

Nest and brood stage association between ducks and small colonial gulls in boreal wetlands

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Heterospecific grouping is often associated with reduced predation. One example of this phenomenon is birds breeding in association with more aggressive species. Here we report a study of the association between breeding ducks and small colonial gulls during the nesting and brood-rearing periods in boreal wetlands in Finland. Dabbling duck nests were rarely found within gull colonies, while Tufted Duck (*Aythya fuligula*) and Pochard (*Aythya ferina*) nests were exclusively found within gull colonies. During the brood stage, the broods of most duck species were found more often than expected within the colony areas of small gulls, such as the Black-headed Gull (*Chroicocephalus ridibundus*) and Little Gull (*Hydrocoleus minutus*). Dabbling duck broods in particular were associated with gulls. In diving ducks, Tufted Duck broods preferred gull defence areas, whereas Common Goldeneye (*Bucephala clangula*) broods did not. We suggest that colonies of small gulls may be much more important for ducks than previously thought. In recent years, Black-headed Gull populations have decreased in Finland, and the populations of Tufted Duck and Pochard have concurrently decreased. We recommend that the nesting site requirements of small colonial gulls should be taken into account in wetland restoration and when building new wetlands.



1. Introduction

Nest predation is among the most important factors affecting the reproductive output of birds (Newton 1998). In addition to nest predation, breeding females are exposed to an increased predation risk during nesting and brood-rearing. It is therefore obvious that a strong evolutionary pressure has existed to minimize the predation risk during the breeding period. Adaptation against predation has taken many forms, including varying strategies from solitary to group breeding (Lack 1988, Newton 1998, Lima 2009, Martin &

Briskie 2009). Heterospecific grouping of birds is an interesting phenomenon that is in many cases associated with reduced predation risk (Burger 1984, Götmark 1989, Norrdahl *et al.* 1995), although heterospecifics may also provide other information related to habitat quality (e.g., Elmberg *et al.* 1997, Seppänen *et al.* 2007 and references therein).

One fascinating example of heterospecific grouping is birds breeding in association with more aggressive species (e.g., Hildén 1964, Newton & Cambell 1975, Nuechterlein 1981, Larsen & Grundetjern 1997, Pius & Leberg 1998, Kurvinen

et al. 2016). In boreal freshwater wetlands Pochard (*Aythya ferina*) and Tufted Duck (*Aythya fuligula*) are known to nest in association with small colonial gulls, such as the Black-headed Gull (*Chroicocephalus ridibundus*), thereby gaining protection for their nests (Väänänen 2000). Ducklings in their first weeks after hatching are also highly vulnerable to predation and gull colonies could provide protection against predators. Duck broods are additionally highly mobile and can easily reach attractive habitat patches in the wetland complex (e.g., Paasivaara & Pöysä 2008). It can therefore be assumed that ducks may benefit from the presence of gulls not only during the nesting phase, but also during the brood period because small colonial gulls do not prey on ducklings (Cramp & Simmons 1983, Götmark 1984). However, we are not aware of studies addressing the attractiveness of gull colonies to duck broods.

Three hypotheses have been suggested to explain heterospecific breeding associations in birds: (1) an aggressive species defends its breeding area and, hence, the nests of other species in the area gain protection (protector species include e.g., larids, Hildén 1964, Newton & Cambell 1975; raptors, Wiklund 1982, Norrdahl *et al.* 1995), (2) mixed breeding colonies primarily function as an “information centre” for food finding (Ward & Zahavi 1973), (3) birds can use the information contained in alarm calls and defence behaviour, thus avoiding predation (Nuechterlein 1981, Pöysä 1988, Burger 1994, Väänänen 2001). The first hypothesis has been tested experimentally and the results support this hypothesis (Götmark 1989, Norrdahl *et al.* 1995, Pius & Leberg 1998, Väänänen 2000). The second hypothesis is supported by observational data in some species (Krebs 1974, Emlen & Demong 1975), but in experimental work with the Black-headed Gull the information-centre mechanism has been refuted (Andersson *et al.* 1981, Götmark 1990). The third hypothesis has rarely been tested (Burger 1994, Väänänen 2001).

