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# Fine-scale selection of nesting habitat in Little Crake *Porzana parva* and Water Rail *Rallus aquaticus* in small ponds

JAN JEDLIKOWSKI<sup>1\*</sup>, MATTIA BRAMBILLA<sup>2,3</sup> and MAŁGORZATA SUSKA-MALAWSKA<sup>1</sup>

<sup>1</sup>Faculty of Biology, Biological and Chemical Research Centre, University of Warsaw, Żwirki i Wigury 101, 02-089 Warszawa, Poland; <sup>2</sup>Fondazione Lombardia per l'Ambiente, Settore Biodiversità e Aree protette, Largo 10 luglio 1976 1, I-20822 Seveso, MB, Italy; <sup>3</sup>Museo delle Scienze, Sezione Zoologia dei Vertebrati, Corso della Scienza e del Lavoro 3, I-38123 Trento, Italy

**Capsule** The most important factor determining fine-scale selection of nesting habitat in Little Crake and Water Rail is water depth.

**Aims** To evaluate factors affecting nest-site selection and relative inter-specific differences in two poorly studied Rallidae species, the Little Crake and Water Rail.

**Methods** Habitat variables describing water depth, water cover, as well as vegetation type and structure were measured within 3-m radius plots around birds' nests and random points, located in small ponds scattered within a largely cultivated landscape in north-eastern Poland. Descriptive statistics and multi-adaptive regression splines were used to describe nesting habitat and to model nest-site selection in the study species.

**Results** Little Crake nested in sites with deeper water and lower percentage of vegetation cover than Water Rail. Both species chose nest sites according to water depth (probability of Little Crake nests occurrence was the highest around 40 cm and of Water Rail below 12 cm) and vegetation stage in which nests were build (old vegetation was preferred). Little Crake nests were also associated with vegetation height lower than 1.5 m and high percentage cover of old vegetation within a 3-m radius around nests, whereas Water Rail preferred *Carex* spp. and *Juncus effusus* for nesting.

**Conclusion** For both species, water depth was the main driver of nest-site selection, followed by vegetation traits. Water depth was also the variable most important in discriminating between the nesting sites of the two species. The different patterns of habitat selection showed by the two species are likely to be due to different morphology and nest characteristics, and are probably driven by the need to maximize both nest and adult safety.

Habitat selection is the process determining the choice of a particular habitat amongst others available (Patridge 1978), and is often considered as a hierarchical process (Hutto 1985, Saab 1999, Harvey & Weatherhead 2006). Different environmental features (food availability, vegetation structure and social factors) may be responsible for habitat selection at different levels (Burger 1985, Anderson *et al.* 2005, Mayor *et al.* 2009). In birds, during the breeding season, the final step in this hierarchical process is the selection of the nest site, after more general choices at the landscape and territory level (Jones & Robertson

2001, Martinez *et al.* 2003, Bailey & Thompson 2007). In many species, the most important factor for nest-site selection seems to be the vegetation structure in close proximity to the nest (Burger 1985, Orians & Wittenberger 1991). Because for most birds, the main cause of nest failure is predation (Ricklefs 1969), it has been posited that birds choose their nest sites according to the vegetation structure, which has a direct influence on the probability of nest detection by predators, and thus on brood survival (Møller 1989, Martin 1993, Sieving & Willson 1998, Liebezeit & George 2002, Baxter *et al.* 2009).

This study focuses on the nest-site selection process of two marsh-nesting bird species belonging to the Rallidae

\*Correspondence author. Email: [janjedlikowski@biol.uw.edu.pl](mailto:janjedlikowski@biol.uw.edu.pl)

family, the Little Crane *Porzana parva* and the Water Rail *Rallus aquaticus*. Members of this family are specially adapted to live and move smoothly in dense vegetation with their laterally compressed body and relatively long legs and toes (Del Hoyo *et al.* 1996, Taylor & Van Perlo 1998). This high specialization may influence the preferences and selection of particular vegetation types and structure in the breeding site in contrast to other waterbirds. Both Little Crane and Water Rail occupy a wide range of freshwater, usually eutrophic wetlands (natural and semi-natural), with fairly tall and dense aquatic vegetation (Cramp 1980, Taylor & Van Perlo 1998). A few recent studies have investigated landscape and spatial determinants of Water Rail occurrence or abundance (Jenkins & Ormerod 2002, Brambilla & Rubolini 2004, Brambilla *et al.* 2012), but small-scale nest-site preferences of both species are poorly known (Schiermann 1929, Kux 1959, De Kroon 2000, De Kroon & Mommers 2002, De Kroon 2004), although water depth at nest sites has been reported to vary between the two species, with Water Rail nesting in shallower places than Little Crane (Bauer 1960). Nevertheless, virtually no study has quantitatively analysed which habitat features are most likely to drive nest-site selection in these two secretive species.

The aim of the present study was thus (1) to describe the habitat factors within a 3-m radius plot around birds' nests (related to water depth and cover, vegetation structure, type and cover) affecting nest-site selection and (2) to investigate whether the fine-scale nest-site preferences of Little Crane and Water Rail overlap or differ.

