

Relationships between the nest predation rates caused by different waterfowl nest predators: an artificial nest experiment

Jānis Reihmanis*

Laboratory of Ornithology, Institute of Biology, Miera 3, Salaspils LV-2169, Latvia.

*Corresponding author, E-mail: janis.reihmanis@dap.gov.lv

Abstract

Nest predation is crucial process affecting the breeding success of birds and their fitness. Numerous studies have been carried out using natural and artificial nests to test nest failures caused by different predator species. The aim of this study was to investigate the interaction among nest predation rates due to different predators, i.e. how changes in one predator's predation rate and consumption of the nests are related to the predation rate of other predators? Depredation of artificial nests was studied in 5.68 ha and 10.17 ha plot on Lielrova island, in Lake Engure in Latvia, in 2002 and 2003 respectively. This study shows that food availability (e.g. number of nests) and activity of other predators was significantly related to the nest predation rate by interspecific predators in a waterfowl nest predator community. Nest daily mortality rates caused by predators were related to changes in the number of exposed nests. The experimental study showed that predation on artificial nests by competitive nest predators was a significant predictor of the possibility of nest predation by other members of the local predator community.

Key words: artificial nest, corvids, mammals, marsh harrier, nest predation.

Introduction

Nest predation is a major factor affecting nesting success and is a driving force in the evolution of birds (Martin 1988; Ricklefs 2000). As artificial nests are easy to construct they are frequently used to measure the variation in predation rate associated with characteristics of eggs, nests, habitat, location of nests, nest density and season (Major, Kendal 1996). These factors allow the investigators to control variables of interest and to work with adequate samples.

In most studies of nest predation, the nest fate is measured in general (successful vs. depredated) or the study is focused on a single target nest predator species or on a group of species (e.g. avian vs. nonavian; Yahner, Cypher 1987; Yahner, Scott 1988) and the nest predation rates of different nest predator species are overlooked. In the majority of ecosystems there are several nest predator species. Knowledge about interactions among predators is required in order to determine their effect on the prey population. The influence of predators on the risk of nest predation has been investigated in relation to habitat quality (Yahner, Cypher 1987; Eriksson 2001) or predator and nest characteristics (Crabtree et al. 1989; Cresswell 1997; Opermanis et al. 2001), interactions between competitors in waterfowl nest predator assemblages are poorly understood.

The aim of this study was to investigate the interactions between nest predation rates due to interspecific predators depending on nest availability, i.e. how the changes in the predation rate of one predator and the consumption of the nests are related to predation rate of other predators.

Materials and methods

Study area

This study was conducted on Lake Engure, Latvia (57° 15' N, 23° 07' E), an eutrophic wetland encompassing 3,500 ha. About 40 % of the lake is covered by emergent vegetation, mainly common reed *Phragmites australis*, narrow-leaved cattail *Typha angustifolia* and bulrush *Scirpus* spp. The data on artificial nests were collected on Lielrova island and the most accessible small artificial islands. The islands were open, flat and the vegetation was dominated by grasses *Poaceae*, occasionally interspersed with reeds, willow *Salix* spp. (but mostly *Salix repens*) and sedges *Carex* spp. The study area was 5.68 ha and 10.17 ha, in 2002 and 2003 respectively. The size of the experimental plots was selected according to the number of nests necessary to statistically process the data. The area of the study plots was estimated using an aerial photo (1 : 10000 scale) and ArcView version 8 software package. The location and size of the experimental plots were selected so that the plots had sufficient numbers of natural duck nests in the particular year. In the study plots Mallard *Anas platyrhynchos* were common breeders and Gadwall *Anas strepera*, Northern Shoveler *A. clypeata*, Garganey *A. querquedula*, Tufted Duck *Aythya fuligula* and Common Pochard *A. ferrina* nests were rare during the breeding season.

