Duck nests and predators: interaction, specialisation and possible management

Authors: Opermanis, Otars, Mednis, Aivars, and Bauga, Ilmārs

Source: Wildlife Biology, 7(2) : 87-96

Published By: Nordic Board for Wildlife Research

URL: https://doi.org/10.2981/wlb.2001.012

Duck nests and predators: interaction, specialisation and possible management

Otars Opermanis, Aivars Mednis & Ilmārs Bauga

Opermanis, O., Mednis, A. & Bauga, I. 2001: Duck nests and predators: interaction, specialisation and possible management. - Wildl. Biol. 7: 87-96.

Low hatching success due to nest depredation has frequently been reported from waterfowl breeding sites, but current knowledge on relationships between duck nests and their predators, which should form a basis for successful management, remains incomplete. We used a 13-year data set to test whether specific predator species are more successful in finding certain types of natural duck nests and whether there are interspecific differences in nest characteristics. Multinomial logistic regression allowed simultaneous evaluation of the effects of different factors, including their interactions. Significant predictors of duck nest fate were the presence of water edge and 3-way interaction among presence of gull colonies, island type and clutch initiation date. Significant predictors of nest site use by duck species were: 3-way interaction among presence of gull colonies, island type and clutch initiation date, 3-way interaction among presence of gull colonies, island type and presence of water edge and 2-way interaction between presence of water edge and clutch initiation date. The above interactions led to certain associations between duck species and predator species. Corvids (hooded crow *Corvus corone cornix* and raven *Corvus corax*) were responsible for depredating more mallard *Anas platyrhynchos* nests, but fewer common pochard *Aythya ferina* and tufted duck *Aythya fuligula* nests than expected. American mink *Mustela vison* was responsible for destroying more small *Anas* species (northern shoveler *Anas clypeata*, garganey *Anas querquedula* and gadwall *Anas strepera*) and tufted duck nests, but fewer mallard nests than expected. Marsh harrier *Circus aeruginosus* was apparently a generalist predator since we were not able to detect significant associations between this predator and nests of any specific duck species. We believe that examination of interactions between different factors affecting the probability that nests will be either successful or depredated by certain predator species may help waterfowl managers increase management success.

Key words: duck nests, habitat use, management, predators, predator identification, predator-prey relationships

Otars Opermanis & Aivars Mednis, Institute of Biology, Miera 3, Salaspils LV-2169, Latvia - e-mail: otars@parks.lv
Ilmārs Bauga, Lukstenieki, Mārupe LV-2167, Latvia

Received 25 May 2000, accepted 10 November 2000

Associate Editor: Hannu Pöysä

Due to high nest predation rates, waterfowl managers very often need to know which predator species is responsible for nest depredations in order to develop strategies to reduce predation (Pasitschniak-Arts, Clark & Messier 1998, Sargeant, Sovada & Greenwood 1998, Lariviere 1999). Effective management should be based on sound knowledge about factors potentially affecting nest success (van der Lee, Lutz, Hansen & Mathews 1999) and especially on predator behaviour and specialisation, but most waterfowl nesting studies

focus on nest predation rates rather than on the predators themselves.

Different predators use different search tactics (Martin 1987). For example, carrion crows *Corvus corone corone* may search extensively around previously discovered prey (Tinbergen, Impekoven & Franck 1967). Striped skunks *Mephitis mephitis* may apply different strategies (sit-and-wait and widely searching) in different habitats (Crabtree, Broome & Wolfe 1989). In other circumstances, predator movements may be random and nests discovered by chance (Clark & Nudds 1991, Lloyd, Plaganyi, Lepage, Little & Crowe 2000). These different search tactics most likely lead to certain nest types being found more frequently than other nest types.

Therefore, bird species whose nests are subject to predation may be assumed to develop their own strategies to minimise predation (e.g. Martin 1993). Many bird species choose nest sites which are characterised by a number of physical, social and other parameters (Cody 1985, Martin 1995). However, in many places, the local predator community is so diverse that bird species cannot safeguard their nests equally against all types of predators (Brua 1999). Thus, nests of different duck species likely suffer predation by a certain type (or types) of predator.

Current knowledge of these predator-prey relationships is incomplete (Johnson, Sargeant & Greenwood 1989, van der Lee et al. 1999). Except for widely accepted differences between avian and mammalian predators with respect to the importance of nest concealment (Clark & Nudds 1991, Pasitschniak-Arts & Messier 1995, Butler & Rotella 1998), and several detailed studies of a single predominant predator (e.g. Crabtree et al. 1989, Fleskes & Klaas 1993), no assessment has been made regarding the role of individual predators in a predator community. In many studies, predation and predators are considered as a rather anonymous force; typically the objective of these studies was either to estimate hatching success or to reveal the differences between characteristics of successful and depredated nests (Hill 1984, Crabtree et al. 1989, Clark & Wobeser 1997, Guyn & Clark 1997, Pasitschniak-Arts et al. 1998, Brua 1999). Another approach offered by Johnson et al. (1989) compared activity indices of different predators with daily nest predation rates of duck nests for the same time periods; using this approach they succeeded in identifying the most important predators of early and late duck nests in the Canadian Prairie Pothole Region.