In this paper, we report an association study between ducks and colonial gulls during the breeding season in Finnish boreal wetlands. We first give an overview of duck nesting habitats in our study area. Our aim is to demonstrate which duck species nest within gull colonies. We then test the hypothesis that duck broods are associated with

gull colonies. Specifically, we hypothesized that duck broods clump within colony areas defended aggressively by gulls and, hence, gain protection from gulls against predators. Alternatively, gull colonies may attract duck broods simply because these indicate better foraging conditions (i.e. a variety of the “coarse-level local enhancement” hypothesis, see Pöysä 1992). We also provide a test of these two alternative explanations of colony attraction by comparing the distribution of broods (within vs. outside colony) in two lakes during two successive years, with a gull colony present only during one year.

2. Material and methods

Data were gathered in 1985–2014 in Central Finland (63°N, 27°E). The study area consisted of richly vegetated lakes surrounded by cultivated fields. There are also some forest patches near the lakeshores. Characteristics of the study lakes are very similar to those described by Kauppinen & Väänänen (1999) in the same lake district.

Nest data were collected in 1985–2014 (Table 1). Duck nests were effectively searched for in floating vegetation rafts within and outside the colonies of small gulls (for more details see Väänänen 2000). In our study wetlands small colonial gulls only breed on floating rafts surrounded by open-water areas. The spring flood is always much higher than the summer water level, covering shore meadows and partly also fields from icebreak until the end of May. Therefore, if ducks nest within gull colonies they can be easily found on floating rafts. Nests were also searched for in cultivated shore fields and meadows that are not covered by spring floods. Nests in forested areas were found more or less by chance. Hence, our nest data do not allow the study of nest-site selection because calculating the “expected use” for nests found in other habitats than floating rafts was not possible. However, the data are useful for gaining an overview of duck nesting habitats in a landscape of boreal wetlands, forests and cultivated fields. However, because we carefully checked the floating rafts (within and outside colonies) we have good knowledge of the duck species present in gull colonies already during the nesting period. We have monitored breeding numbers of ducks in

Table 1. Number of duck nests found in different nesting habitat types in 1985–2014. *N* gives the total number of nests. Duck nests within gull colonies were always found on floating rafts.

Species	Floating raft		Shore meadow	Cultivated field	Other	<i>N</i>
	Colony	Outside				
Eurasian Wigeon (<i>Anas penelope</i>)	–	–	–	3	7	10
Common Teal (<i>A. crecca</i>)	–	–	–	1	1	2
Mallard (<i>A. platyrhynchos</i>)	1	–	2	1	14	19
Northern Shoveler (<i>A. clypeata</i>)	1	1	2	19	–	22
Pintail (<i>A. acuta</i>)	–	–	2	25	1	28
Garganey (<i>A. querquedula</i>)	–	–	2	–	–	2
Tufted Duck (<i>Aythya fuligula</i>)	33	21	–	–	–	54
Pochard (<i>A. ferina</i>)	12	29	–	–	–	41
Total	47	51	6	51	23	178

the most important study lakes, where we also found all the nests of the *Aythya* species (1985–2014, lakes 1–4 in Table 2). In these study lakes the breeding numbers of Mallard (*Anas platyrhynchos*) (mean 14.4 pair / year), Eurasian Wigeon (*Anas penelope*) (18.3), Northern Shoveler (*Anas clypeata*) (26.1), Pintail (*Anas acuta*) (11.5) and Common Teal (*Anas crecca*) (41.8) were much higher than nesting Pochard (4.1) and Tufted duck (9.8). If dabbling duck species regularly nest on floating rafts we certainly should have found their nests. In our study area at least one gull colony was present each year in 1985–2014, meaning that each study year the ducks had the possibility of selecting a gull colony as their nesting place. Common Goldeneye (*Bucephala clangula*) was not included in the nest data because it nests exclusively in nest boxes and tree cavities.