## METHODS

### Study area

The study was conducted in north-eastern Poland (the Mazurian Lake District), within a typical young post-glacial landscape, characterized by a large number of lakes and by many small inland water bodies (ponds). Until the 1990s, intensive agricultural practices were carried out in this area, which resulted in the draining of many of these wetlands. After the State Agricultural Farms collapsed in 1993, land-use practices changed and many fields were abandoned. Due to the lack of conservation of drainage channels, many small midfield water bodies started to recover in natural depressions. These changes were reinforced by the implementation of water retention and by the

increasing abundance of Eurasian Beavers *Castor fiber* in this region in last two decades (Czech 2010), which has resulted in an increase in flooded sites and ponds.

Data were collected at 20 unnamed water bodies distributed at 53°48'–53°53' N and 21°34'–21°44' E. The area of these water bodies varied from 0.1 to 10.6 ha (mean 2.58 ha), the average depth was usually less than 2 m and water acidity pH ranged from 6.3 to 8.2 (mean 7.11). Most of the ponds were located in depressions filled by organic sediments, mainly peat. The vegetation of the littoral zone was typical for early stages of development. Most of the ponds were strongly dominated by typical hydrophytes such as *Typha* spp., Common Reed *Phragmites australis* and *Carex* spp., with some clumps of Grey Willow *Salix cinerea*. Water bodies were surrounded by agricultural (arable fields, meadows and pastures) or post-agricultural (fallow) lands.

### Data collection

Data were collected from mid-April to the end of July in 2011–2013 by the same observer (J.J.). During these three breeding seasons, nests of Little Crane and Water Rail were searched for and habitat variables were measured around the nests and at the random points in the study area.

The high vocal activity of both species during the breeding season is helpful in estimating rail density and in finding nests (Taylor & Van Perlo 1998). Along the shore line of each water body, birds were stimulated every 50 m (Dombrowski *et al.* 1993) with a playback of their voices in the periods of their highest vocal activity, usually before sunrise and before sunset (Polak 2005, Brambilla & Jenkins 2009). To stimulate birds, we used 30-second long sequences of the announcement call of male Water Rails and of the advertising call of male Little Crakes (Cramp 1980). If birds responded to the vocal stimulation the site was marked on a 1:10000 map. If there was no response within 2 minutes, the stimulation was repeated. Monitoring was conducted every 10–14 days in each site (from mid-April to the end of June) and after confirming that birds responded from the same place during two consecutive controls, the vegetation around the marked places was systematically and carefully investigated. The position of each nest was marked using a handheld GPS receiver (Topcon GRS-1; accuracy less than 0.5 m). Also the stage of the nests was assessed at the time of finding (egg laying,

incubating or nestling period), and the size of the clutch was also checked seven days later.

At each nest site and in a corresponding random point, 16 different habitat variables were recorded. The 'Random points' tool in QGIS 1.8.0 software was used to choose random points and a handheld GPS receiver to find them in the field. The random points were chosen separately for Little Crake and Water Rail in the littoral vegetation at the same water bodies as the birds' nests (for each pond, the number of random points equalled the number of nests for each species). Habitat variables were measured in a circular plot, defined as a 3-m radius around the nest or the random point (nest-site plots and random plots, respectively). The minimum distance between a nest and random point or among neighbouring random points was 6 m, so as to avoid non-independent variable recording due to plot overlap.

At nest-site and random plots the following habitat variables were measured: water depth at the centre of the plot (estimated with 1 cm precision), mean water depth (average value from ten randomly selected points within the plot), standard deviation for water depth, height of emergent vegetation at the centre of the plot (estimated from the water surface with 5 cm precision), mean vegetation height from ten randomly selected points within the plot and standard deviation for vegetation height. Emergent vegetation around nests and random points was identified to particular species, and the stage of vegetation growth was assigned to one of three categories: new (fresh vegetation), old (1 or more year-old vegetation) or mixed (old with new vegetation). The main plant species used as nest material was recorded in all nests. In each plot, the proportional area covered by new and old vegetation, and by open water was recorded. Percentage cover values were estimated with 5% precision. Old and new vegetation cover was estimated separately, because both covers usually overlap in clumped littoral vegetation (new vegetation growing over the old from the same clump). The proportional cover of the following vegetation categories was also determined (with 5% precision) at the nesting-site plots and in random plots: *Typha* spp. (Bulrush *Typha latifolia* and Lesser Bulrush *Typha angustifolia*), Common Reed, *Carex* spp. (mainly Lesser Pond-sedge *Carex acutiformis* and Greater Pond-sedge *Carex riparia*), Soft-rush *Juncus effusus*, Water-plantain *Alisma plantago-aquatica*, Reed Sweet-grass *Glyceria maxima*, Reed Canary-grass *Phalaris arundinacea*, Sweet-flag *Acorus calamus*, Wood Club-rush *Scirpus*

*sylvaticus*, Amphibious Bistort *Persicaria amphibia*, Yellow Iris *Iris pseudacorus*, Water Horsetail *Equisetum fluviatile*, dicotyledon herbs (mainly Skullcap *Scutellaria galericulata*, Bittersweet *Solanum dulcamara* and Gypsywort *Lycopus europaeus*) and Grey Willow. Using these categories, the dominant vegetation was assessed within each plot and habitat heterogeneity was estimated according to Shannon diversity index ( $H = -\sum p_i \ln p_i$ , where  $p_i$  is the proportion of the  $i$ th vegetation category within the nest or the random plot; Magurran 2004). Finally, the distances from the nest sites or the random points to the nearest shore, open water and Grey Willow shrub were measured (with 1 m precision), using QGIS 1.8.0 software and satellite photographs.