In our study, we focused on the interactions between three different predator species, both mammalian and avian, and natural duck nests. Our aim was to test: 1) whether duck species are specialised in nest site use, i.e. does nest type differ among duck species; 2) whether predators are specialised, i.e. are there any associations between predators and nest type, and therefore, 3) whether certain predators are associated with the nests of specific duck species.

Methods

Study area and nest counts

We used data from a long-term duck population study (1985 to 1997) at Lake Engure, Latvia (57°15'N, 23°07'E), a eutrophic wetland encompassing 3,500 ha, of which ca 40% is covered by emergent vegetation. Ducks typically bred on solid islands and on floating mats of emergent vegetation. Island vegetation was dominated by grasses of the order *Poaceae*, occasionally interspersed with reeds *Phragmites communis* and shrubs. Water edges around the islands were mostly covered with sedges *Carex* spp. Floating mats consisted of cattails *Typha* spp. and reeds, occasionally surrounded by bulrush *Scirpus* spp.

Duck nests were found during 2-3 complete nest censuses performed in mid-May and early and late June, on permanent plots covering ca 130 ha. Additional efforts were made during each season to locate new nests by flushing females and watching lone birds of both sexes. Any scrape containing at least two eggs was considered a nest. Nest count methods have been described in detail by Blums, Bauga, Leja & Mednis (1993). All nests were monitored until hatching, depredation or abandonment.

Identification of predator types

The identification of predators was based on detailed examination of eggshells (if present), nest material dislocation and additional signs found in and around the nest. Typical evidence left by the three most common predators marsh harrier *Circus aeruginosus*, corvids and American mink *Mustela vison* is summarised in Table 1. Other nest predators included racoon dog *Nyctereutes procyonoides*, red fox *Vulpes vulpes*, stoat *Mustela erminea*, wild boar *Sus scrofa*, rats *Rattus* spp., goshawk *Accipiter gentilis*, eagle owl *Bubo bubo*, common gull *Larus canus* and herring gull *Larus argentatus*, but these species were rarely responsible for depredation of duck nests or rarely took females from the nests. Given the minimum sample size requirements, nest predation by any of these predators were excluded from our analyses, which thus only included predation events by marsh harrier (hereafter referred to

Table 1. Cues used to determine predators of destroyed nests at Lake Engure, Latvia.

Category	Eggs	Nest	Other evidence
Successfully hatched nest	Eggshells (usually halves) typically have membranes and some amount of small eggshell pieces attached.	Eggshells usually under the nest material (down), rarely uncovered.	Sometimes successfully hatched nest may be 'depredated'; the predator may have searched for unhatched eggs and nest material may be lifted and scattered.
Marsh harrier *Circus aeruginosus*	If eggs are fresh: edges of cuts are not bent inside. Impact marks on the eggshell. If incubated: bloody half-shells.	Predation takes place in the nest. Usually 2-3 eggs are eaten, the rest of clutch left is untouched.	Rarely, large female harriers may eat female ducks, but this is most likely a behaviour adapted by only some individuals
Corvids*: Raven *Corvus corax*, hooded crow, *C. corone*	Eggs absent. Only some fragments of incidentally broken eggs may be found, but usually in the immediate area.	Nest material is lifted and sometimes spread to the closest surroundings.	
American mink *Mustela vison*	Eggs may be untouched. Fresh eggs have distinct holes used for sipping egg contents with toothmarks at edges. Incubated eggs could be chewed, eggshell totally broken and bloody. May transport undamaged eggs to the den. Hatched ducklings may be killed and left uneaten.	In most cases feathers or the whole dead female duck is left with typical bite marks in the back of the head.	Attracted mostly to duck nests at the pipping stage.

* Corvids include also few depredation cases by magpie *Pica pica*.

as 'harrier'), corvids and American mink (hereafter referred to as 'mink'). The fourth predator category used in our analyses was 'unknown', to which we assigned all unclear cases, mostly caused by multi-predator visits or a long time period since the depredation event.

The method of predator identification based on the remains from depredated nests has been criticised (see review by Lariviere 1999), but is still widely used because all alternatives suggested to date (e.g. time-lapse cameras, hair-catchers, ceramic and wax-filled eggs) are either expensive or of limited use (Yahner & DeLong 1992, Pasitschniak-Arts & Messier 1995, Brown, Moller, Innes & Jansen 1998). The difficulties in predator identification are linked to the high variability of evidence left by individuals of one predator species and close similarity to evidence left by individuals of different predator species (Sargeant et al. 1998). We realise that in our study the signs left by predators may have been subjectively interpreted to some extent. However, there are three reasons why we believe that misinterpretations were reduced to a minimum: 1) in unclear cases, we did not hesitate to record the predator as 'unknown' and we specifically included this category in subsequent analyses (details below); 2) the three most common predators occurring at the lake left different cues (see Table 1), thus making it relatively easy to distinguish between them; 3) duck population studies at Lake Engure have been ongoing since 1958, so the field personnel have accumulated considerable experience in distinguishing between predator species. Their experience arises from the offering of duck eggs to captive predators and from the numerous cases when various predators were disturbed during duck nest predation in the field, thus allowing immediate examination of nest remains. Note that the characteristics outlined in Table 1 are very close to those reported from North American studies (Sargeant et al. 1998), comparing mink from both continents and American crows *Corvus brachyrhynchos* with corvids. Our study was based exclusively on natural duck nests, as results based on experiments with simulated nests may be biased (Guyn & Clark 1997, Butler & Rotella 1998).