Data on the distribution of duck females with broods were gathered using the round count method (Kauppinen *et al.* 1991) from eutrophic wetlands (Table 2). Lakes were monitored 1–3 times during the brood season of ducks and small colonial gulls, i.e., from 15 June to 15 July in 1998–2000. The entire lake, including dense stands of emergent vegetation, was carefully checked during the round count using a canoe. Broods without hens were not included in the data. Each study lake had a gull colony in 1998–2000 (Table 2; note that the number of lakes studied per year varied), and the defence area of each colony was assessed by observing the warning and mobbing behaviour of gulls (against corvids, the Marsh Harrier (*Circus*

aeruginosus) and the canoe). Gull defence areas were marked on field maps. The shoreline of each wetland was divided into defended and undefended areas of the colony and corresponding shoreline sections were calculated using Mapinfo (Mapinfo Professional Version 5.0.1, copyright 1985–1998 Mapinfo Corporation). The proportion of shoreline in the gull defence area in relation to the total shoreline was used to calculate the expected use of gull colony areas by duck broods. Colony size varied from 21 to 703 pairs, the most common species being the Black-headed Gull (Table 2). The Little Gull (*Hydrocoleus minutus*) was also abundant and at least one Common Tern (*Sterna hirundo*) pair was present in every colony. These larids are widely distributed in Europe (Hagemeijer & Blair 1997) and do not prey on duck eggs or ducklings (Cramp & Simmons 1983, Götmark 1984). Both duck and gull broods were situated near the shoreline.

The distribution of each female with a brood, i.e. within or outside the defended area of the colony, was ascertained. Brood age was determined using the classification of Pirkola & Högmänder (1974). The Pirkola & Högmänder method is based on the gradually changing shape of small downy ducklings and their feather development. Broods are divided into seven categories depending on their developmental stage. Only the first observation of each brood was included in the data. Pseudoreplication (recounts) was avoided by using brood size and age class information for each lake. Colonies are situated mostly within bays on

Table 2. Colony structure (Black-headed Gull, Little Gull and Common Tern), number of colonies, shoreline within gull defence area (proportion of total shoreline in parentheses) and total shoreline of each lake during each study year, as well as total numbers of dabbling duck and diving duck broods and their density within and outside gull colonies (broods per shore kilometres in parentheses) during each study year.

Lake	Year	B-h Gull, Little Gull Common Tern	Numbers of colonies	Shoreline (km)		Dabbling ducks	Diving ducks
				Colony	Total		
I	1998	300, –, 1	1	0.3	12.4	–	–
II	1998	300, –, 1	1	1.5	11.8	–	–
III	1998	5, 130, 3	1	2.2	5.3	–	–
IV	1998	50, 100, 2	1	0.4	6.6	–	–
Total	1998	655, 230, 7	4	4.4 (12.3%)	35.9	32 (3.18; 0.57)	25 (1.14; 0.63)
I	1999	40, –, 2	2	0.8	12.4	–	–
II	1999	700, 10, 1	1	1.8	11.8	–	–
III	1999	10, 10, 4	1	2.2	5.3	–	–
V	1999	100, –, 1	1	1.4	9.6	–	–
VI	1999	100, –, 1	1	1.8	3.6	–	–
VII	1999	100, –, 1	1	2.0	5.5	–	–
VIII	1999	20, –, 1	1	0.3	3.5	–	–
IX	1999	100, –, 1	1	1.2	5.8	–	–
Total	1999	1170, 20, 12	9	11.5 (20.1%)	57.3	54 (3.04; 0.34)	31 (1.04; 0.34)
I	2000	700, –, 3	3	2.8	12.4	–	–
IV	2000	20, 10, 3	1	0.4	6.6	–	–
Total	2000	720, 10, 6	4	3.2 (17.0%)	19.0	13 (2.81; 0.26)	5 (0.63; 0.19)
Total	1998–2000	2545, 260, 25	17	19.1 (17.1%)	112.2	99 (3.09; 0.43)	61 (0.99; 0.45)

I = Lake Lapinjärvet (Maaninka), II = Lake Valkeinen (Maaninka), III = Lake Hämeenlahti (Maaninka), IV = Lake Keskimäinen (Maaninka), V = Lake Keskimäinen (Ilisalmi), VI = Lake Poskilampi (Ilisalmi), VII = Lake Keskimäinen (Riistavesi), VIII = Lake Pohjalampi (Tervo), IX = Lake Pitkäjärvi (Karttula)

floating vegetation stands and the borders of the colony defence areas were clear (often open-water areas or islands). Testing whether the broods swam inside or outside the defended area of the colony was possible with the help of a canoe. All brood observations in our data are from broods that were clearly either inside or outside the defended area.