Experimental design and field procedures

The artificial nest experiment was carried out from July 11 till October 8 in 2002 and from August 30 till October 17 in 2003. To minimize interference to the natural predator-prey ecosystem and to exclude an increase of predation rate in real duck nests stemming from the attraction of predators, the artificial nests experiment was carried out after the duck breeding season (Association for the Study of Animal Behaviour, Animal Behaviour Society 2001). The lengths of trials were five and seven days. During each trial, 50 and 32 artificial nests were exposed, in 2002 and 2003 respectively. The number of artificial nests in each trial was equal to the number of duck nests in the study area in the same year. Each artificial nest was randomly placed where suitable substrate for duck nesting was present. The minimal distance between nearest neighbouring nests was 10 m. To relocate the nests they were marked using 1.5-m-long willow canes. To decrease the probability that potential nest predators use this mark to locate the nest, the canes were placed 2 m away from the nests (Hein, Hein 1996). The artificial nests were constructed to resemble duck nests. Nest bowls were made by creating a shallow depression in the ground approximately 15 cm in diameter. Six fresh brown hen eggs were placed in each bowl. Bowls were concealed by vegetation so that two or three eggs were visible from above. Since the nests were partly covered by vegetation, they appeared like nests abandoned or from which the female duck was flushed (Opermanis 2004). Since non-cryptic hen eggs were used, their colour was similar to that of duck eggs and they did not affect the detectability of the nests by visually oriented predators (Weidinger 2001).

Nest-site characteristics were recorded in each experimental trial: species of plants in

a 1-m radius around the nest, height of vegetation around the nest estimated using five randomly placed measurements in a 1-m radius around the nest, and location (natural vs. artificial island). The date of the placement of the nest and subsequent relocations were recorded. If the nest was depredated, the number of damage or missing eggs was recorded.

All nests were exposed for 24 or 25 days, which was close to the mean duration of the egg stage of real duck nests. If the nest was successful after this time, it was removed and reset in a different location, keeping total number of the nests in each trial constant.

The fate of the nests was measured at the end of each trial. A nest was considered depredated when at least one egg was damaged or missing. Depredated nests were removed and reset in different locations, maintaining the total number of nests in each trial constant. The nest predators were identified using careful examination of the remaining eggshells and additional signs in and around the nest (Opermanis et al. 2001). The nest predators were divided in four groups using the as precise as possible taxonomical level: (i) 'Harriers' – including Marsh Harrier *Circus aeruginosus*; (ii) 'Corvids' – including Raven *Corvus corax*, Hooded Crow *C. corone cornix* and Magpie *Pica pica*; (iii) 'Mammals' – including American Mink *Mustela vison*, Raccoon Dog *Nyctereutes procyonioides* and Red Fox *Vulpes vulpes*; (iv) 'Unknown' – including all cases where the predator was not possible to identify sufficiently precisely or where multiple predators were present. As mammals as predators were detected only in one trial in 2003, this data was pooled with the 'Unknown' predator group and designated in further as 'Other' predators.

Data analysis

Data from both years were analysed separately, as recommended by Butler and Rotella (1998). The daily mortality rates (hereafter DMR) of nests were estimated by the Mayfield method (Mayfield 1961; Mayfield 1975). DMR of each trial was divided in separate days. The nest-day was used as the unit of exposure because the number of nest exposure days in trials differed – 5 days in 2002 and 7 days in 2003.

To identify interactions between the nest predation rates due to interspecific predators, multiple linear regression analysis was used as follows – one by one the DMR by each predator was used as a dependent variable and the DMR's by the remaining predators were used as predictor variables. In multiple linear regression analyses, the daily mortality rates were arcsine transformed. The significance of the regression models was estimated using ANOVA. The significance of coefficients of multiple linear regression equations was estimated using *t* statistics. The nests availability rate for each predator was calculated as the daily survival probability after depredation by the remaining predators. Spearman rank correlation was used to detect association between the DMR by each predator type and the nest availability rate for a particular predator.

All statistical tests were conducted using SPSS statistical software package. All tests (where were preference) were two tailed.

