

# Comparison of fine-scale spatial distribution and nest-site selection in great crested grebe (*Podiceps cristatus*) and coot (*Fulica atra*)

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Tests were performed for differences in the distribution over the patches of emergent vegetation and in nest-site selection between nesting great crested grebe and coot on lakes Meteliai, Obelija and Žaltytis of southern Lithuania. Coot is more widely dispersed than great crested grebe, however, a significant spatial overlap exists between the two species. The distribution of great crested grebe is much more clumped than that of coot. Patches with nests of both species have larger areas of well-waterlogged reedbeds than those occupied by only one of the species. Coot, in comparison with great crested grebe, builds nests in shallower and more densely vegetated parts of reedbeds.

**Key words:** coot, great crested grebe, nest-site, patch of emergent vegetation, reedbeds, distribution

## INTRODUCTION

Ecologists suggest that organization of animal community is determined by the interaction among species in a given area (MacArthur, 1970; May, MacArthur, 1972; Roughgarden, 1974; Toft, 1982; Begon et al., 1989). Such approach is inevitably related to the problem of resource partitioning. The patterns of such partitioning can be recognized as non-random differences in the use of space and food (Schoener, 1974; Werner, 1977; Toft, 1980; Toft, 1982; Dunham, 1980; Arlettaz et al., 1997; Karlson et al., 2007). With a large overlap in the breeding timing and nesting sites and no competition for food resources, as in the case of great crested grebe and coot, an ecologically meaningful and delicate task is to find out how “nesting habitat resources” are shared. However, we failed to find comparative data on nest-site selection by great crested grebe and coot. It seems that the behavioral aspect of spatial interaction between coot and great crested grebe is a more popular object of investigation (Блум, 1973; Кошелев, 1984; Goc, 1986; Konter, 2002; Stanevičius, Švažas, 2005) than comparison of their habitat characteristics. Ecological separation and microhabitat selection of American Coot and some American native grebe species were compared by Nudds (1982).

In our paper, we explored differences in nest-site choice and spatial distribution between great crested grebe and coot on wetlands where both species are common. To achieve this goal, we investigated: (i) whether the patterns of nest distribution over plant patches differ between the species, (ii) what is the degree of spatial isolation and overlap in the use of plant patches by the species, (iii) differences in some habitat characteristics between patches occupied by great crested grebe only, by Coot only and by both species, (iv) differences in nest-site characteristics between the species.

## MATERIALS AND METHODS

The investigations were conducted in a reed (*Phragmites australis*) and reedmace (*Typha angustifolia*) shore belt on the Meteliai (1288 ha; 54°18'N23°47'E), Obelija (575 ha; 54°18'N23°50'E) and Žaltytis (256 ha; 54°25'N23°24'E) lakes, south Lithuania. Previous year reed and reedmace beds were the only nesting habitats of great crested grebe and coot. In April 1985, the total area of plant cover in lakes Meteliai, Obelija and Žaltytis was approximately 61, 16 and 36 ha, respectively (Станевичюс, 1992). It consisted of an intermittent shore-belt of differently sized and shaped patches.

We used aerial photographs (1 : 5000) made in April 1985 to estimate the area of vegetation patches. For annual water depth measurements, reedbed patches were divided into parallel transects, at an approximately 10 m interval from each other, running from open water to the shore. Water depth, plant height and the density of vegetation were measured at an interval of about 5 m. Based on water depth measurements, well-waterlogged part of patch (20–100 cm water in depth) was separated from those poorly waterlogged (<20 cm). Water depth and the height and density of vegetation were also measured in nest-sites. Vegetation density was measured by counting plant stems within a 1 × 1 m<sup>2</sup> wire frame at the mid-height of plants. Measurements were grouped into five classes, class 1 denoting 20 stems/m<sup>2</sup> and class 5 100 stems/m<sup>2</sup>. The distance from a nest to open water was measured on aerophotos (with mapped nests) or by boat lengths. Plant species composition in reedbed was evaluated visually.

Nest counts were performed twice every season with the first survey in the second half of May and in late May and the second one in early June. Nests were counted moving in a boat

with the help of a long pole through reed stands along the shore. We examined all the territory of a patch. The number of such parallel routes within a patch of emerging vegetation depended on the width of a patch. In addition, routes along the junction of waterlogged and non-waterlogged reed stands were walked.