The *G*-test and Fisher's exact test (depending on sample size) were used to study the differences between observed and expected duck brood numbers within and outside the colony defence area. Spearman rank correlation was used to study the association between colony size and duck brood density within the colony defence area.

3. Results

Dabbling duck nests were only occasionally found within gull colonies (Table 1). The nests of diving ducks, i.e., Tufted Duck and Pochard, were con-

trastingly found only on rafts of floating vegetation within and outside the gull colonies (Table 1).

During the brood stage, most duck species preferred the colony areas of small gulls. Sixty per cent of dabbling duck broods were found within gull colonies although the defended areas of the colonies only amounted to 17% of the shoreline of the study lakes (Tables 2–3; data pooled from all the *Anas* species, *G*-test, $G^2 = 39.33$, $P < 0.001$). Diving ducks were not as strongly associated with gulls as dabbling ducks. The Tufted Duck preferred gull defence areas, whereas the Common Goldeneye did not (Table 3; data pooled from the *Aythya* species, Fisher's exact test, $P = 0.057$). Duck brood density within the gull defence area was not associated with colony size in dabbling ducks (Spearman rank correlation $r_s = -0.062$, $P = 0.832$, $N = 14$) or in diving ducks ($r_s = 0.032$, $P = 0.914$, $N = 14$).

To test between the two alternative explanations of gull colony attraction (see Introduction),

Table 3. Duck brood distribution within or outside the defence areas of gull colonies during 1998–2000. The observed percentages of duck broods within or outside the defended areas are given in parenthesis. The expected brood distribution was calculated by dividing the shorelines in defended (17%) and undefended (83%) areas of the gull colonies. *N* gives the total number of broods. Data sets fewer than 10 observations were not tested.

Species	Number of duck hens with brood		<i>N</i>	Statistical test
	Within colony (%)	Outside colony (%)		
Eurasian Wigeon	10 (66.7)	5 (33.3)	15	Fisher's exact test, $P = 0.025$
Common Teal	21 (61.8)	13 (38.2)	34	G-test, $G^2 = 14.44$, $P < 0.001$
Mallard	4 (44.4)	5 (55.6)	9	–
Pintail	14 (77.8)	5 (22.2)	19	Fisher's exact test, $P = 0.001$
Northern Shoveler	10 (50.0)	10 (50.0)	20	Fisher's exact test, $P = 0.041$
Garganey	–	2 (100.0)	2	–
Tufted duck	10 (50.0)	10 (50.0)	20	Fisher's exact test, $P = 0.041$
Pochard	1 (33.3)	2 (66.7)	3	–
Common Goldeneye	8 (21.1)	30 (78.9)	38	G-test, $G^2 = 0.35$, $P = 0.553$
Total	78	82	160	–

we compared brood distribution (within vs. outside colony defence area) in two wetlands in 1998 and 1999. A gull colony was present in the first wetland in 1998 and absent in 1999; in the other wetland gulls were absent in 1998 and present in 1999. Data from Common Goldeneye were excluded, because the species did not show association with gull colonies (see above). When the colony was present 12 broods were inside the colony defence area and 15 were outside it, while in the absence of gulls 3 broods were inside and 16 broods outside the colony defence area (Fisher exact test, $P = 0.058$). Thus, there was a marginally significant tendency for brood-tending female ducks to use gull colony areas to gain safety rather than food.

4. Discussion

We hypothesized that duck broods are associated with gull colonies to gain protection from gulls against predation. As an alternative explanation, we hypothesized that gull colonies may attract duck broods because these indicate better foraging conditions. We found that dabbling duck broods were strongly associated with gull colonies. However, diving duck broods were not associated with gull colonies, except for the Tufted Duck. Our data additionally supported the hypothesis that colony

attraction was due to protection against predation rather than better foraging conditions. The attraction of dabbling duck broods to gull colonies was underscored by the fact that dabbling duck nests were rarely found within gull colonies, contrary to the two diving duck species, Pochard and Tufted Duck, which nested exclusively within gull colonies.