Variables

Each nest record consisted of six categorical variables. The first variable was duck species (SPEC), which had four categories: tufted duck *Aythya fuligula*, common pochard *Aythya ferina*, mallard *Anas platyrhynchos* and 'small dabbling ducks'. Due to insufficient sample size, nests of northern shoveler *Anas clypeata*, garganey *Anas querquedula* and gadwall *Anas strepera* were pooled in a single category, because nests of these species have several similarities: they are generally well concealed, contain small but numerous eggs and females stay on the nest until the very last moment when approached by humans. This category is referred to as 'small *Anas* ducks'.

The second variable was nest fate (FATE) with successful nest category and four predator categories: harrier, corvids, mink and 'unknown'. All these five categories were included in the main analyses (see Rangen, Clark & Hobson 1999 for a similar approach).

The third variable was nest position in relation to gull colonies (COLO), with two categories: inside and outside. The most common gulls in the area were black-headed gull *Larus ridibundus* and little gull *Larus minutus*; the common tern *Sterna hirundo* also occurs frequently in the area. As the activity of gulls extended beyond colonies, nests within 30 m of colonies were also recorded as being situated inside colonies.

The fourth variable was nest position in relation to water edge (WATE), with two categories: ≤2 m from water (further referred as 'edge') and >2 m from the water.

The fifth variable was nest substrate or type of island (ISLE), with two categories: solid islands and mats of emergent vegetation.

The sixth variable was nest initiation date (INIT), with two categories: before and after the yearly 50% quantile, referred to as 'early' and 'late' nests, respectively. Clutch initiation date was estimated by back-dating based on the total number of eggs in the nest and the stage of incubation. Nest initiation dates were standardised to control for annual variation by expressing them as deviations from the yearly 50% quantile of all nests found (see Blums, Mednis & Clark 1997 for a similar approach).

Data analysis

We used a simple two-way contingency table and χ^2-tests to initially assess possible associations between species and predators of depredated duck nests. Differences between the observed and expected frequencies were standardised so that they approximately followed a standard normal distribution (Andersen 1997). These values (i.e. standardised residuals) were further used to evaluate the strength and direction of associations between variable categories.

We used multinomial logistic regression analysis to test for interspecific differences (SPEC; dependent variable) in nest site use by ducks with respect to ISLE, COLO, WATE and INIT, and to test whether nest fate (FATE; dependent variable) was associated with ISLE, COLO, WATE and INIT. The advantage of this method was that it allowed simultaneous evaluation of the effects of explanatory variables, including their interactions. We checked for all possible main, two and three-way effects. The final models were obtained by stepwise removal of non-significant terms, until only significant predictors ($P < 0.05$) remained. Model interpretation was done through odds ratios that were calculated for pairwise comparisons between two categories of response variable for cases in which the value of some explanatory variable was changed from one category to another. The odds ratio ranged within 0-~. With an odds ratio of 1 there is no association between the variables. For example, if the odds ratio for a comparison between mallard and tufted duck (reference) and early and late (reference) season equals 3.6, then the interpretation is that early nests are 3.6 times more likely than late nests to belong to mallard rather than to tufted duck. By performing a number of mutual comparisons between categories of response variable (species), it was possible to classify predator and duck species according to their relative preferences in accordance with selected parameters.

We tried to design and fit simple models using categorical variables with only few categories, because simple models, which otherwise may ignore substantial amounts of data, often outperform more complex models when parameters have to be estimated and decisions made (Hilborn & Mangel 1997). All tests were performed using the SPSS 10.0.5. program package and according to Norusis (1999) and Stokes, Davis & Koch (1995).

Results

Characteristics of successful and depredated nests

We recorded the fate of 2,426 pochard nests (215 depredated), 1,410 tufted duck nests (136 depredated), 2,006 mallard nests (571 depredated) and 752 (137 depredated) small *Anas* species nests. Of 1,059 predation events, 53.7% were attributed to marsh harrier, 14.7% to corvids, 3.0% to other birds, 9.0% to mink, 0.6% to racoon dog, 3.5% to other mammals, 1.9% were destroyed by humans and 13.6% by unknown predators. After excluding nests lost to predators other than harrier, corvids, mink and 'unknown', the final sample size amounted to 6,500.

A comparison of the characteristics of successful and depredated nests for all species separately reveal that all species benefited from nesting in gull colonies (Fig. 1). In all species, except small *Anas* ducks, the depredation rate was significantly higher on solid islands than on mats of emergent vegetation. Only in the common pochard did depredation occur more often along water edges than in areas away from the edges.