Results

All multiple linear regression models in both years demonstrate significant relationships between the DMR's by different predators (Table 1). Significant negative relations in year 2002 were detected (i.e. significant unstandardized coefficient in multiple linear model

Table 1. Multiple regression analysis of the effects of the predation rates of different predator species (predictor variable) on the nest daily mortality rates by specific predator groups (dependent variable) in an artificial nests experiment at the Lake Engure, Latvia in 2002 and 2003

Year	Regression model estimation				Regression equation coefficient estimation				
	Dependent variable r^2	Coefficient of determination d.f.	Degree of freedom	F-value	Significance P	Predictor variable	Unstandardized coefficient	Student's t test	Significance P
2002	Harriers	0.666	89	57.091	< 0.001	Constant	0.099	20.260	< 0.001
						Corvids	-0.615	-9.461	< 0.001
	Corvids	0.623	89	47.337	< 0.001	Mammals	0.209	1.079	0.284
						Unknown	-0.609	-4.042	< 0.001
						Constant	0.097	11.179	< 0.001
						Mammals	-0.444	-2.002	0.048
	Mammals	0.352	89	15.577	< 0.001	Unknown	-0.026	-0.136	0.892
						Harriers	-0.829	-9.461	< 0.001
						Constant	0.002	0.043	0.966
						Unknown	0.458	6.008	< 0.001
Unknown	0.448	89	23.252	< 0.001	Harriers	0.064	1.079	0.284	
					Corvids	-0.100	-2.002	0.048	
					Constant	0.037	5.556	< 0.001	
					Harriers	-0.262	-4.042	< 0.001	
2003	Harriers	0.200	48	5.756	0.006	Corvids	0.645	6.008	< 0.001
						Constant	0.044	3.240	0.002
	Corvids	0.832	48	113.603	< 0.001	Corvids	-0.745	-0.870	0.389
						Other	-0.204	-0.565	0.575
						Constant	0.015	11.877	< 0.001
						Other	0.373	13.192	< 0.001
	Other	0.830	48	112.326	< 0.001	Harriers	-0.022	-0.870	0.389
						Constant	-0.025	-5.078	< 0.001
						Harriers	-0.034	-0.565	0.575
						Corvids	2.118	13.192	< 0.001

Table 2. Spearman rank correlations between daily mortality rate by each nests predator and the availability of remaining nests after depredation by the other predators, in an artificial nest experiment during 2002 and 2003 at Lake Engure, Latvia

Nest predator	Year	Spearman rank correlation coefficient r_s	Number of observations (days)	Significance P (two tailed)
Harriers	2002	0.763	90	< 0.001
Corvids	2002	0.549	90	< 0.001
Mammals	2002	-0.055	90	0.609
Unknown	2002	0.012	90	0.907
Harriers	2003	0.555	49	< 0.001
Corvids	2003	-0.430	49	0.002
Other	2003	-0.382	49	0.007

equitation) between Harriers and Corvids, and between Harriers and Unknown predators: an increasing daily mortality rate due to Corvids and Unknown predators was related with a decrease in the Harrier-caused nest depredation rate (or vice versa). An increasing daily mortality rate by Corvids occurred with a decrease in Mammal nest predation rate (or vice versa). A significant positive relation between Mammals and Unknown predators was identified in 2002. In 2003 a significant positive relation was found only between Corvids and Other (Table 1).

The total nest exposure to possible depredation significantly increased the likelihood of nest mortality by Harriers and Corvids in both years and by Other only in 2003 (Table 2).

Discussion

The artificial nest experiment demonstrates that nest predators can affect predation rates of each other. Although the nest predators were not identified to species, probably most of the Unknown predators in 2002 were mammals, as the late summer was dry and the water level was low. These conditions enable Raccoon Dogs and Foxes to use small ridges to reach the island from the lake shore, which was confirmed by Mammalian faeces found on the island. In 2003 Ravens were believed to be responsible for majority of depredated nests by Other predators, since all eggs were absent in some nests and there were no additional signs. The above explain the positive relationships between Mammals and Unknown in 2002 and between Corvids and Other in 2003.