Benefits of breeding in heterospecific colonies are not well studied. Väänänen (2000) showed that Pochard and Tufted Duck have much lower nest predation rates when nesting within gull colonies. Brzeziński (2012) demonstrated that Coot (*Fulica atra*) and Great Crested Grebe (*Podiceps cristatus*) appear to breed predominantly in colonies and in the vicinity of built-up areas after American Mink (*Neovison vison*) invasion in Poland. Both species survive better when nesting within colonies.

It has been suggested that nesting timing and nest site requirements are important factors affecting the evolution of nesting association between ducks and gulls (see Götmark 1989, Väänänen 2000, 2001). In our study area the Mallard, Pintail and Common Teal are already incubating when gulls begin to build their nests. These duck species cannot therefore actively seek to nest within gull colonies, although that is possible for re-nesting females. In eutrophic boreal lakes, floating vegetated rafts and wet shore vegetation do not appear

to fulfil the nest-site requirements of dabbling ducks.

Dabbling duck broods in particular appeared to clump within the defence areas of gulls. We also have direct evidence of dabbling duck brood movements from nests to gull colonies. In two cases Pintail ducklings ringed at nests were later found within a gull colony, with distances of 1.7 and 2.2 kilometres, respectively, between the nests and the colony. In general, diving ducks showed lower association with gulls than dabbling ducks. The Tufted Duck preferred gull colonies, whereas Common Goldeneye broods were found within gull colonies in the same proportion as colonies occur in our study wetlands. This is expected because Common Goldeneye females aggressively defend their brood-rearing territories against conspecific females with broods (Savard 1984, Ruusila & Pöysä 1998).

Aythya broods were not very strongly associated with gull colonies possibly due to their foraging behaviour. Diving duck ducklings begin searching for food by diving soon after hatching and are also able to use deeper waters for foraging. It is probable that diving duck ducklings simply do not find enough good foraging patches within or near gull colonies.

We found that duck brood numbers in the gull colony defence area were higher when the gulls were present than when they were absent. This is expected because ducks and Black-headed Gulls mostly use different prey, although there are also common characteristics in their diets. Dabbling ducks use large amounts of aquatic invertebrates, such as Water Louse (*Asellus aquaticus*), Gastropods and Chironomid larvae, whereas Black-headed Gulls prey on earthworms and insects flying over water or fields and their foraging areas reach distances of up to 5–20 km from the nesting area (Street 1977, Götmark 1984, Nummi & Väänänen 2001, and references therein). Gull colonies can therefore not function as “information centres” for food finding as described by Ward & Zahavi (1973). Nor did we find support for the idea that gull colony areas simply indicate good foraging areas for duck broods (i.e., the “coarse-level local enhancement” hypothesis, Pöysä 1992). We conclude that duck broods were associated with gull colonies because of gaining protection rather than food.

5. Management implications

In recent years, populations of Tufted Ducks, Pochards, Eurasian Wigeons, Pintails and Common Teals have decreased in Finland, especially in eutrophic lakes (Pöysä *et al.* 2013, Lehtikoinen *et al.* 2016). We have recognized a similar trend in our study lakes (Väänänen unpubl.). Interestingly, all these species (excluding the Pochard with insufficient data) were associated with gulls during the brood stage in our study lakes.

During recent years the community structure and species abundance of ducks have changed much in our yearly monitored study lakes (Lakes 1–4 in Table 2). During the last 15 years the number of gull colonies has also decreased and in 2011–2014 only one gull colony has been present. Black-headed Gulls and Little Gulls have additionally nested more commonly in cultivated fields in recent years. This is extremely harmful for the *Aythya* species that we found nesting only on the floating rafts within or outside the gull colonies. The numbers of breeding *Aythya* species in our study area peaked in 1985: 19 Pochard pairs and 31 Tufted Duck pairs. In the period of 1985–2014, the numbers of *Aythya* species have decreased steadily, and in 2014 there was only one Tufted Duck pair left (Väänänen unpubl.). A very similar population development for Pochard, Tufted Duck and Black-headed Gull has been found in other eutrophic lakes in the same lake district (Kauppinen & Reinikainen 2011, Kauppinen 2012).