The association between FATE and SPEC was highly significant ($\chi^2 = 174.14$, df = 9, $P < 0.001$). There were no significant associations between harriers and the nests of any duck species (Fig. 2). Corvids depredated more mallard nests, but fewer common pochard and tufted duck nests than expected. The mink destroyed more small *Anas* species and tufted duck nests, but few-

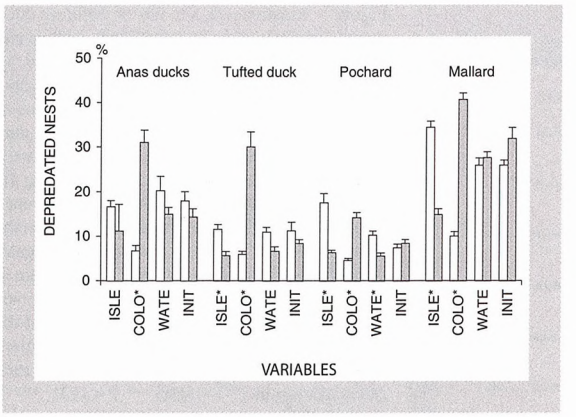

Figure 1. Proportion of depredated nests (+S.E.; %) of small *Anas* ducks, tufted ducks, pochards and mallards at Lake Engure, Latvia. White bars indicate for COLO: nests in gull colonies; for WATE: nests ≤ 2 m from the water; for INIT: early nests; and for ISLE: nests on solid islands. Grey bars indicate for COLO: nests outside gull colonies; for WATE: nests >2 m from the water; for INIT: late nests; and for ISLE: nests on mats of emergent vegetation. Statistically significant differences are indicated by * ($P < 0.05$).

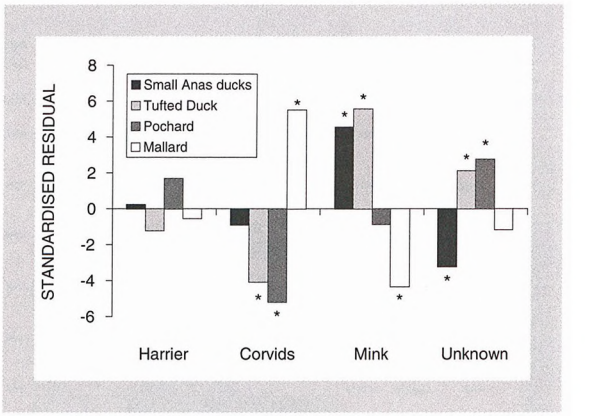

Figure 2. Associations between duck species (small *Anas* ducks, tufted duck, mallard and pochard) and predators of depredated nests at Lake Engure, Latvia. Significant deviations exceeding the value 2, which corresponds to the 97.5% percentile of the standard normal distribution, are indicated (*).

er mallard nests than expected. Unknown predators depredated more tufted duck and common pochard nests, but fewer small *Anas* species' nests than expected.

In order to examine the above associations in more detail, we tested for interspecific variation in nest site use (Table 2a) and whether predator species depredated specific nest types (Table 2b). In both models we used statistically significant predictors at the highest interaction level (3-way) for further examination of interactions using odds ratios. Pairwise comparisons among duck species and among predators were performed in order to rank species according to their relative preferences (Figs. 3 and 4).

Three-way effects of type of island, presence of gull colony and nest initiation date on interspecific nest site use and nest fate

The interaction ISLE*COLO*INIT appeared to be a statistically significant predictor for variation both in SPEC and FATE (see Table 2). This allowed us to present predator and duck species rankings together (see Fig. 3), which although arbitrary regarding the positioning of SPEC categories along with FATE categories, may explain some of the associations shown in Figure 2.

Duck nests on islands were most likely to be depredated by corvids. Mink was classified as the most significant predator on islands only in the late season and

Table 2. Sources of variation in A) nest site use by different duck species (with species (SPEC) as dependent variable) and B) duck nest fate (with nest fate (FATE) as dependent variable), i.e. the probability of being successful or depredated by a certain predator type. Analyses were based on multinomial logistic regressions. In the table, predictors used in the model interpretation are separated from the rest of the predictors in the model. See Methods for abbreviations of predictors.

A) SPEC as dependent variable Model goodness-of-fit P = 0.51			B) FATE as dependent variable Model goodness-of-fit P = 0.86		
Predictor	χ^2_3	P	Predictor	χ^2_4	P
ISLE*COLO*WATE	25.87	<0.001	ISLE*COLO*INIT	14.53	<0.01
ISLE*COLO*INIT	8.60	<0.05	WATE	45.92	<0.001
WATE*INIT	21.65	<0.001			
ISLE*INIT			ISLE*COLO		
ISLE*WATE			ISLE*INIT		
ISLE*COLO			COLO*INIT		
COLO*INIT			ISLE		
COLO*WATE			COLO		
ISLE			INIT		
COLO					
WATE					
INIT					

