltmarsh, mangroves, estuaries and tidal channels, through to open water with reeds, rush-filled ditches, drainage channels and farm dams. Permanent wetlands were thought to be favoured, although the species has often been recorded at ephemeral wetlands (Emison *et al*. 1987; Marchant & Higgins 1993; McMahon & Franklin 1993; Quinn & Lacey 1999; Seaman 2003). On rare occasions, it has been recorded far from open water (Emison *et al*. 1987; R.H. Loyn pers. comm.), and on some offshore islands of Australia it inhabits dry, but densely vegetated, habitats (Milledge 1972).

The objective of this study was to develop a predictive model for the occurrence of Lewin's Rail that might allow suitable wetland habitat to be identified, primarily across the Port Phillip and Western Port region (close to the large city of Melbourne, population approaching 5 million). This should allow more accurate assessment of potential impacts on this species of urban developments and other habitat modification or disturbance and more effective targeting of areas for on-ground surveys, such as camera-trapping (e.g. Znidersic 2017).

Methods

Study area

The study area was centred on the Port Phillip and Western Port region of Victoria, although part of this study was undertaken within the adjoining Corangamite region (Figure 1). Covering ~1.28 million ha (5.5 % of Victoria), the Port Phillip and Western Port region is a highly urbanised hub of commercial, industrial and transport infrastructure, as well as an economically important agricultural area for Victoria. It also contains some of the most significant coastal waterbird habitat in Victoria, and supports a high diversity and abundance of waterbirds, particularly during summer when inland wetlands dry out (ANCA 1996). There are >900 wetlands greater than 1 ha in the region, including the tidal flats of Western Port Bay, with a combined area of >40 000 ha (PPWCMA 2004). The Corangamite region covers ~ 1.33 million ha of primarily (70%) agricultural land, although urbanisation is increasing rapidly around regional centres. This region supports ~1400 wetlands greater than 1 ha, covering a total area of 65 000 ha, which includes the Western District Lakes Ramsar wetlands (Harding & Callister 2005).

Site selection

The cryptic nature of Lewin's Rail means that it may be easily overlooked at wetlands where it does occur. To