Since the artificial nest experiment was carried out beyond the breeding season (i.e. no real duck nests) the study area had a higher density of nests. Aggregation of predators (mainly magpies) was observed during the experiment. Bendekoff et al. (1997) demonstrated that *Corvidae* successfully apply 'Spatial information processing' to make their own foraging more effective. This has also been confirmed in studies where corvids were natural (Erikstad et al. 1982) or artificial (Picozzi 1975) nest predators. Therefore, it is possible that corvids changed their feeding behaviour, thereby significantly affecting other predators. Predators use prey selection according to prey species, age or sex and

interindividual variations in hunting behavior, and predatory behavior may differ not only between habitats, but also within similar environments (Mitani et al. 2001). Sparrowhawk *Accipiter nisus* consistently selectively decides to hunt the weakest and most vulnerable individuals in a population (Götmark 2002; Quinn, Cresswell 2004), but nests with openly visible eggs are vulnerable to visually oriented nest predators (Opermanis 2004). Thus, openly placed artificial nests, as immobile and vulnerable prey, are more susceptible to successful attack of a predator. The Harrier is a generalist predator, feeding on a wide variety of prey (Cramp, Simmons 1980) and can change its foraging behaviour and composition of the diet according to changes in the availability of different food items (Underhill-Day 1985), which is also true for other bird species (Bryant et al. 1999; Murakami 2002). Non-specific predation on nests of some duck species with different appearances, location and temporality showed that Harriers were generalist predators on waterfowl nests (Opermanis et al. 2001). Quartering hunting flights have been described earlier (Schipper 1977) and if predators find nests by random or systematic search, nests should be equally vulnerable. In our experiment similar hunting techniques were most frequently observed, but Harriers usually used transect searching flights to follow habitat edges (open water/reed stand) in late summer. Since waterfowl eggs contribute a small part of the Harrier diet (Kasparsons 1960; Schipper 1973; Underhill-Day 1985), there is a weak response to artificial nests as supplementary food items.

Norrdahl and Korpimäki (2002) demonstrated a response of diurnal raptors to a change of prey availability following cyclic fluctuations in rodent populations. They found a short time lag response in late summer, when non- and post-breeding individuals were free to search for patches with a high prey density. In this context, it was possible that Harriers prefer young waterfowl and reed breeding passerines, as they were abundant in the study area in late summer. Therefore, artificial nests in our experiment were not an important part of the Harrier diet and Harriers were likely pronounced opportunistic nests predators. This confirms an earlier observation by Opermanis (2001) that Harriers never consume entire egg contents. Thus, Harriers are generally weak competitors for artificial nests as a food item.

Mammal predation on artificial nests on islands have a chance character because of the difficulty in arriving on the island. Depredation by American Mink was low in both years because they depredate nests more frequently near hatching eggs or ducklings (A. Mednis, personal communication). DMR due to Mammals were analysed separately only in 2002, when foxes were observed on the island. The data are still insufficient, but it is clear that there is no relation between DMR by Mammals and DMR by specific avian predators – Harriers and Corvids (Table 1). Avian nest predators use visual cues to locate nests (Dwernychuk, Boag 1972) while mammals are olfactory oriented predators, resulting in a low possibility for an interaction between the predation rates. However further study is still required in this context.

Since the nest availability had a significant positive correlation with the daily mortality rates by Harriers and Corvids in both years (Table 2), the daily mortality rates by these predators influenced food availability and the success of nest searching by other predators.

Our experiment and other studies (Sutherland 1996; Krebs, Davies 1997) provide evidence that the interactions between nest predation rates by interspecific predators in the waterfowl nest predator community result from competition between different

predators for food, depending on the importance of eggs in the diet of the predator species. Predation on artificial nest by competitive nest predators was a significant predictor of the possibility of nest predation by other predators. The nest failure may be affected by area-dependent changes in predator assemblages on the landscape-level, and other factors also may be important. As the nests were only partly covered, the daily mortality rates more represented the activity of predators than successful searching for the nests. The experiment showed that the effects of food availability (e.g. numbers of nests) and the activity of one predator may influence nest predation rate by another predator in a waterfowl nest predator community. This study suggests that the traditional measure of nest success (failed vs. fledged at least one young) may not be appropriate in investigating predation, without careful validation of the experiment design and results, because changes in the predation rate by one predator may influence predation rate of another predator.

As this study presented the response of predators on artificial nests beyond real duck breeding season, future experiments should be carried out to examine whether the pre-breeding season determines the nest search behaviour of different predators.