### Statistical analyses

Multi-adaptive regression splines (MARS) were used to model habitat association in the study species, relating their occurrence to the set of environmental variables listed above. MARS is a recent machine-learning technique (Friedman 1991, Hastie *et al.* 2009), and thanks to its flexibility and ability to model non-linear relationships (Elith & Leathwick 2007), MARS is now increasingly used in ecology (Leathwick *et al.* 2005, Mac Nally *et al.* 2008, Heinanen & von Numers 2009, Brambilla & Gobbi 2014). This regression method fits non-linear functions by fitting linear segments (or piecewise linear basis functions) to the data, breaking predictors at knots, allowing the slope of segments to vary between knots and connecting adjacent segments at knots, thus keeping the full fitted function without gaps or steps. Model fitting is achieved by a forward procedure that identifies many potential predictors and knots, on the basis of a specified increase in model performance (the 'threshold'), followed by backward pruning that reduces the number of predictors and knots on the basis of a penalty value.

Prior to multivariate analyses, variable correlations were checked. Although variable autocorrelation has been reported to be less problematic for machine-learning than for statistical methods, it may still affect models (Merow *et al.* 2013) and in particular the interpretation of the effects of habitat factors on species' response. Therefore, for pairs of variables which were highly intercorrelated ( $r > 0.7$ ,  $P < 0.05$ ), only one of the two was alternatively entered in the analyses, and thus different sets of models were tested, excluding different variables each time (see Supplementary online

material). The earth package version 3.2-1 (<http://cran.r-project.org/web/packages/earth/index.html>) in R 3.0.1 (R Development Core Team 2013) was used. The earth package allows MARS analyses for different types of distribution, including binomial distributions (Milborrow 2011a), which was used for the model with nest and random plots of Little Crake and Water Rail, respectively, as the dependent variable. The following settings, commonly adopted as default values, were used for model selection: threshold = 0.001, penalty = 2 and degree of interactions = 1 (no interaction allowed among variables). The model was subjected to cross-validation, which was used to estimate model performance over different subsets of the data. The number of folders for cross-validation was five for Water Rail, and two for Little Crake, given that for the latter increasing the number of folders resulted in too high a standard deviation. The discriminatory ability of the models was evaluated by means of the area of the curve of the receiver operating characteristic plot, calculated considering the cross-validation output. Variable importance was evaluated on the basis of the evimp command (Milborrow 2011a, Brambilla *et al.* 2013). The evimp command estimates variable importance in a MARS model according to three criteria: (1) the number of model subsets generated by the pruning pass, which include a given variable: variables included in more subsets are considered more important; (2) the decrease in the residual sum of squares (RSS) for each subset relative to the previous subset: for each variable evimp sums these decrease over all subsets that include the variable and rescales the summed decreases to a percentage scale (largest one equal to 100); (3) the generalized cross-validation (GCV) of the model, calculated using the penalty argument, which considers the increase or decrease in the GCV associated with a variable being added to the model; the evimp command uses GCV criterion exactly like the RSS criterion (Milborrow 2011a). The plotmo package version 1.3-1 (<http://cran.r-project.org/web/packages/plotmo/index.html>) was used to plot the fitted functions (Milborrow 2011b). After repeating the same procedure for all subsets of variables, the models which showed both the inclusion of relevant variables and good cross-validation statistics were selected, indicating model robustness and consistency across data (Supplementary online material). When two models received the same statistical support, the simplest one was selected. The two most correlated variables were water depth and mean water depth. Models including the latter were preferred, because it seemed that depth

in the close surroundings of the nest could be more important in determining nest accessibility (both to breeding species and predators), rather than the depth at a very specific point. In any case, all models tested are reported in the Supplementary online material.

To assess what factors differ in habitat selection between the two species, we built a further model using all data, with nest presence/absence as dependent variables, and as predictors the most relevant (according to species-specific models) and weakly correlated habitat variables (mean water depth, vegetation height, vegetation type, vegetation stage, distance from bank, distance from open water, distance from bushes and percentage of old vegetation) and species as a factor. We then tested the effect of the interaction of habitat predictors by species, to evaluate variables subjected to different selection by the two species. We adopted the same MARS procedure described above also for this analysis.