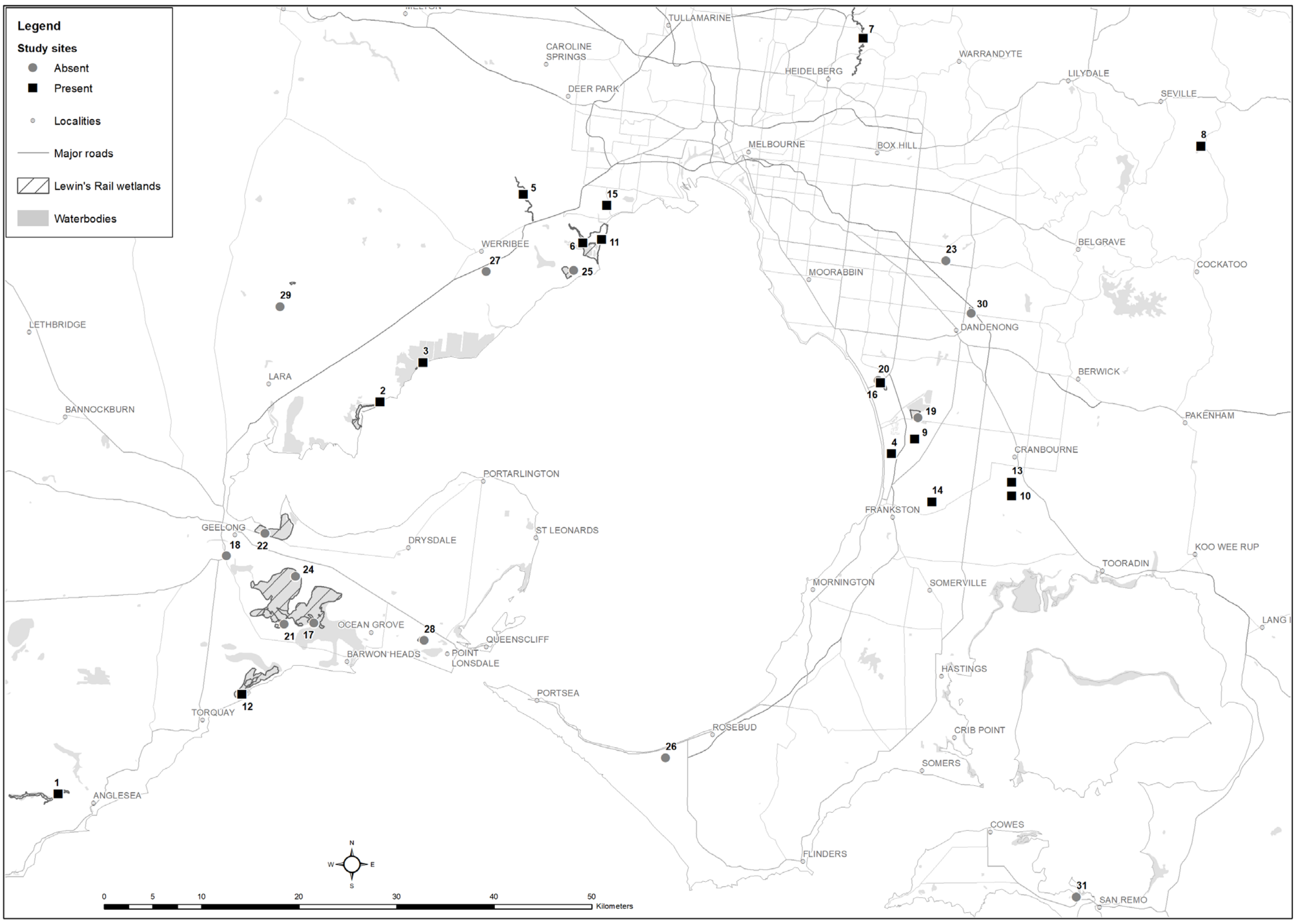

Figure 1. Lewin's Rail 'presence' and 'absence' sites selected for the Port Phillip, Western Port and Corangamite regions of Victoria. See Appendices 1–2.

overcome the problems associated with low detection probabilities, and to avoid the possibility of recording a false 'absence' of this species in the field, we used previously surveyed sites for the measurement of habitat variables. We collated distributional records of crake and rail species in the Port Phillip and Western Port region from the Atlas of Victorian Wildlife (DSE 2007a), BirdLife Australia's Bird Atlas database and Melbourne Water's Wetland database. Additional localities thought likely to provide habitat suitable for Lewin's Rail were selected after discussions with local ornithologists and from unpublished data, including field surveys for this species that we undertook in the region between 2005 and 2007 (Ecology Australia 2005, 2006, unpubl. data). A total of 31 wetlands with a high likelihood of supporting crake or rail species at times was selected (Figure 1, Appendices 1–2). These included 15 sites ('absence' sites) where Lewin's Rail had not been recorded in at least four repeat surveys during which at least two other crake or rail species had been recorded. It is acknowledged that this selection process was biased towards larger, more visited wetlands and that small wetlands in wooded landscapes are likely to be under-represented. Sixteen 'presence' sites were selected at which Lewin's Rail had been recorded one or more times between 2004 and 2008. To ensure independence of data, wetland sites were separated by a minimum distance of 1 km.

Habitat measurements

The selected sites were assessed between October 2007 and February 2008. Habitat variables were recorded at two spatial scales: landscape and site scales. Landscape variables for each site were extracted from Geographic Information System (GIS) data layers (1:250 000). These included wetland size (ha); the area of land covered by other waterbodies within a 5-km radius of the site; the area of urbanised land within a 5-km radius of the site; and the dominant Ecological Vegetation Class (EVC) mapped at the site, as categorised and mapped by the Victorian Department of Sustainability and Environment (DSE 2007b).

Additional site-scale habitat variables were then sampled in the field from within a circular plot of radius 30 m for wetlands and a linear plot 60 m long for waterways, centred as closely as possible on the coordinates for the crake or rail sighting, as given in the databases. Within each plot, we estimated the percentage cover of seven functional vegetation groups: trees, shrubs, ground-cover, and fringing, emergent, submerged and floating vegetation (see Table 1). The percentage cover of each functional vegetation group was estimated visually as a proportion of the total area. Similarly, we estimated the percentage cover of open water, with or without submerged vegetation, and the percentage cover of exposed mud. Several of these habitat parameters vary considerably over time. Our assessments could estimate these parameters only at the time of our site visits and therefore may not represent the wetland at the time that Lewin's Rail was, or was not, recorded. We assumed that our estimates provide some comparative indication of the state of a site's vegetation over the period for which we had rail records.

To obtain a measure of vegetation density and structure, we used a graduated height pole, marked at 10-cm intervals.

Table 1. Definitions used for functional vegetation groups assessed at each of the selected sites in this study.