Acknowledgements

This study was financed by the Latvian Council of Science (grant No. 01.0342). I thank Otars Opermanis for support and has invaluable advice on experimental design and Jānis Priednieks for provided encouragement. Vita Šalavejus assisted in the fieldwork, Gunta Krastiņa helped with ArcView and Aija Klupša improved the language. For comments on earlier draft of this paper I thank Oskars Keišs, Aivars Mednis, Otars Opermanis and Jānis Vīksne, and two anonymous referees.

References

- Association for the Study of Animal Behaviour, Animal Behaviour Society. 2001. Guidelines for the treatment of animals in behavioural research and teaching. *Anim. Behav.* 61: 271–275.
- Bendekoff P.A., Balda R.P., Kamill A.C., Hile A.G. 1997. Long-term spatial memory in four seed-caching corvid species. *Anim. Behav.* 53: 335–341.
- Bryant R., Jones I.L., Hipfner J.M. 1999. Responses to changes in prey availability by Common Murres and Thick-billed Murres at the Gannet Islands, Labrador. *Can. J. Zool.* 77: 1278–1287.
- Butler M.A., Rotella J.J. 1998. Validity of using artificial nests to assess duck-nest success. *J. Wildlife Manage.* 62: 163–171.
- Crabtree R.L., Broome L.S., Wolfe M.L. 1989. Effects of habitat characteristics on gadwall nest predation and nest-site selection. *J. Wildlife Manage.* 53: 129–137.
- Cramp S., Simmons K.E.L. (eds.) 1980. *Handbook of the Birds of Europe, the Middle East, and North Africa: the Birds of the Western Palearctic*. Vol. 2. Oxford University Press, Oxford.
- Creswell W. 1997. Nest predation: the relative effects of nest characteristics, clutch size and parental behaviour. *Anim. Behav.* 53: 93–103.
- Dwernychuk L.W., Boag D.A. 1972. How vegetative cover protects duck nests from egg-eating birds. *J. Wildlife Manage.* 36: 955–958.
- Eriksson L.M. 2001. Nest-predation at the edge: an experimental study contrasting two types of edges in the dry Chaco, Paraguay. *CBM:s Skriftserie* 3: 39–52.
- Erikstad K.E., Blom R., Myrberget S. 1982. Territorial hooded crows as predator on willow ptarmigan nests. *J. Wildlife Manage.* 46: 109–114.
- Hein E.W., Hein W.S. 1996. Effect of flagging on predation of artificial duck nests. *J. Field Ornithol.*