To compare the distribution of the coot and great crested grebe over the patches of emergent vegetation, patches were assumed as "sampling units". To compare nest-site selection, a sampling unit was considered a nest site. Nest patch and nest site habitat characteristics were related to the fine-scale level of distribution and habitat selection.

Chi-square analysis of contingency tables was used to test for differences in the numbers of reed patches occupied by one of the two or both species. This method was also used to examine differences in the distribution between great crested grebe and coot over different plant communities in particular lakes. To compare the variability in nest distribution over reedbed patches between great crested grebe and coot, variances of nest distribution for each species were calculated. Further, F-test was used to check the significance of differences between these variances. Also, a variance was compared with a mean in order to check for clumpiness in spatial nest distribution for great crested grebe and for coot in each of the study lakes. Mann-Whitney (when compared between two lakes) or Kruskal-Wallis ANOVA (when compared among three lakes) tests were performed in order to check differences in some characteristics of emergent vegetation patches occupied by one or both species. Series of Mann-Whitney tests were performed to test differences in nest-site characteristics between great crested grebe and coot on particular lakes in particular years.

The statistical analysis was performed using the StatSoft, Inc. 1999 software package.

**RESULTS**

**1. Range of spatial distribution of nests**

Coot was more widely spread on all the three lakes than the great crested grebe i.e. occurred in a larger number of patches of emergent vegetation (Fig. 1). In each lake, these differences were statistically significant ( $\chi^2 = 48.43$ ,  $df = 1$ ;  $P < 0.0001$ ;  $\chi^2 = 6.906$ ,  $df = 1$ ;  $P < 0.01$ ;  $\chi^2 = 11.121$ ;  $df = 1$ ;  $P < 0.001$  on Meteliai, Obelija and Žaltytis, respectively).

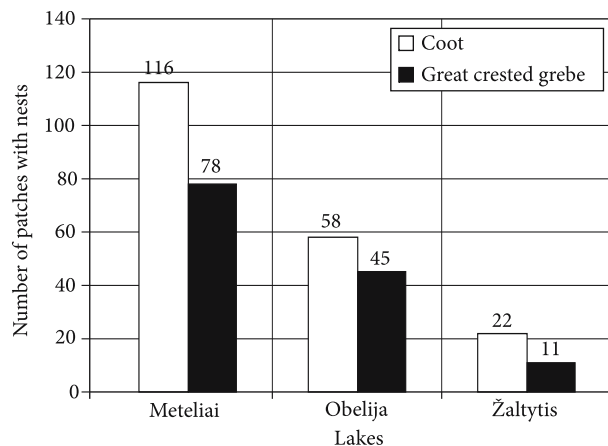


Fig. 1. Distribution of great crested grebe and coot nests over patches of emergent vegetation in lakes

**2. Variations in the numerical distribution of nests**

Most frequently patches were occupied by single pairs of birds. Nevertheless, there were patches occupied by several tens of grebes, whereas coots formed no such colonies there (Fig. 2). As a consequence, even 422 grebe pairs nested in only 70 helophyte patches on Meteliai, whereas only 248 coot pairs were distributed over 116 patches. The calculated variances were 104.48 for great crested grebe and only 9.24 for coot.

The F-test confirmed a significant difference between variances in great crested grebe and coot nest distribution ( $F = 11.31$ ;  $df = 115$  and  $69$ ;  $P < 0.01$ ). For great crested grebe, the variance was much more higher than the mean (variance 104.48 vs mean 2.14), indicating a high clumpiness in the distribution of breeding pairs. For coot, the difference between the mean and variance values (9.24 vs 6.06) was less than that for great crested grebe.

In Lake Obelija, 158 pairs of great crested grebe nested in 45 patches, whereas 124 pairs of coot in 58 patches. The variances were 19.1 and 3.68, respectively. F-test confirmed this difference in nest distribution variability ( $F = 5.19$ ;  $df = 44$  and  $57$ ;  $P < 0.01$ ). The variance for great crested grebe was much larger than the mean (19.31 vs 3.51), indicating a clumped distribution. Again, in coot, the variance was somewhat higher than the mean (3.68 vs 2.14).