Functional vegetation group	*Definition*
Ground-cover	Non-woody plants below the shrub-layer
Trees	Woody plants with few stems, taller than 4 m
Shrubs	Multi-stemmed woody plants, up to 4 m in height
Fringing vegetation	Terrestrial plants within 1 m of water's edge
Emergent vegetation	Aquatic plants with foliage growing primarily above water-surface
Submerged vegetation	Aquatic plants with foliage growing below water-surface
Floating vegetation	Aquatic plants with foliage that floats on water-surface

Measurements were taken in four subplots located 15 m apart along a 60-m transect that ran through the centre of the circular or linear plot. Each subplot had a radius of 3 m. Measurements were taken in the four cardinal directions at the 3-m edge of the circular subplot (n = 16). Vegetation structure and density were measured by calculating the number of contacts with vegetation on the measuring pole at four different height intervals: 0–20, 21–50, 51–70 and 71–100 cm above ground- or water-level. The greater the density of vegetation, the greater the number of contacts with the pole. The average of each of the measurements provided a measure of vegetation density and horizontal cover. At each of the four points, we also measured the maximum vegetation height and water depth.

Each wetland was also assigned a wetland type under the classification system of Corrick & Norman (1980), on the basis of depth and duration of inundation and salinity. The degree of fluctuation in water-levels (e.g. tidal influence and stream flows), and therefore inundation and exposure of wetland substratum, was estimated from the location of the site and degree of connectivity to a water source and possible extent of inundation. The substratum was determined by samples taken in the field, and classified as mud, silt, sand, pebble or rock. The presence of seven different degrading factors was assessed at each site: presence of access tracks, eroded banks, evidence of Red Foxes or Cats, altered hydrology, rubbish, cleared buffers and stock grazing.

Statistical analysis

We used logistic regression analysis to model the occurrence of Lewin's Rail, using the presence or absence of this species at a site as the dependent variable and the landscape and site habitat variables as predictors. Logistic regression assumes that data are binomially distributed and that, if there are more than two predictor variables, there will not be a significant correlation between them (Quinn & Keough 2002). We calculated bivariate correlation coefficients for the variable matrix, to explore co-linearity

Table 2. Types of wetlands and watercourses at which Lewin's Rail has been recorded in the Port Phillip, Western Port and Corangamite regions of Victoria, and the Ecological Vegetation Classes (EVCs) in which the individual was recorded. The EVCs include the newly expanded and refined typologies for Victorian saltmarsh communities recognised by Boon *et al.* (2011).

Wetland category/watercourse	*EVCs*
Permanent Saline	Wet Saltmarsh Shrubland (Shrubby Glasswort *Tecticornia arbuscula* shrubland)
Freshwater Meadow	Tall Marsh, Aquatic Herbland
Deep Freshwater Marsh	Swampy Riparian Woodland
Permanent Open Freshwater	Swamp Scrub, Aquatic Sedgeland, Tall Marsh
Semi-permanent Saline	Wet Saltmarsh Shrubland (Shrubby Glasswort shrubland)
Shallow Freshwater Marsh	Tall Marsh, Riparian Scrub
River	Riparian Scrub, Brackish Wetland, Tall Marsh, former Riparian Forest
Creek	Brackish Wetland, Tall Marsh

and reduce the number of candidate variables for the models. Where two variables were significantly correlated, we eliminated the variable that made the least biological sense from subsequent analyses. Statistical significance was determined at the 5% level.

Modelling was based on the information-theoretic approach, as described by Burnham & Anderson (2002), which provides a rational alternative to null hypothesis testing. Rather than selecting a single best model, the information-theoretic approach acknowledges that all models are simplistic representations of reality and thus all are wrong to varying degrees. Instead, there are several well-supported hypotheses, represented by the models (Anderson *et al*. 2000; Burnham & Anderson 2002).

All possible subsets of the six predictor variables were modelled and then ranked according to Akaike's Information Criterion corrected for small sample size (AIC_c). Rankings are based on both the weight of evidence in favour of each model (ω_i), and an estimate of the relative distances between each model and the true, unknown relationships. Model selection was based on best inference, given the data. In addition, we generated 5000 bootstrap samples to test each model. By sampling with replacement from the original data, this method calculates the frequency with which each model is selected as the best fit (returns the lowest AIC_c value). The percentiles provide a measure of relative support for alternative models that are robust to the effects of sampling error in the original data (Burnham & Anderson 2002).

When no single model is clearly superior (maximum $\omega_i \leq 0.9$), Burnham & Anderson (2002) recommended model averaging, a model selection process that accounts for uncertainties because of model structure, by averaging over all possible models and combining information from the entire set of candidate models. Using the weighted averages allows formal inferences to be made from more than one model (a multi-model inference approach). Model averaging reduces bias and provides more precision in predictive models when compared with the originally selected models (Burnham & Anderson 2002).