- 67: 604–611.
- Götmark F. 2002. Predation by sparrowhawks favours early breeding and small broods in great tits. *Oecologia* 130: 25–32.
- Kasparsons Ģ. 1960. Feeding of Marsh Harrier (*Circus aeruginosus*) at Lake Engure during summer 1958. In: Spuris Z. (ed.) *Bird Life of Latvia*. Latvijas PSR ZA izdevniecība, Rīga, 45–51 p. (in Latvian – Niedru lījas (*Circus aeruginosus*) barošanās Engures ezerā 1958. gada vasarā)
- Krebs J.R., Davies N.B. 1997. *Behavioural Ecology. An Evolutionary Approach*. 4th Ed. Blackwell Science. 456 p.
- Major R.E., Kendal C.E. 1996. The contribution of artificial nest experiments to understanding avian reproductive success: a review of methods. *Ibis* 138: 298–307.
- Martin T.E. 1988. Processes organizing open-nesting bird assemblages: competition or nest predation? *Evol. Ecol.* 2: 37–50.
- Mayfield H.F. 1961. Nesting success calculated from exposure. *Wilson Bull.* 73: 255–261.
- Mayfield H.F. 1975. Suggestions for calculating nest success. *Wilson Bull.* 87: 456–466.
- Mitani J.C., Sanders W.J., Lwanga J.S., Windfelder T.L. 2001. Predatory behaviour of crowned hawk-eagles (*Stephanoaetus coronatus*) in Kibale National Park, Uganda. *Behav. Ecol. Sociobiol.* 49: 187–195.
- Murakami M. 2002. Foraging mode shifts of four insectivorous bird species under temporally varying resource distribution in a Japanese deciduous forest. *Ornithol. Sci.* 1: 63–69.
- Norrdahl K., Korpimäki E. 2002. Seasonal changes in the numerical responses of predators to cyclic vole populations. *Ecography* 25: 428–438.
- Opermanis O. 2001. Marsh Harrier *Circus aeruginosus* predation on artificial duck nests: a field experiment. *Ornis Fennica* 78: 198–203.
- Opermanis O. 2004. Appearance and vulnerability of artificial duck nests to avian predators. *J. Avian. Biol.* (in press)
- Opermanis O., Mednis A., Bauga I. 2001. Duck nests and predators: interaction, specialisation and possible management. *Wildlife Biol.* 7: 87–96.
- Picozzi N. 1975. Crow predation on marked nests. *J. Wildlife Manage.* 39: 151–155.
- Quinn J.L., Cresswell W. 2004. Predator hunting behaviour and prey vulnerability. *J. Anim. Ecol.* 73: 143–154.
- Ricklefs R.E. 2000. Density dependence, evolutionary optimization, and the diversification of avian life histories. *Condor* 63: 9–22.
- Schipper W.J.A. 1973. A comparison of prey selection in sympatric Harriers, *Circus* sp., in Western Europe. *Le Gerfaut* 63: 17–121.
- Schipper W.J.A. 1977. Hunting in three European harriers (*Circus*) during the breeding season. *Ardea* 65: 53–72.
- Sutherland W.J. 1996. *From Individual Behaviour to Population Ecology*. Oxford University Press, Oxford.
- Underhill-Day J.C. 1985. The food of breeding Marsh Harriers *C. aeruginosus* in East Anglia. *Bird Study* 32: 199–206.
- Yahner R.H., Cypher B.L. 1987. Effects of nest location on depredation of artificial arboreal nests. *J. Wildlife Manage.* 51: 178–181.
- Weidinger K. 2001. Does egg colour affect predation rate on open passerine nests? *Behav. Ecol. Sociobiol.* 49: 456–464.

Sakarības starp dažādu ligzdu postītāju veikto ūdensputnu ligzdu postījumu apjomu: mākslīgo ligzdu eksperiments

Jānis Reihmanis*

Ornitoloģijas laboratorija, Latvijas Universitātes Bioloģijas institūts, Miera 3, Salaspils LV-2169, Latvija

*Korespondējošais autors, E-pasts: janis.reihmanis@dap.gov.lv

Kopsavilkums

Ligzdu postījumiem ir nozīmīga ietekme uz putnu ligzdošanas sekmēm un to izdzīvošanu. Lai izpētītu dažādu plēsēju sugu veiktos ligzdu postījumus, ir veikti daudzi pētījumi, izmantojot gan dabīgās, gan mākslīgās ligzdas. Šī darba mērķis bija noskaidrot atsevišķu ligzdu postītāju veikto ligzdu postījumu mijiedarbību, t.i., vai izmaiņas viena plēsēja veikto ligzdu postījumu biežumā un ligzdu patēriņā izmaina citu plēsēju veikto ligzdu postījumu biežumu. Mākslīgo ligzdu postījumu eksperiments tika veikts Engures ezera Lielrovas salā 2002. un 2003. gadā, attiecīgi 5,68 ha un 10,17 ha lielos parauglaukumos. Eksperiments parādīja, ka barības pieejamība (t.i., ligzdu skaits) un citu plēsēju darbība būtiski ietekmē pārējo ūdensputnu ligzdu postītāju sabiedrības sugu veikto ligzdu postījumu apjomu. Plēsēju veikto ligzdu postījumu biežums bija atkarīgs no tiem pieejamo ligzdu skaita. Iegūtie eksperimenta rezultāti parādīja, ka izmaiņas savstarpēji konkurējošu mākslīgo ligzdu postītāju veikto ligzdu postījumu biežumā būtiski ietekmē citu šajā teritorijā sastopamo plēsēju veikto ligzdu postījumu biežumu.