Several reasons are apparent for the population decreases of small colonial gulls and ducks in Finland (Valkama *et al.* 2011, Pöysä *et al.* 2013, Lehtikoinen *et al.* 2016). Predation caused by invasive alien predators, the Raccoon Dog (*Nyctereutes procyonoides*) and American Mink is one probable reason (Nordström *et al.* 2002, 2003, Väänänen *et al.* 2007). Both of these predators prey on the nests of gulls and ducks as well. Food competition between fish and ducks may also have affected duck numbers (Nummi *et al.* 2012, Väänänen *et al.* 2012). Competition may be direct or indirect, fish presence decreasing the amount of aquatic invertebrates in both cases (Nummi *et al.* 2016). It is worth noting that also Black-headed and Little Gulls forage on flying aquatic insects. Hence, there may also be competition between fish and small colonial gulls.

We suggest that small gull colonies may be much more important for ducks than previously thought. We recommend that the nest-site requirements of small colonial gulls should be taken into account in wetland restoration and when building new man-made wetlands. In recent years, man-made wetlands have become increasingly popular for increasing waterfowl breeding habitats. Preventing access by fish to the new wetlands is very important (Väänänen *et al.* 2012).

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Sorsien ja pienten lokkilintujen pesimäaikainen yhteiselämä rehevillä kosteikoilla

Tässä tutkimuksessa tarkasteltiin rehevien sisävesien sorsien ja yhdyskunnissa pesivien pienten lokkilintujen (nauru- ja pikkulokki sekä kalatiira) välisiä suhteita pesimäkauden aikana. Aineisto on kerätty Maaningalta vuosina 1985–2014. Tutkimuksen sorsanpesäaineiston mukaan vain tukka- ja punasotka hakeutuivat pesimään lokkiyhdykseen kelluville turvelautoille. Sotkien lisäksi aineistossa oli vain kaksi havaintoa yhdyskunnan sisällä pesineistä puolisukelajasorsista. Kelluvat turvelautat eivät siis näytä täyttävän useimpien sorsalintujen pesäpaikkavaatimuksia sen enempää lokkiyhdyksessä kuin niiden ulkopuolella.

Poikueaikana varsinkin puolisukelajasorsat kerääntyivät lokkiyhdyksunnan puolustusalueen sisään. Sorsapoikueita havaittiin puolustusalueilla enemmän kuin mitä niiden kattama osuus järvien rantaviivasta antaisi olettaa. Tutkimuksessa testattiin kahta selitysvaihtoehtoa sille, miksi sorsapoikueet kerääntyvät lokkiyhdykseen. Aineistomme tukivat vaihtoehtoa, jonka mukaan sorsapoikueet hakevat aggressiivisesti pesiään ja poikasiaan puolustavien pienten lokkilintujen tarjoamaa suojaa petoja vastaan. Naurulokin viimeaikainen taantuminen on saattanut välillisesti vaikuttaa rehevillä vesillä pesivien sorsien, erityisesti sotkien taantumiseen.