We used hierarchical partitioning to examine the independent contributions of each variable to variation in the data (Mac Nally 2000), and compared the final sets of predictor variables selected from the information-theoretic approach and the hierarchical partitioning approach.

We used a Receiver Operating Characteristic (ROC) curve to assess the predictive performance of the model-averaged equation. The technique creates a curve of true-positive cases (or sensitivity) on the *y*-axis against corresponding false cases (or 1-specificity) on the *x*-axis, across a range of threshold values (Fielding & Bell 1997). The area under the curve (AUC) provides a measure of the model's discriminatory ability, where 0.5 is no better than random and 1.0 is perfect. The calculation of the AUC and standard error was based on a non-parametric assumption.

Data analyses were run in the *R* computing environment (Ihaka & Gentleman 1996) using algorithms to calculate AIC_c, bootstrap frequencies and model-averaged outputs of standard error (M. Scroggie, Arthur Rylah Institute for Environmental Research, unpubl. data), and to run the hierarchical partitioning (Walsh & Mac Nally 2003). Correlation analyses and the ROC curve were carried out in SPSS v 11.5 (SPSS 1998).

Results

Table 2 lists the types of wetlands and the EVCs for 'presence' sites where Lewin's Rail has been recorded in the Port Phillip, Western Port and Corangamite regions.

Given the relatively small number of sites surveyed (n = 31), only a limited number of predictor variables could be used in the modelling to avoid over-fitting the data and biasing the modelling (Harrell 2001; Burnham & Anderson 2002). Following preliminary analyses, we selected six variables to construct the models: number of vegetation contacts between 0 and 20 cm on the graduated height pole, percentage cover of fringing vegetation, percentage cover of exposed mud, percentage cover of shrubs, area of water (ha) within a 5-km radius of the site, and the number of degrading factors.

Four candidate models were identified as the best approximating models (with AIC_c differences <2), from a set of 63 possible models (Table 3). According to Burnham & Anderson (2002), models with AIC_c differences between 0 and 2 have substantial support, differences between 4 and 7 have considerably less, but models with differences

Table 3. Ranking of the four best models for predicting the presence of Lewin's Rail based on Akaike's Information Criterion corrected for small sample size (AIC_c) and showing the maximised log-likelihood function [*log (L)*], number of predictor variables (*K*), AIC_c, AIC_c differences (Δ_i), Akaike weights (ω_i), bootstrap selection frequencies (π_i) and goodness of fit (R^2). The variables in the models are T = number of vegetation touches on the graduated pole between 0 and 20 cm, S = percentage cover of shrubs, D = number of degrading factors, W = area of water within 5 km of the record (ha), and M = percentage of exposed mud.

Rank	*Model*	*Log (L)*	*K*	AIC_c	Δ_i	ω_i	π_i	R^2
1	T + S	–14.13	3	35.14	0.0000	0.1387	0.144	0.25
2	T + S + D	–12.99	4	35.53	0.3844	0.1145	0.113	0.28
3	T + S + W	–13.66	4	36.87	1.7223	0.0586	0.010	0.28
4	T + S + M	–13.76	4	37.06	1.9127	0.0533	0.039	0.27

>10 have virtually no support in terms of explaining the variation in the data. Table 3 shows the maximised log-likelihood values, number of predictor variables, AIC_c values, AIC_c differences, relative Akaike weights, bootstrap frequencies and goodness of fit for the four models for which there was considerable support.

The models in Table 3 are ranked according to their AIC_c differences, from most favoured (1) to least favoured (4), as it is the relative not absolute size of AIC_c values that are important (Burnham & Anderson 2002). Model 1 is the most supported of the four models as it has the lowest AIC_c difference (Δ_i = 0.0000). Of the 5000 bootstrap samples generated, Model 1 was selected as the best fit 14.4% of the time (π_i = 0.144), and Model 2 as the best fit 11.3 % of the time (π_i = 0.113).

Model 1 has the variables of number vegetation contacts on the graduated pole at 0–20 cm and percentage cover of shrubs. These two variables were common to all four supported models. Models 2–4 are close to the best approximating model, with AIC_c differences <2, demonstrating substantial support, as they contain a third added variable rather than being competitive. This is illustrated by the similarity of the log-likelihood values of the four models (Table 3). These results indicate that model averaging was appropriate, as no one model was clearly the best (maximum ω_i <0.9). Burnham & Anderson (2001) suggested that when a certain parameter is common across models or when the goal of the modelling is prediction, model averaging should also be conducted. The model-averaged logistic regression coefficients are given in Table 4, together with unconditional standard errors (not conditional on any particular model) and conditional standard errors (conditional on the most supported model, i.e. Model 1). Unconditional standard errors are calculated by multiplying the conditional sampling variances from each model by their Akaike weights (Burnham & Anderson 2001).