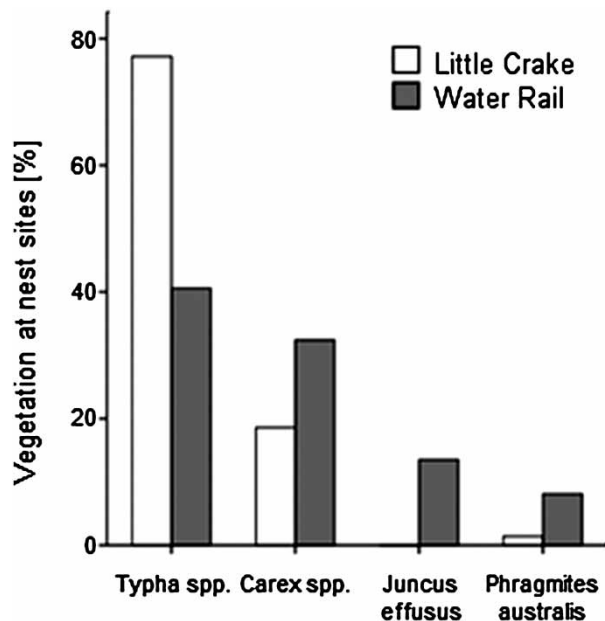
## RESULTS

### Nest-site features

During the three breeding seasons, 70 nests of Little Crake and 37 nests of Water Rail were found. The earliest nests were found on 30 April for Water Rail and on 6 May for Little Crake. The latest nests were found on 11 July for Water Rail and on 25 July for Little Crake. Nineteen nests of Little Crake and 30 nests of Water Rail were recorded during the egg-laying period. Five nests of each species were found as abandoned after predation. The rest of the nests were recorded during the incubation period. Distance between neighbouring nest of Little Crake averaged 75.9 m (sd  $\pm$  43.3 m,  $n$  = 58), between Water Rail nests averaged 122.4 m (sd  $\pm$  36.0 m,  $n$  = 16) and between two nearest nests of both species was an average of 80.3 m (sd  $\pm$  49.8 m,  $n$  = 31). Little Crake nested on 14 water bodies with mean density 1.07 pairs/ha and Water Rail on 16 water bodies with mean density 0.75 pair/ha. Water Rail and Little Crake co-occurred on half of the water bodies studied with overall breeding density 1.64 pairs/ha.

Both species nested mainly in *Typha* spp. and *Carex* spp. (Fig. 1). Single nests of Little Crake were also found in Common Reed, Water-plantain and in Reed Sweet-grass (each 1.4%). Water Rail nested occasionally in Soft-rush (13.5%), Common Reed (8.1%), Reed Canary-grass (2.7%) and in Sweet-flag





**Figure 1.** Frequency of the most common vegetation types at nesting sites of Little Crane and Water Rail.

(2.7%). The vegetation category around the nests was the same as the dominant vegetation within the 3-m radius plots in 92.9% of plots for Little Crane and in 75.7% of plots for Water Rail. Little Crane and Water Rail built nests mostly in mixed (respectively, 62.8% and 48.6%) and old vegetation (respectively, 32.9% and 46.0%), and only sporadically in new vegetation (respectively, 4.3% and 5.4%). The commonest nest materials used by both species were old leaves of *Typha* spp., found in 87.1% of Little Crane nests and in 75.7% of Water Rail nests (the rest of the nests were built with *Carex* spp. and two nests of Water Rail were built with Common Reed). Comparing nest material with dominant vegetation in nest plots, the ratio between *Typha* spp. and other vegetation categories did not significantly differ for Little Crane ( $\chi^2_1 = 0.2$ ,  $P = 0.63$ ) and for Water Rail ( $\chi^2_1 = 3.8$ ,  $P = 0.051$ ).

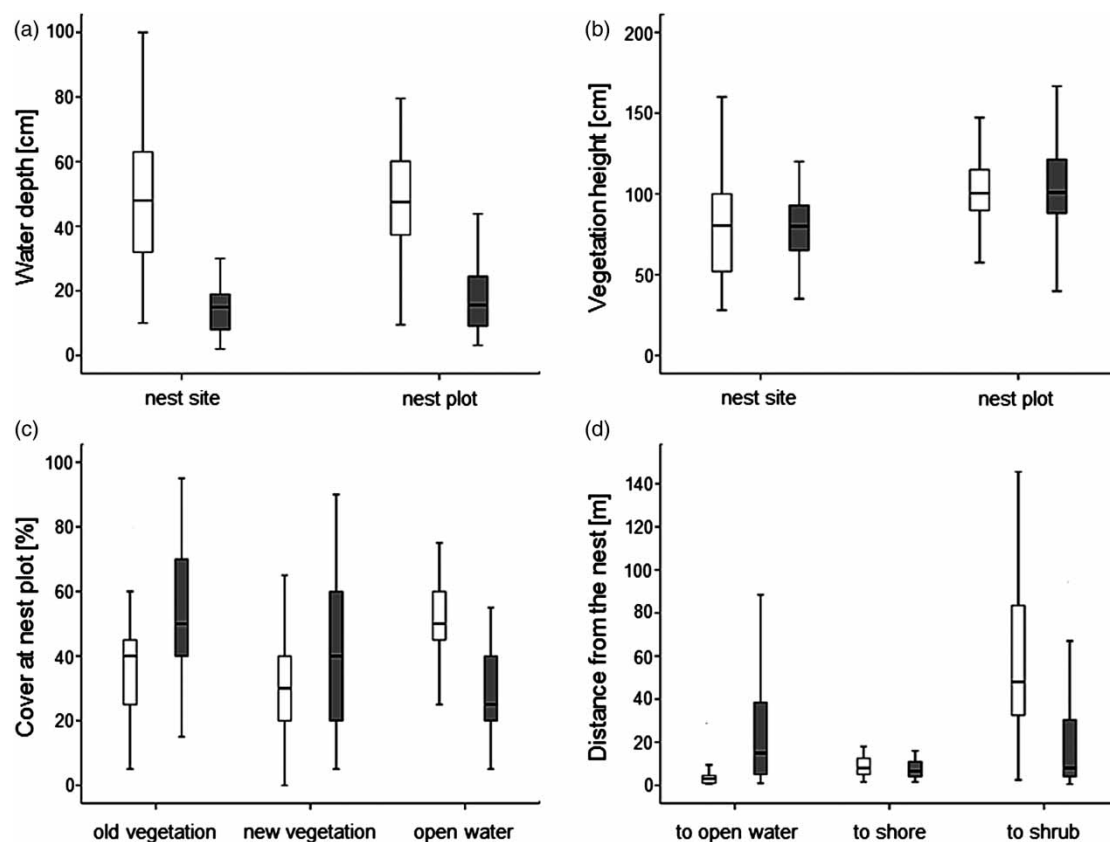
Water depth (mean  $\pm$  se) at Little Crane nest sites was  $48.5 \pm 2.25$  cm (range 10–100 cm) and  $14.4 \pm 1.31$  cm (range 2–30 cm) at Water Rail nest sites, and the former preferred also deeper mean water depth (Fig. 2a). Emergent vegetation height at Little Crane nest sites was  $81.4 \pm 3.67$  cm and  $81.7 \pm 4.42$  cm at Water Rail nest sites (the average height of vegetation within nest plots were slightly higher; see Fig 2b). The nest plots of Little Crane were characterized also by  $36.6 \pm 1.86\%$  of old vegetation cover,  $32.4 \pm 1.97\%$  of new vegetation cover and by  $51.1 \pm 1.43\%$  of open