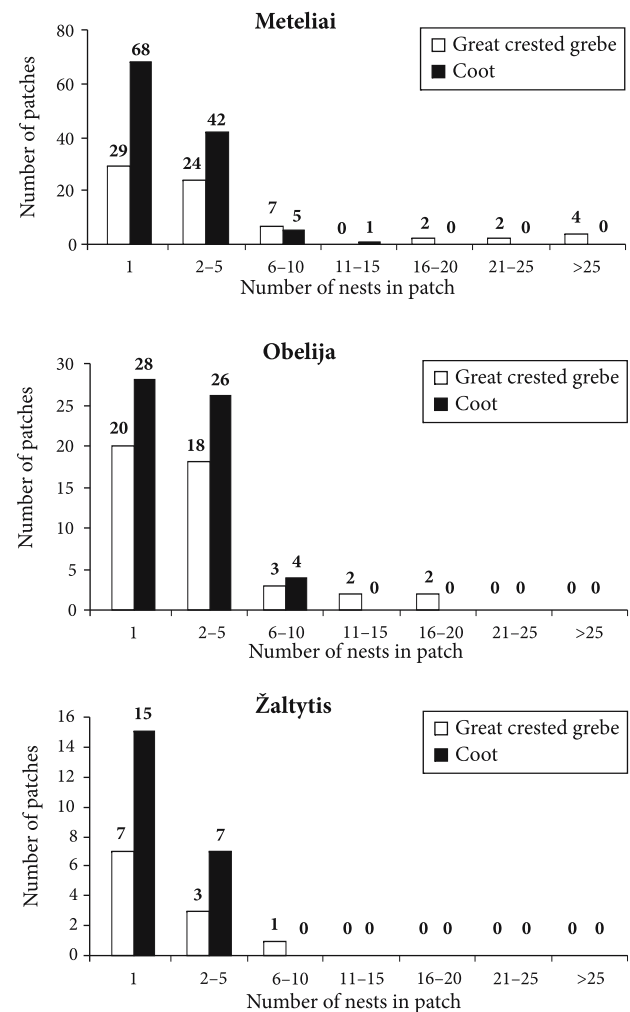


Fig. 2. Numerical distribution of great crested grebe and coot nests over patches of emergent macrophytes in Meteliai, Obelija and Žaltytis lakes

In Lake Žaltytis, 29 grebe pairs nested in 11 patches, whereas 25 coot pairs nested in 22 patches. The difference in the variance of nest distribution (4.84 and 0.23, respectively) was statistically significant ( $F = 21.04$ ,  $df = 10$  and  $21$ ,  $P < 0.01$ ). For great crested grebe, the variance of nest distribution over patches was higher than the mean (4.84 vs 2.27). For coot, the variation in nest distribution over emergent vegetation patches was lower than the mean (0.23 vs 1.32), indicating a not clumped distribution.

**3. Spatial overlap and isolation**

There were very few emergent vegetation patches used as nest sites only by great crested grebe, more with coot nests only, and most frequently both species nested in the same patches (Fig. 3). A chi-square analysis of the contingency table revealed that this pattern was similar in Meteliai and Obelija plus Žaltytis ( $\chi^2 = 3.01$ ,  $df = 1$ ,  $P > 0.05$ ). In this analysis, we aggregated data from Obelija and Žaltytis because inspection of the contingency table revealed that the values of expected frequencies for great crested grebe were less than 5 in both Obelija and Žaltytis. Further, we tested whether some of the parameters differed between patches with grebe nests only, with coot nests only and those with nests of both species. The area of the waterlogged part of a patch between the these three patch groups in Meteliai and Obelija differed significantly. Patches with both species breeding together contained the largest area of waterlogged vegetation in these lakes, whereas patches occupied exclusively by coots took the smallest one. For Žaltytis, differences in this characteristic of patch groups were insignificant (Table 1).

The difference in plant density of patch types was significant only for Lake Žaltytis (Table 1).

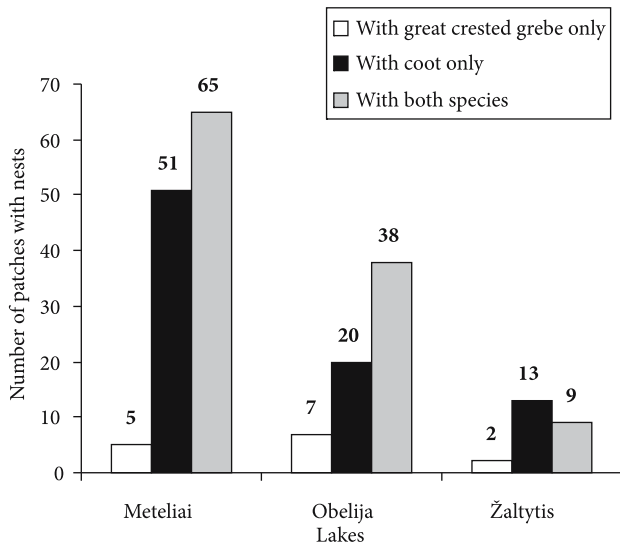


Fig. 3. Numbers of patches with great crested grebe nests only, with coot nests only and with nests of both species