Overall, small differences in the conditional and unconditional standard errors show good support for the four best models out of all the candidate models. The comparatively high unconditional standard error of variable *D* (degrading factors) demonstrates some uncertainty on the true effects of this variable on the dependent variable. Unconditional standard errors better reflect the precision of model coefficients (Burnham & Anderson 2002), because the variance from model selection uncertainty has been included, following model averaging (Burnham & Anderson 2001).

Hierarchical partitioning analysis showed that both the number of vegetation touches on the graduated pole between 0 and 20 cm and the percentage cover of shrubs made significant independent contributions towards explaining variation in the dependent variable, based on 100 randomisations (Table 5). This result is

Table 4. Model-averaged coefficients, unconditional standard errors, and standard errors conditional on the best model (Model 1) for each variable for predicting the occurrence of Lewin's Rail. Variables are: W = area of water within 5 km of the record (ha), M = percentage of exposed mud, T = number of vegetation touches on the graduated pole between 0 and 20 cm, F = percentage cover of fringing vegetation, S = percentage cover of shrubs, and D = number of degrading factors.

Variable	*Coefficient*	*Standard error*	
		Unconditional	*Conditional*
Constant	–2.5663	2.7411	2.1344
W	–0.0003	0.0013	0.0006
M	0.0234	0.0532	0.0387
T	0.2881	0.2221	0.2056
F	–0.0046	0.0172	0.0103
S	0.0544	0.0408	0.0343
D	0.3215	0.7002	0.4832

Table 5. Results of hierarchical partitioning, showing the independent contributions, *z*-scores and significance levels based on the upper 0.95 confidence limit in the model for predicting the occurrence of Lewin's Rail. The variables are: W = area of water within 5 km of the record (ha), M = percentage of exposed mud, T = number of vegetation touches on the graduated pole between 0 and 20 cm, F = percentage cover of fringing vegetation, S = percentage cover of shrubs, and D = number of degrading factors; significance levels: * = significant at the 0.05 level, ns = not significant.

Variable	*Contribution*	*z-score*	*Significance*
W	6.836	–0.4232	ns
M	7.809	0.6161	ns
T	35.478	1.4010	*
F	4.028	–0.4464	ns
S	38.488	1.5856	*
D	7.361	0.6653	ns

consistent with the information-theoretic approach, where these two variables alone constituted the best model and were common in the next best three models, which had considerable support in terms of explaining variation in the data. The percentage cover of shrubs made the largest contribution to variation in the data.

The area under the ROC curve was 0.75 ± 0.09 for the most supported model, suggesting that the model correctly discriminated between the presence and absence of Lewin's Rail 75% of the time. Values of 0.7–0.9 have useful applications in predicting habitat suitability (Manel *et al*. 1999).

The logistic regression equation of the selected best model is:

$$Y = 0.2881(T) + 0.0544(S) - 2.5663$$

where Y = the linear predictor, T = number of vegetation touches on the graduated pole between 0 and 20 cm, S = percentage cover of shrubs, and probability of Lewin's Rail occurrence = e (Y) / (1 + e (Y))

Discussion

The best-supported habitat models developed here indicate that dense vegetation and a high cover of shrubs increase the probability of encountering Lewin's Rail at a wetland. Vegetation density up to 20 cm above the ground and percentage cover of shrubs were found to be the best indicators of presence as shown by both logistic regression and hierarchical partitioning analyses. Our findings concur with those of Gibson (2017), who found that high levels of lateral cover (a measure reflecting vegetation density), particularly by long grasses, with a canopy up to 0.6 m above ground were the main factors influencing habitat selection by Lewin's Rail in Brisbane, Queensland. Although Gibson (2017) found this species to be associated generally with tall grasses and reeds, she also reported it at sites with a very different composition of plant species but similar levels of lateral cover. Thus wetlands and watercourses with little shrub cover, but where tall grasses, reeds, sedges and/or rushes may perform a similar function, should not be totally discounted as suitable habitat for Lewin's Rail.

The findings of the present study are also consistent with studies of habitat use by a related species, the New Zealand Auckland Rail *Lewinia muelleri*, which occurs in vegetation types associated with wet or damp ground, and with a dense canopy up to 1 m off the ground and open 'runways' beneath (Elliott *et al*. 1991). Most sites where Lewin's Rail has been recorded also have dense vegetation with open runways or clear spaces at ground-level.