water cover. Respective values for Water Rail nest plots were  $54.3 \pm 3.33\%$ ,  $41.6 \pm 4.56\%$  and  $28.9 \pm 2.39\%$  (Fig 2c). Habitat heterogeneity was higher within Water Rail nest plots ( $0.54 \pm 0.05$ ) than within Little Crane nest plots ( $0.19 \pm 0.04$ ). Finally, the nests of Little Crane were situated closer to the open water than Water Rail nests (respectively,  $4.0 \pm 0.52$  m and  $23.7 \pm 3.99$  m), further from willow shrubs (respectively,  $56.8 \pm 4.59$  m and  $23.5 \pm 5.02$  m) and at a similar distance to dry areas (respectively,  $10.0 \pm 0.90$  m and  $9.6 \pm 1.62$  m; see Fig. 2d). Despite these recorded differences, the range of values for all environmental variables recorded at Little Crane and Water Rail nest sites overlapped. The summary of all measurements taken in nest sites of Little Crane and Water Rail, as well as in random points are shown in the Supplementary online material.

### Habitat selection models

The selected MARS model for Little Crane included four variables: mean water depth, percentage cover of old vegetation within a 3-m radius plot, vegetation height and vegetation stage at the centre of the plot (Table 1). Nest occurrence probability peaked at sites with mean water depth equal to 42 cm, vegetation height lower than 146 cm, percentage cover of old vegetation higher than 40% and vegetation stage old or new (not mixed, see Fig. 3). The evimp command for the evaluation of the variable importance confirmed model strength, indicating that the included variables were the ones considered as more important (Table 1), whereas possible importance is additionally suggested for distance to bushes (number of subset 1, RSS 13.2 and GCV 30.4), that was not included in the chosen model. This model was very close (the same variables were selected and with the same effect) to a model obtained using water depth at nesting sites/random points instead of mean water depth (see Supplementary online material), further suggesting the model's validity.

The selected MARS model for Water Rail included mean water depth, vegetation stage and vegetation category at the centre of the plot (Table 1). Nest occurrence probability was highest at sites with mean water depth lower than 12 cm, vegetation stage old or new (not mixed) and in sites with *Carex* spp. or *J. effusus* (Fig. 4). The evimp command for the evaluation of variable importance confirmed model strength, indicating that the included variables were the ones regarded as more important (Table 1).



**Figure 2.** Comparison of habitat variables at nesting sites and nesting plots (area within 3-m radius around nest) of Little Crane (white box plots) and Water Rail (grey box plots): (a) water depth at nest site and mean water depth at nest plot; (b) vegetation height at nest site and mean vegetation height at nest plot; (c) percentage cover of old and new vegetation, and open water cover at nest plot; (d) distances from the nest to the nearest shore, open water and Grey Willow shrub. The band inside the box represents the median and whisker plots represent range of values without outliers.

The MARS model considering the effects of species-habitat interactions revealed that the variable most important in discriminating between the two nest-site selection processes was mean water depth (details not shown), in agreement with the variable's importance separately for both Little Crane and Water Rail, and with the different effect on nest occurrence probability for the two species shown by the species-specific models.