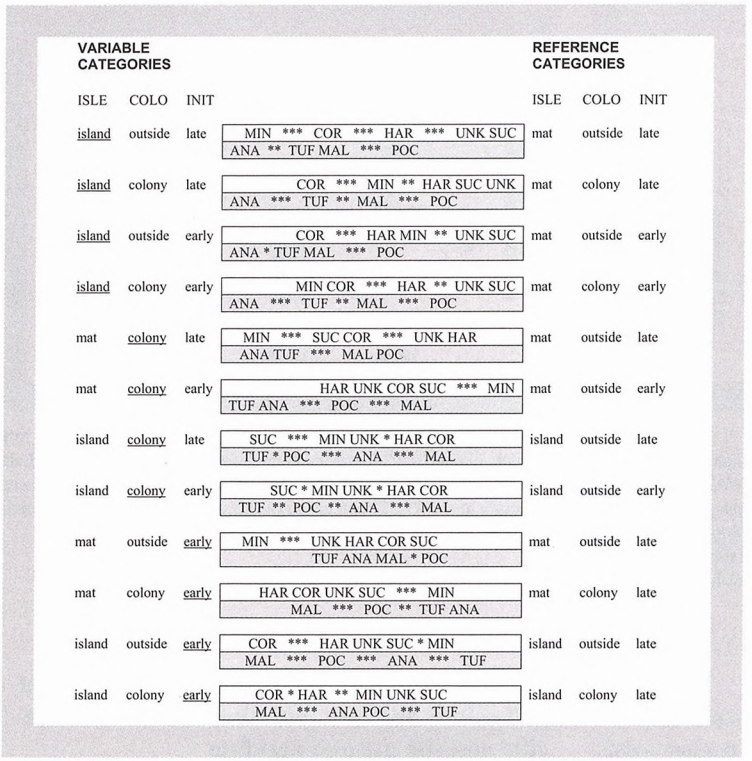

Figure 3. Relative nest site use of different duck species (small *Anas* ducks, tufted duck, mallard and pochard) and relative nest type preferences by different predator species at Lake Engure, Latvia, with respect to type of island (ISLE), presence of gull colonies (COLO) and clutch initiation date (INIT). The categories of the explanatory variables in different combinations are listed along the margins of the figure so that there is a difference only in one variable's category if one compares the left side with the right side (reference); this category is underlined on the left side. The change in this variable (from one category to another, see Methods) allows us to rank the categories of the response variable along the left-right gradient based on significance of odds ratios between each of category pairs (* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$). For example, referring to the first row of duck species there have been six odds ratios obtained: ANA vs TUF ($P<0.01$), ANA vs MAL ($P<0.01$), ANA vs POC ($P<0.001$), TUF vs MAL (n.s.), TUF vs POC ($P<0.001$) and MAL vs POC ($P<0.001$), which eventually gives the ranking of species, as shown in the figure. Consequently, as closer the species lies to some end of the line, the greater is the species' relative association with the combination of variable categories on that side. Abbreviations: HAR - harrier, COR - corvids, MIN - mink, UNK - unknown predator, SUC - successful nests, ANA - small *Anas* ducks, TUF - tufted duck, POC - common pochard, MAL - mallard.

outside gull colonies. Nests on mats of emergent vegetation were most likely to be either successful or depredated by unknown predators. Among ducks, islands were most preferred by small *Anas* species, whereas mats of emergent vegetation were most used by common pochards.

Duck nests in gull colonies and on solid islands were most likely to be successful. However, duck nests in gull colonies on mats and in the late season were most likely to be depredated by mink. Otherwise, mink were less likely to affect duck nests in gull colonies on mats in the early season. For duck nests outside gull colonies, the main threat, except for the above example, was avian predators (harrier and corvids). Gull colonies were most preferred by tufted ducks, whereas mallards used gull colonies less frequently.

Early nests were most likely to be depredated by corvids, except those on mats and outside gull colonies where the mink was prevalent. Among ducks, the mallard was the earliest breeder and the tufted duck generally the latest breeder.

The above interactions explain to a large extent the positive associations between corvids and mallard, mink and small *Anas* ducks, mink and tufted duck, and unknown predators and common pochard (see Fig. 2).

Three-way effects of type of island, presence of gull colony and water edge on interspecific nest site use

Nest sites on islands were most likely to be used by small *Anas* species, and nest sites on mats of emergent vegetation were most likely to be used by common pochards (see Fig. 4a). Nest sites in gull colonies were most likely to be used by tufted ducks, whereas nest sites outside gull colonies were most likely to be used by nesting mallards. Water edges on mats of emergent vegetation were mostly used by tufted ducks, whereas water edges on islands were mostly used by common pochards. Nest sites far away from the water edges were most likely to be used by small *Anas* species, but on mats with no gull colonies the common pochard was prevalent.

Two-way effects of water edge and nest initiation date on interspecific nest site use

Water edges were most often used by tufted ducks and mallards whereas areas far from the edges were most used by common pochards (see Fig. 4b). Again, mallards were the earliest breeders and tufted ducks the latest breeders.