**4. Nest site selection**

In Lake Meteliai, in three years of four, great crested grebe built nests in higher vegetation than did coot. In two years these differences were significant and one year insignificant. Only in one year coot nested in a significantly higher vegetation than great crested grebe. On Lake Obelija, coots built nests in higher ve-

getation during two out of three years, whereas grebes did so during one year. None of these differences were statistically significant. On Lake Žaltytis, in 1984, coots built nests among higher vegetation than grebes, but this difference was not significant (Table 2).

Table 1. Medians of some habitat characteristics of different patch groups (sample sizes are given in brackets)

Lake, patch characteristics	Patches with great crested grebe nests only	Patches with coot nests only	Patches with nests of both species	Significance of difference
<b>Meteliai</b>				
Area of waterlogged vegetation per patch, ha	0.32 (5)	0.24 (51)	0.62 (65)	$P < 0.001^*$
Plant density per patch, steams/m <sup>2</sup>	2 (5)	3 (51)	3 (65)	n. s. *
<b>Obelija</b>				
Area of waterlogged vegetation per patch, ha	0.32 (9)	0.19 (20)	0.45 (38)	$P < 0.05^*$
Plant density per patch, steams/m <sup>2</sup>	3 (9)	3 (20)	3 (38)	n. s. *
<b>Žaltytis</b>				
Area of waterlogged vegetation per patch, ha	– (0)	0.26 (13)	0.33 (9)	n. s.**
Plant density per patch, steams/m <sup>2</sup>	– (0)	3 (13)	4 (9)	$P < 0.05^{**}$

\* Kruskal–Wallis ANOVA test.

\*\* Mann–Whitney test.

n. s. – not significant.

Table 2. Medians of plant height (in cm) in great crested grebe and coot nests. Sample sizes are given in brackets

Lake, year	Great crested grebe	Coot	Significance of difference
<b>Meteliai</b>			
1983	165 (21)	208 (42)	*
1984	250 (154)	170 (63)	**
1985	198 (36)	192 (34)	n. s.
1986	208 (112)	200 (45)	*
<b>Obelija</b>			
1983	128 (17)	155 (20)	n. s.
1984	160 (60)	140 (43)	n. s.
1986	170 (55)	170 (18)	n. s.
<b>Žaltytis</b>			
1984	108 (41)	102 (12)	n. s.

\*  $P < 0.05$ ; \*\*  $P < 0.0001$  (Mann–Whitney test).

n. s. – not significant ( $P > 0.05$ ).

Most frequently, a higher vegetation density was recorded around coot nests than around great crested grebe nests. However, only in three cases of six these differences were significant (Table 3).

Table 3. Medians of plant density (stems/m<sup>2</sup>) at great crested grebe and coot nests (sample sizes are given in brackets)

Lake, year	Great crested grebe	Coot	Significance of difference
<b>Meteliai</b>			
1983	40 (21)	50 (42)	*
1984	30 (154)	30 (63)	n. s.
1985	28 (36)	33 (34)	*
<b>Obelija</b>			
1983	37 (17)	39 (20)	n. s.
1984	30 (60)	32 (43)	*
<b>Žaltytis</b>			
1984	33 (41)	41 (12)	n. s.

\*  $P < 0.05$ ; \*\*  $P < 0.0001$  (Mann–Whitney test).

n. s. – not significant ( $P > 0.05$ ).

In all cases, grebes built nests in deeper places than coots. However, these differences were significant only for lakes Obelija and Žaltytis (Table 4). Nevertheless, the same tendency for all the lakes allow the assumption that this is rather a regular preference. Additionally, it can be confirmed indirectly by the fact that great crested grebe tends to nest in sparser vegetation than coot (return to Table 3) because reedbeds, as a rule, are sparse in deeper places and denser in shallow places heaped with plant stems of many previous generations.