## DISCUSSION

Our work represents one of the first quantitative descriptions of nesting habitat in these poorly investigated Rallid species (Stermin 2012). Despite the overlap in the range of values recorded for habitat features at nest sites and nesting plots of the two species, the average nesting habitat of the two species was quite different. The most pronounced differences were found in water levels, consistent with earlier

studies reporting water levels at Little Crane nest sites ranging from 30 to 60 cm (Kux 1959, Dittberner & Dittberner 1990), and at Water Rail nest sites ranging from 3 to 16 cm (De Kroon 1999). According to our results, the water depth at Little Crane nest sites was, on average, 34 cm higher than that found at Water Rail nest sites, although 17% of Little Crane nests were located in places potentially acceptable for Water Rail too (water depth lower than 30 cm). This result suggests that nest sites of both species may potentially co-occur in places where the water level is between 10 and 30 cm. In summary, water level was the most important factor driving nest-site selection and was clearly associated with a different response pattern from the two species (see Results and Figs 3 & 4).

For marsh-nesting birds, water depth is related to the pressure of terrestrial predators and deeper zones ensure greater nesting success (Jobin & Picman 1997, Hoover 2006). On the other hand, denser vegetation cover

**Table 1.** Summary of selected MARS models (see text and Supplementary online material) for the two studied species.

Variable	Coefficient	No. of subsets	RSS	GCV
<b>Little Crane</b>				
$(R^2 = 0.28, \text{cv } R^2 \pm \text{sd} = 0.17 \pm 0.01, \text{AUC} \pm \text{sd} = 0.74 \pm 0.00)$				
Intercept	2.66			
Mean water depth (below 42 cm)	0.05	100.0	5	5
Mean water depth (above 42 cm)	-0.08			
Vegetation height (above 146 cm)	-0.12	1	11.7	29.8
Old vegetation cover (below 40%)	0.04	1	11.7	29.8
Vegetation stage mixed	-1.18	3	45.1	60.0
<b>Water Rail</b>				
$(R^2 = 0.52, \text{cv } R^2 \pm \text{sd} = 0.36 \pm 0.09, \text{AUC} \pm \text{sd} = 0.86 \pm 0.07)$				
Intercept	2.54			
Mean water depth (above 12 cm)	-0.12	4	100.0	100.0
Vegetation type <i>Carex</i> spp.	2.67	2	37.9	46.1
Vegetation type <i>J. effusus</i>	17.68	1	25.5	31.4
Vegetation stage mixed	-2.73	3	48.7	58.9

For complex hinge functions, the effect for the specified range of values is reported; see Figs 3 & 4 for a detailed description of the species-habitat variables. Abbreviation: no. of subset, number of model subsets generated by the pruning pass, which include a given variable; RSS, decrease in the residual sum of squares; GCV, generalized cross-validation of the model;  $R^2$ , model's  $R^2$ ;  $\text{cv } R^2 \pm \text{sd}$ : model's  $R^2$  calculated over the cross-replicated models and the relative standard deviation;  $\text{AUC} \pm \text{sd}$ : the area under the curve (and its standard deviation) calculated over the cross-replicated models. See text for explanation.

provides security against bird predators (Dwernychuk & Boag 1972), as well as terrestrial predators (Schranck 1972). For the Water Rail and Little Crane predator pressure is still poorly known, but it seems that in the Mazurian Lakeland the main nest predators are the Marsh Harrier *Circus aeruginos* and species belonging to the Mustelidae family (J. Jedlikowski, unpubl. data), suggesting that the safest places should be in deeper water, surrounded by dense vegetation cover. As the water depth in ponds was negatively correlated with the density of vegetation cover ( $r > 0.7$ ,  $P < 0.001$  for both species), birds had to optimize their choice between these two variables during nest-site selection.

One of the main differences in breeding biology between both species, which may potentially be related to the process of nest-site selection, is nest size and egg pigmentation. Water Rail nests are bigger than Little