Weller & Spatcher (1965) first suggested that a bird's mode of locomotion may determine its distribution in the horizontal vegetation strata. Lewin's Rail, a ground-dwelling bird that rarely flies and instead darts into cover to escape danger, requires a vegetation structure that provides protection from predators as well as facilitating movement on the ground. The vegetation communities where it was found in the present study—including Wet Saltmarsh Shrubland, Tall Marsh, Swampy Riparian Woodland, Swamp Scrub and Riparian Scrub EVCs—have these attributes of dense cover and open runways.

Similar findings have been made in western New York State, United States of America (USA), where habitat modelling indicated that large areas of emergent vegetation (~70% cover) and 'horizontal' vegetation cover, together with shallow water, improved the chances of encountering nesting marsh birds (Lor & Malecki 2006).

The occupancy of wetlands by marsh birds, such as Lewin's Rail, is also likely to vary in response to temporal fluctuations in wetland condition. A study of marsh birds at 475 sites across the Lake Ontario–St Lawrence River system of the USA and Canada found that water-levels influenced the presence of the Virginia Rail *Rallus limicola* (Desgranges *et al*. 2006). Based on our current knowledge of Lewin's Rail, water-level probably also has a strong influence on habitat suitability for this species. Lewin's Rail forages on mudflats and in soft mud amongst vegetation or in shallow water (<5 cm deep) (Marchant & Higgins 1993), and the cover of exposed mud tends to increase with shallow water. Marchant & Higgins (1993) suggested that wetlands with fluctuating water-levels, and periodically exposed mudflats, may be favoured, and our fourth supported model (AIC_c difference <2) shows some support for this, although the full influence of this variable might not have been realised because we used past records of Lewin's Rail to measure habitat attributes. As the exposure of mudflats is likely to vary over time, the levels of exposed mud might have made a greater contribution to the modelling if it had been measured at the time of sighting of the bird. Some habitats occupied by Lewin's Rail are subject to regular or frequent fluctuations in water-levels associated with tidal inundation, fluctuating streamflows or wetting (e.g. saltmarsh communities, stormwater-fed wetlands and watercourses with Tall Marsh).

Contrary to what would be expected, the second supported model for Lewin's Rail contained the number of degrading factors as a third added variable, in a positive sense. This may reflect the heavily populated nature of the region which, despite ongoing human pressures, continues to support threatened waterbirds in urban areas (e.g. Plenty River, Montmorency, and Skeleton Creek at Altona and Hoppers Crossing). It is possible that the presence of access tracks to many wetland sites might have been a bias with this habitat attribute. The cryptic nature of the species means that it is regularly overlooked during routine fauna surveys, and this is reflected in the low reporting rate in Victoria (Emison *et al*. 1987; Barrett *et al*. 2003). Visibility and survey effort are likely to be higher at more-accessible sites. However, there is no reason to suspect that detection of Lewin's Rail would differ between sites within the Port Phillip and Western Port region. Degraded areas, which are often weedy, may provide the densely structured vegetation that it requires. Our results confirm that wetlands in urbanised or degraded areas should not be disregarded as potential habitat.

There was no significant relationship between the presence of Lewin's Rail and the area of water within 5 km of the study site, which was also confirmed by the hierarchical partitioning analysis (Table 5). This result might have been heavily influenced by the Lonsdale Lakes complex, which comprised some of our study sites (e.g. Reedy Lake, Lake Connewarre, Hospital Swamp). There might have been other unassessed reasons for the apparent absence of this species from this diverse group of adjacent sites.

The sixth variable applied to the logistic regression (percentage cover of fringing vegetation) was not included in any of the four best models. This is surprising, given that Lewin's Rail is considered to spend most of its time skulking amongst fringing vegetation (Marchant & Higgins 1993). There was little relationship between this variable and the presence of this species (Table 5). The much stronger relationship with vegetation density and percentage of shrub cover indicates that, overall, 'horizontal' or lateral cover may be more important than the total amount of fringing vegetation.

Our study revealed low dense vegetation at 20 cm above ground to be the main indicator of wetland habitat suitability for Lewin's Rail. The information-theoretic approach and hierarchical partitioning both agreed on which variables to retain in the final model (vegetation contacts between 0 and 20 cm and percentage cover of shrubs). This suggests that these are both biologically meaningful variables.