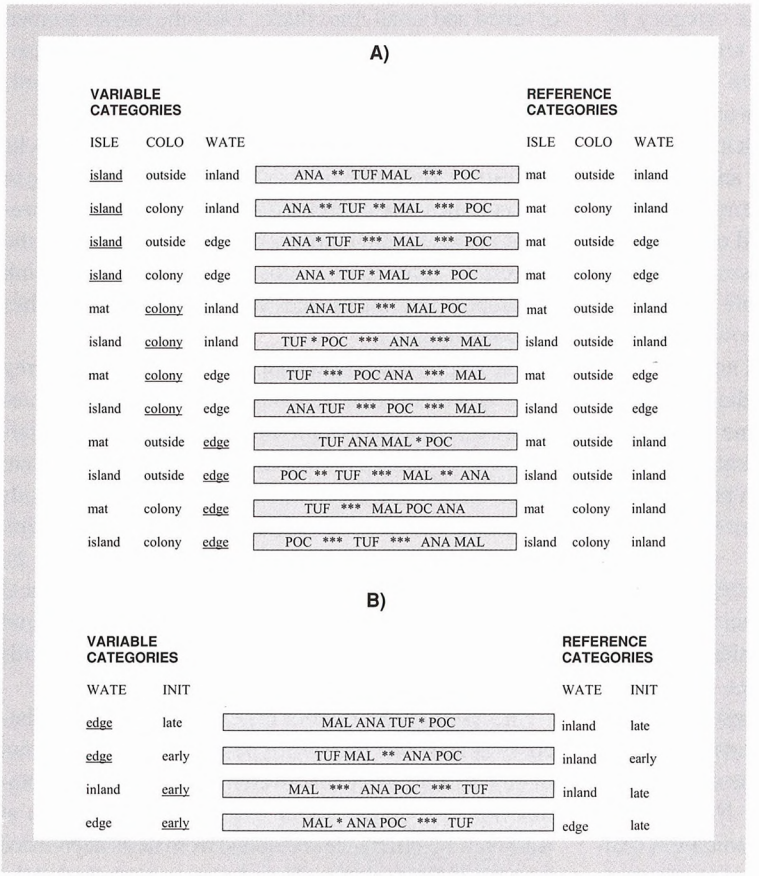

Figure 4. Relative nest site use of different duck species (small *Anas* ducks, tufted duck, mallard and pochard) with respect to A) type of island (ISLE), presence of gull colonies (COLO) and water edge (WATE), and B) presence of water edge (WATE) and clutch initiation date (INIT). Duck species rankings are based on statistical significance of odds ratios (* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$). Underlined categories (left) are compared with the reference (right). See also the legend to Figure 3.

One-way effect of water edge on nest fate

Nests at water edges were most likely to be depredated by mink, harrier or unknown predators, whereas nests more than two metres away from the edge were most likely to be depredated by corvids. Successful nests were less likely ($P < 0.001$) to be situated at edges than the nests depredated by mink, harrier or unknown predators, however, successful nests were more likely ($P < 0.01$) to be situated at edges than those depredated by corvids.

Assessment of unknown predators

The predation pattern of unknown predators seemed to be quite different from that of the known predators (see Fig. 3): only in six cases (out of 12) did it not differ from that of harrier, in three cases from that of mink and in three cases from that of corvids. Accordingly, we could not attribute depredation cases by unknown predators to any known predators.

Discussion

Methodological considerations

Most waterfowl studies have addressed predation only by comparing characteristics of successful and depredated nests or estimating habitat-specific nesting success (Hill 1984, Crabtree et al. 1989, Guyn & Clark 1997, Pasitschniak-Arts et al. 1998, Brua 1999). However, current knowledge does not include detailed analyses of depredated nests which could provide answers to the question which duck nest predators are most important and why. Apparently, most researchers have refrained from analysing depredated nests due to the unreliability of predator identification methods based on egg remains found at depredated nests. Nevertheless, we believe that this line of research has some value, at least in areas like Lake Engure, where few predator species predominate, and the cues they leave at nests are relatively easily recognised. For future studies, we recommend that unclear cases be recorded as 'unknown' and analysed together with other data. Furthermore, it

should be possible to make use of this category by comparing it with predation patterns of known predator types, unless the category 'unknown' constitutes too large a proportion of all records. Unfortunately, in our study (see Fig. 3) there was no convincing similarity between the 'unknown' predator category and any of the known predator species. Therefore it seems likely that the 'unknown' category mainly consisted of other predators not included in the main analyses. However, marsh harrier could actually be responsible for many of the nest depredations recorded as 'unknown', because it usually consumes only a few eggs and not the whole clutch (see Table 1). This may increase the probability that other predators will find and consume the remainder of the nest contents later, thereby making it difficult for a researcher to judge correctly which predator species came first or making predation patterns totally unrecognisable.

Our study, like many others, was not perfect in its initial design, and other potentially important factors may have been overlooked. The role of supplementary (or buffer) prey whose presence or absence may correspondingly increase or decrease duck nesting success (e.g. van der Lee et al. 1999), was not considered. Nor did we carry out an analysis of the effects of duck nest spacing patterns which may (Clark & Nudds 1991, Elser & Grand 1993) or may not affect predation (Andrén 1991). Added variables such as 'distance to the nearest nest' could reveal some search patterns of certain predator types, however, we hope to address this question elsewhere. In order to obtain better modelling, it is essential to attain more knowledge about predator searching success. For example, in our study we assume that all nest types are equally exposed to the search of all predator species, which may, of course, be wrong.

Interpretation of the findings

Our assessment of predator-prey interactions at Lake Engure was based on two models with different response variables (SPEC and FATE), but the same explanatory variables and data set. This allowed a parallel analysis of these response variable levels (see Fig. 3) and description of the relationships between duck species (using certain sites for nesting) and predator type (finding certain nests to depredate). Our study demonstrated high relative specialisation among predators in finding certain duck nest types, and strong differences among duck species in relation to sites used for nesting. Because some duck species had typical nest appearances, which obviously affected their discovery by certain predators, we were able to record several associations, e.g. between corvids and nests of mallard; between mink and nests of tufted and small *Anas* ducks. Only the harrier seemed to be a generalist predator, because no significant associations with nests of certain duck species were recorded (see Fig. 2).