Table 4. Comparison of medians of water depth (in cm) at nests between Great Crested Grebe and Coot. Sample sizes are given in brackets

Lake, year	Great crested grebe	Coot	Significance of difference
<b>Meteliai</b>			
1983	83 (21)	50 (42)	n. s.
1984	52 (154)	48 (63)	n. s.
1985	68 (36)	67 (34)	n. s.
1986	90 (112)	76 (45)	n. s.
<b>Obelija</b>			
1983	87 (17)	55 (20)	***
1984	90 (60)	79 (43)	*
1986	110 (55)	93 (18)	*
<b>Žaltytis</b>			
1984	110 (41)	32 (12)	**

\*  $P < 0.05$ ; \*\*  $P < 0.001$ ; \*\*\*  $P < 0.0001$  (Mann–Whitney test).

n. s. – not significant ( $P > 0.05$ ).

Grebes on Lake Meteliai built nests at a larger distance from open water than coots (Table 5).

For three out of four years, this difference was highly significant. Less evident was the preference on Lake Obelija (Table 5). There, only one year grebes built their nests significantly further from water than coot, whereas in two years both species nested at practically the same distance from open water. On Lake Žaltytis, both species built their nests at a very short distance from wa-

Table 5. Medians of nest distance to open water (in m) for great crested grebe and coot (sample sizes are given in brackets)

Lake, year	Great crested grebe	Coot	Significance of difference
<b>Meteliai</b>			
1983	40 (21)	14 (42)	***
1984	15 (154)	8 (63)	***
1985	17 (36)	16 (34)	n. s.
1986	32 (112)	18 (45)	**
<b>Obelija</b>			
1983	18 (17)	20 (20)	n. s.
1984	16 (60)	13 (43)	**
1986	25 (55)	26 (18)	n. s.
<b>Žaltytis</b>			
1984	0 (41)	1.5 (12)	*

\*  $P < 0.01$ ; \*\*  $P < 0.001$ ; \*\*\*  $P < 0.0001$  (Mann–Whitney test).

n. s. – not significant ( $P > 0.05$ ).

ter (Table 5). All nests of great crested grebe were found on rigid floating structures, immediately by the water edge. However, coots nested significantly further.

Finally, the distribution of great crested grebe and coot nests over different emergent vegetation communities was compared (Table 6). On Lake Meteliai, the largest number of nests of both species was obviously built in reed patches, and this is consistent with the dominance of reed (90%) in the zone of emergent vegetation. However, great crested grebe more frequently than coot preferred reed. Otherwise, we found more coot nests in reedmace and mixed reedmace and reed patches (Table 6). The above-mentioned disproportions in the selection of different plant communities by great crested grebe and coot are highly significant ( $\chi^2 = 68.51$ ;  $df = 2$ ;  $P < 0.0001$ ). Reed on Lake Obelija occupy about 50% of the total area of emergent macrophytes and only a relatively small part of both populations nested in reed patches. The majority of both great crested grebe and coot nests were found in mixed reedmace and reed stands, although the latter covered only about 20% of the zone of emerged macrophytes (Table 6). No significant difference in nest-site selection and plant composition between the two species was found for this lake ( $\chi^2 = 52.26$ ;  $df = 2$ ;  $P > 0.05$ ). On Lake Žaltytis, where the area of reeds is the smallest (only 8%) and that of mixed reed

Table 6. Numbers of great crested grebe and coot nests built in reed, reedmace and mixed reed / reedmace. In parentheses, the share (in %) of reed, reedmace and mixed reed/reedmace stands in emergent vegetation of particular lakes is shown

Lake, years	Reed	Reedmace	Reed / Reedmace
<b>Meteliai, 1984–1986</b>			
Great crested grebe	307 (90)	6 (8)	8 (2)
Coot	132 (90)	32 (8)	27 (2)
<b>Obelija, 1983–1984, 1986</b>			
Great crested grebe	13 (50)	12 (30)	63 (20)
Coot	26 (50)	13 (30)	52 (20)
<b>Žaltytis, 1984–1986</b>			
Great crested grebe	18 (30)	31 (24)	3 (46)
Coot	4 (30)	10 (24)	5 (46)



and reedbed is the largest, the majority of nests of both species were built in pure reedbed (Table 6). Differences between great crested grebe and coot in plant community selection were statistically insignificant for this lake ( $\chi^2 = 5.93$ ;  $df = 2$ ;  $P > 0.05$ ).