Additional variables influencing habitat suitability are certain to exist; however, the small sample size (16 'presence' and 15 'absence' sites) restricts the number of variables that can be used in the modelling process (e.g. Harrell 2001). A larger number of 'presence' sites would be required to explore a greater number of variables (Burnham & Anderson 2001). The shortage of sites at which Lewin's Rail has been recorded, because of its cryptic habits and rarity, was a major limitation of our study, and is one of the main difficulties of habitat modelling for threatened species.

This model represents a first step towards better understanding the wetland habitat requirements of Lewin's Rail. However, work is needed to further explore additional variables and possible differences in habitat use for breeding and foraging. As demonstrated by the four models, there may be other factors that influence wetland use on a temporal scale, depending on environmental conditions and resource availability. The presence of Lewin's Rail at some wetlands is likely to be sporadic in response to wetland condition and resource availability. Few wetlands seem likely to meet all the needs of this species at any one time, and the birds probably move between a variety of wetlands to satisfy all of their requirements.

In regions subject to the increasing pressures of urbanisation and land-use intensification, the conservation of Lewin's Rail depends on identifying conflicts between proposed developments and maintaining suitable habitat. Although models are invariably incomplete representations of reality, for rare species models provide useful baseline indicators that can allow assessments of habitat suitability to be made more confidently, in the absence of other data. Our model provides a means to identify locations for follow-up surveys using effective field-survey techniques such as call-playback (see Ecology Australia 2005, 2006) or camera-traps (Znidersic 2017; M. Antos, Parks Victoria, pers. comm.).

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Appendix 1. Wetland sites selected for survey where Lewin's Rail had been previously recorded ('presence' sites); area of each site (ha); wetland category; Ecological Vegetation Classes (EVCs) and salinity at the survey sites. EVCs were as assigned by the Department of Sustainability and Environment (DSE 2007b) and verified in the field, and include the new typologies for the former Coastal Saltmarsh (aggregate) EVC, recognised by Boon *et al.* (2011). Species recorded: LR = Lewin's Rail *Lewinia pectoralis pectoralis*, BR = Buff-banded Rail *Hypotaenidia philippensis*, ASC = Australian Spotted Crake *Porzana fluminea*, BC = Baillon's Crake *Zapornia pusilla*, and SC = Spotless Crake *Z. tabuensis*. NA = not applicable. See Figure 1 map.

Site (and map no.)	*Area*	*Wetland category*	*EVCs*	*Salinity*	*Species recorded*
1. Salt Creek, Anglesea Estate Heathlands	125.8	NA (creek)	Riparian Scrub	Freshwater	LR
2. The Spit Nature Conservation Reserve	107.9	Permanent Saline	Wet Saltmarsh Shrubland (Shrubby Glasswort *Tecticornia arbuscula* shrubland)	Saline	LR, ASC
3. Wetland at Little River Bird Hide, Western Treatment Plant	6	Permanent Saline	Wet Saltmarsh Shrubland (Shrubby Glasswort shrubland)	Saline	LR, ASC, SC
4. Seaford Swamp (zone 1), Edithvale–Seaford Wetlands	6.7	Freshwater Meadow	Tall Marsh	Freshwater, brackish at low levels	LR, BR, ASC, BC, SC
5. Skeleton Creek, Hoppers Crossing	15.6	NA (creek)	Brackish Wetland, Tall Marsh	Brackish	LR, ASC, SC
6. Skeleton Creek, Altona Meadows	46.2	NA (creek)	Brackish Wetland, Tall Marsh	Brackish	LR, ASC
7. Plenty River, Montmorency	19	NA (river)	Formerly Riparian Forest	Freshwater	LR
8. Cockatoo Swamp, Yellingbo Nature Conservation Reserve	170	Deep Freshwater Marsh	Swampy Riparian Woodland–Mountain Swamp Gum *Eucalyptus camphora* Swamp Community	Freshwater	LR, SC
9. Banyan Swamp, Bangholme	10.7	Freshwater Meadow	Wetland Formation	Freshwater	LR
10. Wylie's Creek Wetland, Royal Botanic Gardens (south), Cranbourne	1.2	Permanent Open Freshwater	Aquatic Sedgeland, Swamp Scrub	Freshwater	LR
11. Cheetham Wetlands, Point Cook	447.2	Permanent Saline	Wet Saltmarsh Shrubland (Shrubby Glasswort shrubland)	Saline	LR, ASC
12. Point Impossible	NA	Semi-permanent Saline	Wet Saltmarsh Shrubland (Shrubby Glasswort shrubland)	Dry	LR, ASC
13. Heathland patch, Royal Botanic Gardens (north), Cranbourne	NA	NA (heath)	Heathy Woodland, Grassy Woodland	NA	LR
14. Tamarisk Reserve	1	Shallow Freshwater Marsh	Tall Marsh	Freshwater	LR
15. Mount St Joseph Wetland, Altona	0.5	Permanent Open Freshwater	Tall Marsh	Freshwater	LR, BR, ASC, BC, SC
16. Edithvale South (zone 2), Edithvale–Seaford Wetland	31.6	Freshwater Meadow	Aquatic Herbland	Freshwater	LR, BR, ASC, BC, SC