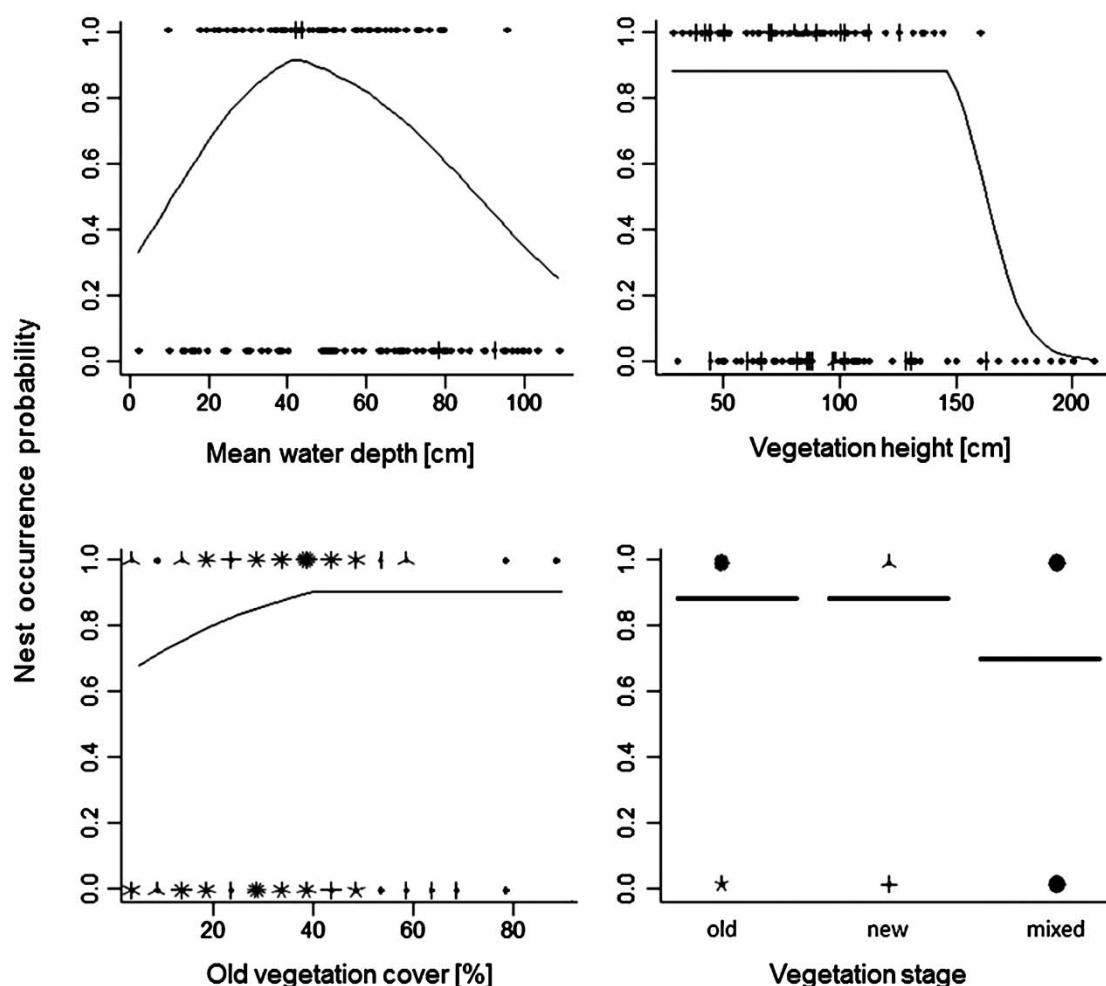
Crane nests (the average outside diameter is 20 cm (De Kroon 2004) and 13 cm (J. Jedlikowski, unpubl. data), respectively), and contain off-white eggs different from the more cryptic and smaller brown-buff eggs of Little Crane (Taylor & Van Perlo 1998). This suggests that a Water Rail clutch is probably more visible (especially by aerial predators) and thus birds have to choose places with denser vegetation cover.

Furthermore, both species are adapted to walking through littoral vegetation and they use floating plant material (leaves and stems) as a walking path. They prefer running through dense vegetation than swimming or flying when they are threatened (Taylor 1980, Taylor & Van Perlo 1998, own observations). Because Water Rail are at least 15% larger and on average twice as heavy as the biggest Little Crane (Cramp 1980), the buoyancy of this species is less. In deeper zones of littoral vegetation, cover and floating plant material are less dense (Grace 1989), therefore Water Rail would have to swim and fly more often there, and so may be more vulnerable to predation. The Little Crane is lighter and moves more easily even in places with scarce floating plant material.

Considering these two differences: in morphology and in clutch characteristics, it can be supposed that each species then selects the safest nesting sites in relation to their respective characteristics. Water Rails nested in shallow plots with vegetation cover 16% denser than random plots and 22% denser than Little Crane plots, which may reduce visibility of the nest and provide better security also for adult birds. Little Cranes can nest in deeper littoral waters, which provide better protection from terrestrial mammalian predators, likely because of its lighter weight which enables the use of sparser floating stems and leaves of the deeper areas.

The different predominance of vegetation types around the nest sites of the two species may also reflect different anti-predator strategies in Water Rail and Little Crane. The compact clumps of old *Typha* spp., which were 17.2% more frequent at Little Crane nest sites than at comparative random points, may well hide the nest, and enable safe movements of adult birds. In contrast, nests situated in Common Reed patches are characterized probably by a higher level of vertical visibility, and thus may be more easily found by terrestrial mammals. Similar results for Little Crane were obtained by Glutz von Blotzheim *et al.* (1973), who found 58% (15) nests in *Typha* spp. and only 19% (5) nests in Common Reed. The preferences for particular vegetation at nest sites are probably driving





**Figure 3.** Graphical summary of the MARS model for nesting-site selection in Little Crake. Species–habitat relationships show the probability of nest occurrence in relation to mean water depth (cm), vegetation height (cm), vegetation stage (old, new, mixed) and percentage cover of old vegetation (% cover in the 3-m radius around the nest). Sunflower plots (upper row: nests; lower row: random points) are also shown in each graph.