References

- Andersson, M., Götmark, F. & Wiklund, C.G. 1981: Food information in the Black-headed Gull, *Larus ridibundus*. — Behavioral Ecology and Sociobiology 9: 199–202.
- Brzeziński, M., Natorff, M., Zalewski, A. & Zimihorski, M. 2012: Numerical and behavioral responses of waterfowl to the invasive American mink: A conservation paradox. — Biological Conservation 147: 68–78
- Burger, J. 1984: Grebes nesting in gull colonies: protective association and early warning. — American Naturalist 123: 327–337.
- Cramp, S. & Simmons, K.E.L. (ed.) 1983: The Birds of Western Palearctic. — Vol 3. Oxford University Press, Oxford.
- Elmberg, J., Pöysä, H., Sjöberg, K. & Nummi, P. 1997: Interspecific interactions and co-existence in dabbling ducks: observations and an experiment. — Oecologia 111: 129–136.
- Emlen, S.T. & Demong, N.J. 1975: Adaptive significance of synchronized breeding in a colonial bird: a new hypothesis. — Science 188: 1029–1031.
- Götmark, F. 1984: Food and foraging in five European *Larus* gulls in the breeding season: a comparative review. — Ornis Fennica 61: 9–18.
- Götmark, F. 1989: Costs and benefits to Eiders nesting in gull colonies: a field experiment. — Ornis Scandinavica 20: 283–288.
- Götmark, F. 1990: A test of the information-centre hypothesis in a colony of sandwich terns *Sterna sandvicensis*. — Animal Behaviour 39: 487–495.
- Hagemeijer, E.J.M. & Blair, M.J. (ed.) 1997: The EBCC Atlas of European Breeding Birds; Their distribution and abundance. — T & A. D Poyser, London.
- Hildén, O. 1964: Ecology of duck populations in the island group of Valassaaret, Gulf of Bothnia. — Annales Zoologici Fennici 1: 153–279.
- Kauppinen, J. 2012: Pochard and tufted duck in Central Finland – from winners to losers. — Suomen Riista 58: 42–49. (In Finnish with English summary)
- Kauppinen, J. & Reinikainen, A. 2011: Long-term variation of the breeding Black-headed Gull populations in eutrophic lakes in Northern Savo, Finland. — Linnut-vuosikirja 2010: 117–121. (In Finnish with English summary)
- Kauppinen, J., Koskimies, P. & Väisänen, R.A. 1991: Waterfowl round count. — In Monitoring bird populations (ed. Koskimies, P. & Väisänen, R.A.): 45–52. Zoological Museum of Natural History, Helsinki.
- Kauppinen, J. & Väänänen, V.-M. 1999: Factors affecting changes in waterfowl populations in eutrophic wetlands in the Finnish lake district. — Wildlife Biology 7: 73–81.
- Krebs, J.R. 1974: Colonial nesting and social feeding as strategies for exploiting food resources in the great blue heron (*Ardea herodias*). — Behaviour 51: 99–134.