The mink was most associated with small *Anas* ducks and especially tufted duck, which preferred nesting in gull colonies. We interpret this result to mean that predator access to gull colonies can be reduced due to the aggressive behaviour of gulls (Kruuk 1964). The mink apparently was most successful, because it approaches a colony by land.

Our results also show that predators and their prey were spaced in time. Corvids were the principal predators on early nests, and mink on late nests; similarly the earliest breeders were mallards, but the latest were tufted ducks (see Figs. 3 and 4b). As a result corvids were associated with mallard nests, whereas mink were associated with nests of tufted ducks (see Fig. 2). Other studies similarly report corvids to be typical predators on early nests (e.g. Johnson et al. 1989) and late nests to be more successful in areas where corvids were the only duck nest predators (e.g. Hill 1984).

Successful nests did not differ from nests depredated by at least one predator type in 10 comparisons out of 12 (see Fig. 3) and in different circumstances (combinations of categories of explanatory variables) at least once no difference was found from nests depredated by each of the predators. Therefore we conclude that the nest variables used in this study did not clearly explain the differences between successful and depredated nests, leading to the suggestion that duck nests may largely have been found and depredated by chance. If this was not the case, nest site characteristics of successful nests should not match those of depredated nests as was the case for nests situated in gull colonies on solid islands. Here nests had a significantly higher probability of being successful, obviously either because predators had limited access to duck nests within colonies because they were mobbed by gulls or because gull nests and chicks act as buffer prey between duck nests and predators. However, this makes it difficult to explain why nesting in gull colonies was not safe on mats of emergent vegetation.

An important conclusion may be drawn from comparing Figure 1 (two-way assessment of differences between successful and depredated nests) with Figure 3 (multi-way assessment of the same differences). In the first, significant differences were present in three variables (COLO, ISLE, WATE) while in the second comparison only the presence or absence of gull colonies (COLO) affected nest fate so that successful nests were different from nests depredated by all predator species

involved. This shows that analysis of only main effects may overestimate the differences between successful and depredated nests and further studies should focus on the interaction of multiple factors which probably is what happens in nature.

Management implications

The patterns observed are of potential value in decision-making in management of waterfowl production areas. If waterfowl managers are concerned about low reproduction rates of certain species, management efforts should be directed towards associated predator species. For example, previous studies have shown that early nests are most important for population recruitment (Mihelsons, Mednis & Blums 1986, Dzus & Clark 1998). Thus, local managers may be particularly interested in increasing hatching success early in the nesting season. To achieve this, removal of corvids could be considered first, but as this action would mostly benefit mallards (see Figs. 2 and 3), it might prove valuable to remove mink from mats of emergent vegetation with no gull colonies, as this would probably increase the hatching rates of more duck species, i.e. small *Anas* ducks and tufted ducks, in the early season. If non-lethal means of management are preferred, the creation of better breeding duck micro-habitats which are unsuitable for predators, should be considered. In order to minimise nest depredation by corvids, managers should create more edges (islands of curved coastline), attract more gulls (see Fig. 3) and, finally, remove vertical elements (trees, bushes, poles), which can be used by crows as perching sites (e.g. Galbraith 1989).

Unfortunately, predator elimination does not always increase waterfowl hatching success, possibly because of compensatory predation by other predator species or recolonisation by new individuals of the same predator species (Clark, Meger & Ignatiuk 1995, Sargeant, Sovada & Shaffer 1995, Beauchamp, Nudds & Clark 1996). Further studies should investigate these aspects, because no management plans based on the above assessment would fulfill expectations if compensatory predation and/or recolonisation were likely to happen.

Acknowledgements - we thank P. Blums, M. Janaus, Y. Kats, J. Kazubiernis, P. Leja, G. Lejins (deceased), A. Stipniece, J. Viksne and many other people for assistance with field work. We are grateful to P. Blums, A. Aunins, P.E. Rasmussen, J. Viksne, J. Ozolins and two anonymous referees for valuable comments on earlier drafts of this paper. R. Sloan improved the English language. The study was financed from a Latvian Council of Science grant No. 96.0125.

References

Andersen, E.B. 1997: Introduction to the Statistical Analysis of Categorical Data. - Springer, Heidelberg, 265 pp.

Andrén, H. 1991: Predation: an overrated factor for over-dispersion of birds' nests? - Animal Behaviour 41: 1063-1069.

Beauchamp, W.D., Nudds, T.D. & Clark, R.G. 1996: Duck nest success declines with and without predator management. - Journal of Wildlife Management 60: 258-264.

Blums, P., Bauga, I., Leja, P. & Mednis, A. 1993: Breeding population of ducks on Engure Lake, Latvia for 35 years. - Ring 15: 165-169.

Blums, P., Mednis, A. & Clark, R.G. 1997: Effect of incubation body mass on reproductive success and survival of two European diving ducks: a test of the nutrient limitation hypothesis. - Condor 99: 916-925.

Brown, K.P., Moller, H., Innes, J. & Jansen, P. 1998: Identifying predators at nests of small birds in a New Zealand forest. - Ibis 140: 274-279.

Brua, R.B. 1999: Ruddy duck nesting success: do nest characteristics deter nest predation? - Condor 101: 867-870.

Butler, M.A. & Rotella, J.J. 1998: Validity of using artificial nests to assess duck-nest success. - Journal of Wildlife Management 62: 163-170.