## DISCUSSION

Great crested grebe and coot most frequently nested together in the same patches of emergent vegetation. Nevertheless, a large number of patches were occupied by coot only. Patches with only great crested grebe nests were very rare (Fig. 1). As a consequence, coot was spatially more widely distributed than great crested grebe. Also, great crested grebe and coot demonstrated different patterns of the numerical distribution of nests over emergent vegetation. For great crested grebe the distribution was much more clumped than for coot. Both above findings relate to a strong territoriality of the coot. Intra-specific territorial competition is often an important factor for the spatial dispersion of a population (Begon et al., 1989), and vice versa, great crested grebe is a semi-colonial species. Previous investigations revealed that the majority of nesting populations of great crested grebe on the Meteliai, Obelija and Žaltytis lakes were concentrated in a few colonies (Станевичюс, 1992; Stanevičius, Švažas, 2005).

Coots more often than grebes built nests in denser and shallower (therefore more marshy) habitats (Table 3). This fact can be explained by the practical inability of great crested grebe to move over a firm substrate. As a consequence, it avoids shallow and densely vegetated parts of reedbeds.

Both species tended to nest in patches with a large area of well water-logged vegetation. Such places present an optimal water depth and plant density gradients for both species (Stanevičius, 2002).

The results of comparison of the plant species composition, the height of plants and nest distance to open water were often contradictory and difficult to interpret. The complicated interactions between various habitat characteristics and inter-lake differences most frequently are the major reasons (e.g., Melde, 1968; Блум, 1973; Недзинскас, 1993).

We conclude that both great crested grebe and coot have a great potential to breed practically side by side (large overlap on vegetation patch level) despite some differences in the nest-site characteristic. This is in accordance with other authors' reports (e.g., Блум, 1973) that in some water bodies great crested grebe and coot share practically the same nest sites.

A common situation in Lithuania is when the whole small or medium-sized wetland is occupied only by coot or (to a much lesser extent) only by great crested grebe. Such inter-wetland (or macrohabitat level) isolation can be explained by strict requirements for some minimal water area by great crested grebe (Сташайтис, Шаблевичюс, 1984; Fjeldså, Lammi, 1997). Also, the ability of coot to nest in shallower and more densely vegetated reedbeds than great crested grebe, as was obtained in our study, confirms the suggestion made by Stašaitis and Šablevičius (1984) on the reasons that attribute to cases of spatial separation between the two species at a lake level in the Aukštaitija National Park.

We also conclude that the scale of investigation (at a microhabitat or macrohabitat level) can lead to different conclusions with respect to the degree to which bird species are spatially or

habitually separated; this is in accordance with other authors' reports (e.g., Wiens, Rotenberry, 1979; Nudds, 1980).

A large spatial overlap on the emergent vegetation patch level between great crested grebe and coot reveals the case of niche complementarity – a high overlap in one resource dimension associated with a low overlap in another (Huey, 1979). The diet and brood-rearing grounds of these species are very different (Кошелев, 1984) and thus allow their wide-spread, side-by-side breeding.

Received 26 November 2007

Accepted 22 February 2008

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**ERDVINIO PASISKIRSTYMO IR LIZDO VIETOS PASIRINKIMO PALYGINIMAS TARP AUSUOTOJO KRAGO (*PODICEPS CRISTATUS*) IR LAUKIO (*FULICA ATRA*) MIKROBUVEINIŲ LYGMENYJE**

*S a n t r a u k a*

Buvo tirta, ar skiriasi ausuotojo krago ir laukio pasiskirstymas ir lizdo vietos pasirinkimas viršvandenėje augalijoje Metelio, Obelijos ir Žaltyčio ežeruose, Pietų Lietuvoje. Laukys plačiau paplitęs (aptinkamas daugiau viršvandenės augalijos guotų) nei ausuotasis kragas, tačiau abi rūšys labai dažnai peri ir tuose pačiuose guotuose. Ausuotasis kragas yra daug netolygiau pasiskirstęs nei laukys. Guotai, kuriuose peri abi rūšys, pasižymi didesniu gerai apsemtos augalijos plotu, nei guotai, kuriuose peri tik viena iš rūšių. Laukys krauna lizdus seklesnėse ir tankesnėse viršvandenės augalijos vietose nei ausuotasis kragas.

**Raktažodžiai:** laukys, ausuotasis kragas, lizdavietė, viršvandenių augalų guotas, nendrynai, paplitimas