DOI: 10.17242/MVvK_3.36

ARE NORTHERN BREEDING DABBLING DUCKS RESOURCE LIMITED?

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ABSTRACT

We describe patterns relating breeding waterfowl to habitat structure as well as to abundance and diversity of aquatic food invertebrates in 60 lakes in six regions in Sweden and Finland. Based on these patterns we studied the possible role of resource limitation and competition by a field experiment in which wing-clipped mallards were released to augment wild dabbling duck populations in 16 lakes in each of two years. Preliminary results of the experiments indicate no competition at the time of nest-building (pair counts), but that intra- as well as interspecific effects are possible later on in the breeding season (brood counts).

INTRODUCTION

Regulation of species richness and relative abundance in animal communities has been a central topic in ecology for a long time (cf. MacArthur, 1972; Cody, 1975). In this respect waterfowl have been fairly extensively studied in North America as well as in Europe (e.g. Nudds, 1992). Birds are problematic as well as challenging study objects, though, because patterns observed may depend on processes occurring in breeding, staging or wintering areas, as well as on different spatial scales (e.g. Wiens, 1989). Hence, there is still controversy as to when, where and what regulates waterfowl populations and communities (Nudds and Wickett, 1994). We here report on extensive field studies describing relationships between communities of breeding waterfowl and habitat variables, and the devising of an experiment testing for resource limitation among dabbling ducks on their breeding grounds in boreal Europe.

METHODS

In 1990 and 1991 we studied breeding waterfowl in six regions in Sweden and Finland along a gradient from broadleaved deciduous forest to northern coniferous forest (see map in Elmberg *et al.* 1993). In each region we selected 10 lakes to represent its gradient from oligotrophic to eutrophic conditions. Waterfowl were censused by two pair counts in spring and two brood counts in early summer. Abundance and diversity of benthic, nectonic and emerging invertebrate prey in the lakes were measured by activity and emergence traps (Elmberg *et al.* 1992, 1993). At the end of the breeding season the floating and the emergent vegetation in each lake were identified, mapped and measured. Subsequently, prey data were pooled to different composite measures, and the 18 variables of vegetation type, height and width were combined in a principal component analysis, in which the first axis explains 25.7% of the variation. Each lake's score on the axis is termed "habitat structural diversity". Details about the methods used are found in Elmberg *et al.* 1992, 1993, 1994.

RESULTS AND DISCUSSION

Our study concerns all waterfowl (i.e. the orders *Gaviiformes*, *Podicipediformes* and *Anseriformes*, and the Coot *Fulica atra*), but we here deal mainly with the dabbling ducks (*Anas*) and some functional groups of possible competitors. Species richness and pair density (relative abundance) of dabbling ducks varied among regions, but showed no consistent latitudinal or longitudinal trend (Elmberg *et al.* 1993, **Table 2**). In pairwise correlation analysis, species richness as well as relative abundance of dabbling ducks increased with overall abundance of activity trap invertebrates and emerging *Diptera*, with habitat structural diversity, and with the percentage of *Equisetum*-dominated shoreline (**Table 1**). Species richness also correlated positively with mean size class of activity trap invertebrates and with lake area. However, stepwise multiple regression analysis showed that the best set of predicting variables for species richness was habitat structural diversity, abundance of emerging *Diptera*, and the abundance of activity trap invertebrates. For the relative abundance of dabbling ducks the same type of analysis show that the percentage of *Equisetum* shore type, habitat structural diversity, and the abundance of emerging *Diptera* constituted the best set of predictors.

Table 1: Pairwise Pearson correlation coefficients between environmental variables and aspects of dabbling duck communities in 60 lakes in Sweden and Finland. Only statistically significant correlations are given.