Appendix 2. Wetland sites selected for survey where Lewin's Rail had not been recorded but at least two other crake or rail species had been recorded ('absence' sites); area of each site (ha); wetland category; Ecological Vegetation Classes (EVCs) and salinity at the survey sites. EVCs were as assigned by the Department of Sustainability and Environment (DSE 2007b) and verified in the field, and include the new typologies for the former Coastal Saltmarsh (aggregate) EVC, recognised by Boon *et al.* (2011). Species recorded: LR = Lewin's Rail *Lewinia pectoralis pectoralis*, BR = Buff-banded Rail *Hypotaenidia philippensis*, ASC = Australian Spotted Crake *Porzana fluminea*, BC = Baillon's Crake *Zapornia pusilla*, and SC = Spotless Crake *Z. tabuensis*. NA = not applicable. See Figure 1 map.

Site (and map no.)	*Area*	*Wetland category*	*EVCs*	*Salinity*	*Species recorded*
17. Lake Connewarre	987.2	Semi-permanent Saline	Estuarine Wetland/Wet Saltmarsh Shrubland (Marsh Saltbush *Atriplex paludosa* shrubland)/ Coastal Saline Grassland (Australian Salt-grass *Distichlis distichophylla* grassland) Mosaic	Saline	BR, ASC
18. Jerringot Wetland, Belmont Common	2	Deep Freshwater Marsh	Floodplain Riparian Woodland	Freshwater	BR, ASC, BC, SC
19. Emergency Holding Basin, Eastern Treatment Plant	70.3	Sewage Ponds	Wetland Formation (artificial)	Freshwater	BR, ASC, BC, SC
20. Edithvale North (zone 5), Edithvale–Seaford Wetlands	2	Freshwater Meadow	Aquatic Herbland	Freshwater, brackish at low levels	ASC, BC, SC
21. Hospital Swamp	124.3	Shallow Freshwater Marsh	Tall Marsh/Brackish Wetland Mosaic	Freshwater, brackish at low levels	BR, ASC, BC, SC
22. Cheetham Saltworks, Moolap	448.6	Saltworks	Wet Saltmarsh Shrubland (Shrubby Glasswort shrubland)	Saline	BR, ASC
23. Mulgrave Reserve Wetlands, Wheelers Hill	2.7	Shallow Freshwater Marsh	Swampy Riparian Woodland	Freshwater	BR, ASC, BC, SC
24. Reedy Lake	1491.4	Deep Freshwater Marsh	Reed Swamp, Coastal Saltmarsh/Mangrove Shrubland Mosaic	Freshwater	BR, ASC, BC
25. RAAF Lake, Point Cook Coastal Park	88.4	Semi-permanent Saline	Coastal Hypersaline Saltmarsh (*Tecticornia pergranulata* shrubland)	Dry	ASC, SC
26. Tootgarook Wetlands	1.9	Deep Freshwater Marsh	Aquatic Sedgeland, Tall Marsh, Swamp Scrub	Freshwater	BR, ASC, BC, SC
27. Channel at Werribee Open Range Zoo	0.4	NA (artificial channel)	Floodplain Riparian Woodland	Freshwater	BR, ASC, BC, SC
28. Freshwater Lagoon	26.9	Semi-permanent Saline	Coastal Saline Grassland (Australian Salt-grass grassland)/Wet Saltmarsh Herbland (Beaded Samphire *Sarcocornia quinqueflora* sub-shrubland)/Coastal Tussock Saltmarsh (Chaffy Saw-edge *Gahnia filum* sedgeland) Mosaic	Saline	ASC, SC
29. Barros Pit, You Yangs Regional Park	7.6	Shallow Freshwater Marsh	Wetland Formation (artificial)	Freshwater	BR, ASC, SC
30. Healthy Bay Wetlands, Mulgrave	12.3	Shallow Freshwater Marsh	Tall Marsh, Aquatic Herbland	Freshwater	BR, BC
31. Fisher's Wetland, Phillip Island	10	Semi-Permanent Saline	Brackish Aquatic Herbland, Estuarine Wetland, Swamp Scrub	Brackish	BR, ASC