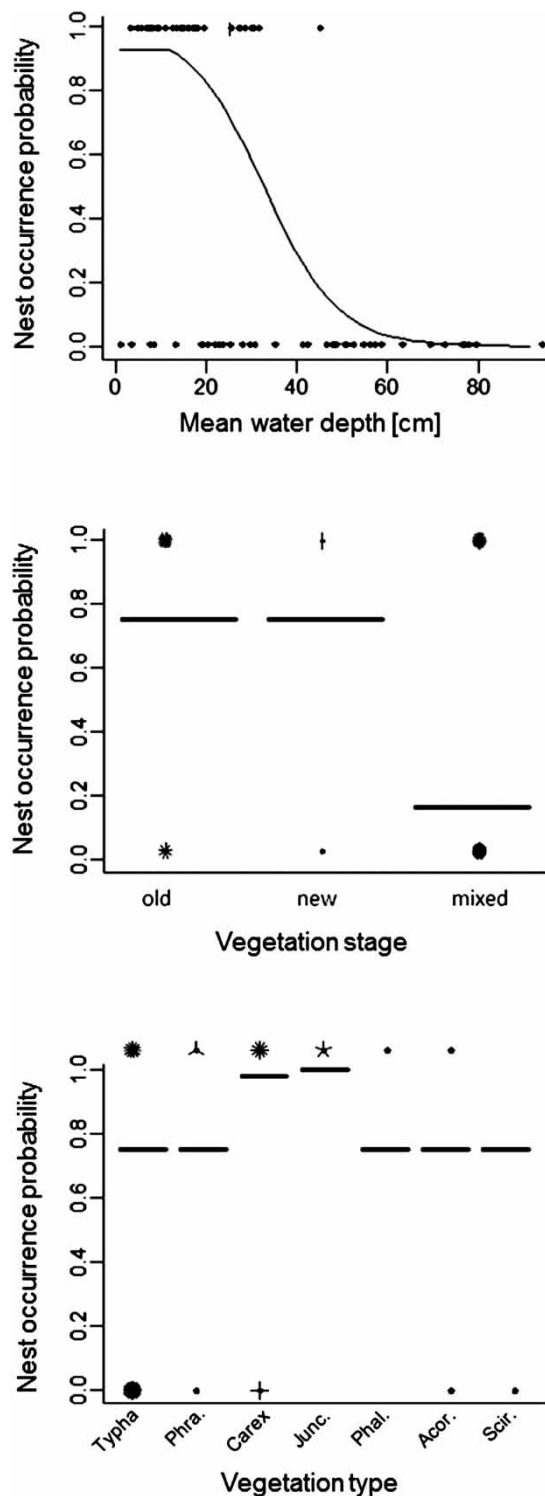
the association with vegetation height too. A decreasing probability of nest occurrence in places with vegetation height above 150 cm corresponds to the maximum height of *Typha* spp. stems – 160 cm, in contrast to Common Reed stems, which had an upper limit of 210 cm.

Similarly, Water Rails nested mainly in *Typha* spp. and *Carex* spp. Slightly different results were obtained by De Kroon (1999), who found most nests in *Carex* spp. (73%) and the rest in Common Reed (27%). However, in our study the highest probability of Water Rail nest occurrence was in Soft-rush and *Carex* spp. (Fig. 4). A large clump of *Juncus* spp. and *Carex* spp. may provide excellent protection of nests from all sides, and reduce its vulnerability. Accordingly, De Kroon (2004) found that nests and eggs of Water Rail placed in Sea Rush

*Juncus maritimus* were less visible than those situated in Common Reed mixed with *Carex* spp.

Both species show a preference for nesting in old vegetation. At the beginning of the breeding season old vegetation is the only type where birds may find sufficient cover to build nests, and even later in the season the compacted clumps of dead stems create an excellent ‘roof’, which may protect against predators and severe weather conditions (hot sun and rain). The previous year’s stems and leaves seem to be also crucial as nest material for both species. All the nests found in this study were built using old plant material. Probably such material is easier to collect by the birds than fresh stems and leaves.

Previous studies have reported that Water Rail nests are usually situated in close proximity to bushes



**Figure 4.** Graphical summary of the MARS model for nest-site selection in Water Rail. Species–habitat relationships show the probability of nest occurrence in relation to mean water depth (cm), vegetation stage (old, new and mixed) and vegetation category (in the order: *Typha* spp., *P. australis*, *Carex* spp., *J. effusus*, *P. arundinacea*, *A. calamus* and *S. sylvaticus*). Sunflower plots (upper row: nests; lower row: random points) are also shown in each graph.

(Huygens 1954, De Kroon 2000). Such places are used as roosting sites and provide safe havens for chicks and adult birds (pers. obs.). Our study shows that nests of Water Rail were closer to willow shrubs than random points, nevertheless this factor was not included in the habitat-preference models. In the case of Little Crake, nests were located further from willow shrubs than random points, but values varied a lot, and the MARS model did not provide a definitive confirmation for such a pattern and thus a real avoidance of shrubs is questionable.

Our results may have some implications for the conservation and management of habitats with breeding Little Crakes and Water Rails. Potentially, the most important factors to be considered for their conservation through habitat management are avoiding the complete removal of old vegetation, such as dead stems or leaves, keeping a fine-scaled mosaic of open water and vegetation cover and managing water level consistent with the two species' different requirements.

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## SUPPLEMENTAL DATA

Supplementary online material comparing vegetation and habitat variables of Little Crake and Water Rail nests with random sites, and details of the MARS models of nest-site selection can be accessed at <http://dx.doi.org/10.1080/00063657.2014.904271>

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