Food resurce variables	Species richness of dabbling ducks	Relative abundance of dabbling ducks
Abundance of activity trap invertebrates	r = 0.453, P<0.01	r = 0.348, P<0.01
Mean size class of activity trap invertebrates	r = 0.328, P<0.01	
Abundance of emerging *Diptera*	r = 0.274, P<0.05	r = 0.324, P<0.01
Habitat variables		
Lake area	r = 0.267, P<0.05	
Habitat structural diversity	r = 0.528, P<0.001	r = 0.398, P<0.01
Shore with *Equisetum* (%)	r = 0.409, P<0.001	r = 0.432, P<0.001

In a biogeographical analysis of all waterfowl, the observed species richness pattern did not fit the random placement null model, suggesting that factors other than lake area per se were also important in affecting species number (Elmberg *et al.* 1994). We related species richness of different functional groups of waterfowl to environmental variables. In pairwise correlations, overall species richness, species richness of one-lake species (species not moving broods between lakes) and 'intermediate species' (those sometimes moving broods) were positively related to lake area. Overall species richness and species richness of non-piscivore birds and species which move the brood between lakes correlated positively with habitat structural diversity, whereas species richness of one-lake species and intermediate species did not. Except for in one-lake species, species richness also correlated positively with the number of prey taxa. Stepwise multiple regression revealed clearer differences between the functional groups. Overall species richness was best explained by the number of prey taxa and lake area, and that of non-piscivores by the number of prey taxa alone. Lake area was the best single predictor of species richness in both one-lake-species and intermediate species, whereas the number of prey taxa and habitat structural diversity was the best predictor set for species richness of lake changing species.

Our results thus indicate that species richness as well as abundance of breeding waterfowl communities are affected by a set of environmental factors. At least food resources, habitat diversity and lake area are important. However, the importance of these factors varies between different functional groups of waterfowl.

Thus far we have only described patterns, which in turn seem complex and not always very consistent. One reason for this being the case could be that the communities studied are not resource limited, i.e. that the patterns observed is a mesh of overlaid species-specific responses to different environmental variables. To approach the processes behind the patterns we thus devised a field experiment to test for resource limitation.

We selected 32 lakes in Västerbotten and Ångermanland, North Sweden, in which Mallard *Anas platyrhynchos* and Teal *Anas crecca* were the only dabbling ducks known to have bred regularly in the previous years. Lakes were generally smaller than 10 hectares, and they were poor to intermediate with respect to the local oligotrophic-eutrophic gradient. Six Mallards were introduced to each of 16 of the lakes in 1993, utilization by mallard and teal was recorded, and the intra- and interspecfic relations were compared with the situation in the remaining 16 lakes to which no birds were added. In 1994 the experiment was reversed, i.e. reference lakes became experimental lakes and vice versa.

The idea behind the experiment is simple. If there is resource limitation in the breeding lakes our introducing six mallards will be a test of intra- and interspecific competition. Assuming resource limitation the predicted outcome of intraspecific competition is that conspecifics (mallards) will utilize the lake less and/or have a lower reproductive success than mallards in control lakes, and the outcome of interspecific competition is that teal will utilize the lake less or have lower reproductive success.

Interestingly, occurrence of neither species differed markedly between experimental and control lakes in the early phase of breeding (**Table 2**; pair counts). However, inter- as well as intraspecific utilization was lower in experimental lakes than in reference lakes during the brood-rearing period, thus indicating resource limitation at this stage.

Table 2: Accumulated utilization of breeding lakes by wild ducks from two censuses in each census period. Sixteen lakes were experiment lakes in 1993, and reference lakes the next year. The remaining sixteen received the reversed treatment. m=male, f=female, p=pair, d=duckling

Census period	Experiment Mallard	Experiment Teal	Reference Mallard	Reference Teal
Pair count	49p	19p	43p	18p
Brood count	1m 9f 55d	3m 17f 40d	1m 14f 72d	1m 23f 76d

One interpretation is that adult birds respond less to the observable abundance of food or scarcity of nest sites, and commence nesting regardless of the situation encountered. By the time broods hatch and forage actively they have incurred higher mortality, or they have been moved by the female to a better foraging site.

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