Clark, R.G. & Nudds, T.D. 1991: Habitat patch size and duck nesting success: the crucial experiments have not been performed. - Wildlife Society Bulletin 19: 534-543.

Clark, R.G., Meger, D.E. & Ignatiuk, J.B. 1995: Removing American Crows and duck nesting success. - Canadian Journal of Zoology 73: 518-522.

Clark, R.G. & Wobeser, B.K. 1997: Making sense of scents: effects of odour on survival of simulated duck nests. - Journal of Avian Biology 28: 31-37.

Cody, M. 1985: Habitat selection in birds. - Academic Press, Orlando, 420 pp.

Crabtree, R.L., Broome, L.S. & Wolfe, M.L. 1989: Effects of habitat characteristics on gadwall nest predation and nest-site selection. - Journal of Wildlife Management 53: 129-137.

Dzus, E.H. & Clark, R.G. 1998: Brood survival and recruitment of Mallards in relation to wetland density and hatching date. - Auk 115: 311-318.

Elser, D. & Grand, J.B. 1993: Factors influencing depredation of artificial duck nests. - Journal of Wildlife Management 57: 244-248.

Fleskes, J.P. & Klaas, E.E. 1993: Remains of ducks and other prey found near Fox and Mink dens on an Iowa Wildlife Refuge. - Prairie Naturalist 25: 43-50.

Galbraith, H. 1989: Arrival and habitat use by Lapwings Vanellus vanellus in early breeding season. - Ibis 131: 377-388.

Guyn, K.L. & Clark, R.G. 1997: Cover characteristics and success of natural and artificial duck nests. - Journal of Field Ornithology 68: 33-41.

Hilborn, R. & Mangel, M. 1997: The ecological detective: confronting models with data. - Princeton, New Jersey, 315 pp.

Hill, D.A. 1984: Factors affecting nest success in the Mallard and Tufted Duck. - Ornis Scandinavica 15: 115-122.

Johnson, D.H., Sargeant, A.B. & Greenwood, R.J. 1989: Importance of individual species of predators on nesting success of ducks in the Canadian Prairie Pothole Region. - Canadian Journal of Zoology 67: 291-297.

Kruuk, H. 1964: Predators and anti-predator behaviour of the black-headed gull (Larus ridibundus L.). - Behaviour Supplement 11: 1-130.

Lariviere, S. 1999: Reasons why predators cannot be inferred from nest remains. - Condor 101: 718-721.

Lloyd, P., Plaganyi, E., Lepage, D., Little, R.M. & Crowe T.M. 2000: Nest-site selection, egg pigmentation and clutch predation in the ground-nesting Namaqua Sandgrouse Pterocles namaqua. - Ibis 142: 123-131.

Martin, T.E. 1987: Artificial nest experiments: effects of nest appearance and type of predator. - Condor 89: 925-928.

Martin, T.E. 1993: Nest predation and nest sites. - BioScience 43: 523-532.

Martin, T.E. 1995: Avian life history evolution in relation to nest sites, nest predation, and food. - Ecological Monographs 65: 101-127.

Mihelsons, H., Mednis, A. & Blums, P. 1986: Populyacionnaya ekologiya migriruyuschih utok v Latvii. (In Russian with English summary: Population ecology of migratory ducks in Latvia). - Publishing House Zinatne, Riga, 111 pp.

Norusis, M.J. 1999: SPSS Regression Models 10.0. - SPSS Inc., 215 pp.

Pasitschniak-Arts, M., Clark, R.G. & Messier, F. 1998: Duck nesting success in a fragmented prairie landscape: is edge effect important? - Biological Conservation 85: 55-62.

Pasitschniak-Arts, M. & Messier, F. 1995: Predator identification at simulated waterfowl nests using inconspicuous hair catchers and wax-filled eggs. - Canadian Journal of Zoology 73: 984-990.

Rangen, S.A., Clark, R.G. & Hobson, K.A. 1999: Influence of nest-site vegetation and predator community on the success of artificial songbird nests. - Canadian Journal of Zoology 77: 1676-1681.

Sargeant, A.B., Sovada, M.A. & Greenwood, R.J. 1998: Interpreting evidence of depredation of duck nests in the Prairie Pothole Region. - U.S. Geological Survey, Northern Prairie Wildlife Research Center, Jamestown, ND and Ducks Unlimited, Inc., Memphis, TN, 72 pp.

Sargeant, A.B., Sovada, M.A. & Shaffer, T.L. 1995: Seasonal predator removal relative to hatch rate of duck nests in waterfowl production areas. - Wildlife Society Bulletin 23: 507-513.

Stokes, M.E., Davis, C.S. & Koch, G.G. 1995: Categorical data analysis using the SAS system. - SAS Institute Inc., 499 pp.

Tinbergen, N., Impekoven, M. & Franck, D. 1967: An experiment on spacing-out as a defence against predation. - Behaviour 28: 307-321.

van der Lee, B.A., Lutz, R.S., Hansen, L.A. & Mathews, N.E. 1999: Effects of supplemental prey, vegetation, and time on success of artificial nests. - Journal of Wildlife Management 63: 1299-1305.

Yahner, R.H. & DeLong, C.A. 1992: Avian predation and parasitism on artificial eggs in two fragmented landscapes. - Wilson Bulletin 104: 162-168.