- Kurvinen, L., Kilpi, M., Nordström, M. & Öst, M. 2016: Drivers of decline and changed nest-site preference of the Baltic eider: an island-level analysis from south-western Finland. — *Ornis Fennica* 93: 55–66.
- Lack, D. 1968: Ecological adaptations for breeding in birds. — Methuen, London.
- Larsen, T. & Grundtjern, S. 1997: Optimal choice of neighbour: predator protection among tundra birds. — *Journal of Avian Biology* 28: 303–308.
- Lehikoinen, A., Rintala, J. & Pöysä, H. 2016: Habitat-specific population trajectories in boreal waterbirds: alarming trends and bioindicators for wetlands. — *Animal Conservation* 19: 88–95.
- Lima, S.L. 2009: Predators and the breeding bird: behavioral and reproductive flexibility under the risk of predation. — *Biological Reviews* 84: 485–513.
- Martin, T.E. & Briskie, J.V. 2009: Predation on dependent offspring: a review of the consequences for mean expression and phenotypic plasticity in avian life history traits. — *Annals of the New York Academy of Sciences* 1168: 201–217.
- Newton, I. 1998: Population limitation in birds. — Academic press, London.
- Newton, I. & Campbell, R.G. 1975: Breeding of ducks at Loch Leven, Kinross. — *Wildfowl*: 26, 83–103.
- Nordström, M., Högmänder, J., Nummelin, J., Laine, J., Laanetu, N. & Korpimäki, E. 2002: Variable responses of waterfowl breeding populations to long-term removal of introduced American mink. — *Ecography* 25: 385–394.
- Nordström, M., Högmänder, J., Laine, J., Nummelin, J., Laanetu, N. & Korpimäki, E. 2003: Effects of feral mink removal on seabirds, waders and passerines on small islands in the Baltic Sea. — *Biological Conservation* 109: 359–368.
- Norrdahl, K., Suhonen, J., Hemminki, O. & Korpimäki, E. 1995: Predator presence may benefit: kestrel protect curlew nests against nest predation. — *Oecologia* 101: 105–109.
- Nuechterlein, G.I. 1981: Information parasitism in mixed colonies of western grebes and Foster's terns. — *Animal Behaviour* 29: 985–989.
- Nummi, P. & Väänänen V.-M. 2001: High overlap in diets of sympatric dabbling ducks — an effect of food abundance? — *Annales Zoologici Fennici* 38: 123–130.
- Nummi, P., Väänänen, V.-M., Rask, M., Nyberg, K. & Taskinen K. 2012: Competitive effects of fish in structurally simple habitats: perch, invertebrates, and goldeneye in small boreal lakes. — *Aquatic Science* 74: 343–350.
- Nummi, P., Väänänen, V.-M., Holopainen, S. & Pöysä, H. 2016: Duck–fish competition in boreal lakes – a review. — *Ornis Fennica* 93: 67–76.
- Paasivaara, A. & Pöysä, H. 2008: Habitat-patch occupancy in the common goldeneye (*Bucephala clangula*) at different stages of the breeding cycle: implications to ecological processes in patchy environments. — *Canadian Journal of Zoology* 86: 744–755.
- Pirkola, M.K. & Högmänder, J. 1974: The age determination of duck broods in the field. — *Suomen Riista* 25: 50–55. (In Finnish, with English summary)
- Pius, S.M. & Leberg, P.L. 1998: The protector species hypothesis: Do black skimmers find refuge from predators in gull-billed tern colonies? — *Ethology* 104: 273–284.
- Pöysä, H. 1988: Do foraging teals exploit gulls as early warners? — *Ornis Scandinavica* 19: 71–72.
- Pöysä, H. 1992: Group foraging in patchy environments: the importance of coarse-level local enhancement. — *Ornis Scandinavica* 23: 159–166.
- Pöysä, H., Rintala, J., Lehikoinen A. & Väisänen, R.A. 2013: The importance of hunting pressure, habitat preference and life history for population trends of breeding waterbirds in Finland. — *European Journal of Wildlife Research* 59: 245–256.
- Ruusila, V. & Pöysä, H. 1998: Shared and unshared parental investment in the precocial goldeneye (Aves: Anatidae). — *Animal Behaviour* 55: 307–312.
- Savard, J.-P. L. 1984: Territorial behaviour of Common Goldeneye, Barrow's Goldeneye and Bufflehead in areas of sympatry. — *Ornis Scandinavica* 15: 211–216.
- Seppänen, J.T., Forsman, J.T., Mönkkönen, M. & Thomson R.L. 2007: Social information use is a process across time, space, and ecology, reaching heterospecifics. — *Ecology* 88: 1622–1633.
- Street, M. 1977: The food of mallard ducklings in a wet gravel quarry, and its relation to duckling survival. — *Wildfowl* 28: 113–125.
- Valkama, J., Vepsäläinen, V. & Lehikoinen, A. 2011: Suomen III Lintuatlas. — Luonnontieteellinen keskusmuuseumi ja ympäristöministeriö. <<http://atlas3.lintuatlas.fi>> (cited: 12.6.2015) ISBN 978-952-10-6918-5.
- Väänänen, V.-M. 2000: Predation risk associated with nesting in gull colonies by two *Aythya* species: observations and an experimental test. — *Journal of Avian Biology* 31: 31–35.
- Väänänen, V.-M. 2001: Numerical and behavioural responses of breeding ducks to hunting and different ecological factors. — Publications/University of Helsinki, Department of Applied Biology, 4, 21, (50 s.) (Doctoral thesis)
- Väänänen, V.-M., Nummi, P., Rautiainen, A., Asanti, T., Huolman, I., Mikkola-Roos, M., Nurmi, J., Orava, R. & Rusanen, P. 2007: The effect of raccoon dog *Nyctereutes procyonoides* removal on waterbird breeding success. — *Suomen Riista* 53: 49–63. (In Finnish with English summary)
- Väänänen, V.-M., Nummi, P., Pöysä, H., Rask, M. & Nyberg, K. 2012: Fish-duck interactions in boreal lakes in Finland as reflected by abundance correlations. — *Hydrobiologia* 697: 85–93.
- Ward, P. & Zahavi, A. 1973: The importance of certain assemblages of birds as “information-centres” for food-finding. — *Ibis* 115: 517–534.
- Wiklund, C.G. 1982: Fieldfare *Turdus pilaris* breeding success in relation to colony size, nest position and association with merlins *Falco columbarius*. — *Behavioral Ecology and Sociobiology* 11: 165–172.