

COMMON GUILLEMOTS *URIA AALGE*
DIFFERENTIATE THEIR NICHE TO COEXIST WITH
COLONIZING GREAT CORMORANTS
PHALACROCORAX CARBO

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Hjernquist M.B., Hjernquist, M., Hjernquist B. & Thuman Hjernquist, K.A. 2005. Common Guillemots *Uria aalge* differentiate their niche to coexist with colonizing Great Cormorants *Phalacrocorax carbo*. *Atlantic Seabirds* 7(2): 83-89. *Colonization of new species into an established community generally results in interspecific competition over resources between the colonist and existing members of the community. Interspecific competition has been suggested to influence extinction rates, population dynamics, community structure, niche differentiation and evolution. In this study, we observe possible interspecific competition over breeding sites resulting in niche differentiation and coexistence of Great Cormorants Phalacrocorax carbo and Common Guillemots Uria aalge in a seabird cliff community. In Sweden, Great Cormorants have naturally increased and expanded during the last two decades. Here, we show that most Common Guillemots previously bred on cliff ledges with high roof heights before the study-island was colonized by Great Cormorants, but are now mainly found breeding on cliff ledges with lower roof heights. A temporary decline in the Common Guillemot population coincided with the colonization event and we discuss the potential for this decline to be caused by increased nest-site competition combined with high nest-site fidelity.*

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INTRODUCTION

Coexistence of species has interested community biologists for decades and studies of birds have played a major role in understanding inter- and intraspecific competition and how they influence evolution (Lack 1968; Lack 1971; Alatalo *et al.* 1986; Alatalo *et al.* 1987). Interspecific competition over resources has long been argued to influence extinction rates, population

dynamics, community structure, niche differentiation and evolution (Begon *et al.* 1996). Gause's (1934) competitive exclusion principle predicts that competition between two or more species will lead to the extinction of all but one species if competitors do not differentiate their niche. More elaborate versions of Gause's principle suggest a limit to the extent of similarity between species and a limit for the number of species that can utilize a niche within a community (MacArthur & Levins 1967; May 1973).

The availability of nesting sites for seabirds on cliff ledges may not be a limiting resource (Furness & Birkhead 1984; Wittenburger & Hunt 1985; Olsthoorn & Nelson 1990), but because sites vary in quality they should be subject to competition (Ashmole 1962; Porter & Coulson 1987). Interspecific competition over nest sites in seabird cliff communities has previously been shown, as well as potential niche differentiation and competitive exclusion (Kenyon and Phillips 1965; Lack 1968; Maunder & Threlfall 1972; Williams 1974; Squibb & Hunt 1983). Thus, interspecific competition over nest sites is often an important force influencing the habitat used by seabirds. However, there are not always costs associated with coexisting with other species and there might even be fitness benefits associated with interspecific interactions, e.g. increased juvenile survival and number of offspring produced (Forsman *et al.* 2002).

Conservation biologists have considered the immigration of new species into communities, both natural and with help from humans, as a cause for concern with respect to existing biodiversity. The Swedish population of Great Cormorant *Phalacrocorax carbo* has naturally expanded and migrated into new areas over the last two decades (Engström 2001). In 1992, the first pairs of Great Cormorants colonized the bird cliffs on the island of Lilla Karlsö (57°19'N, 18°04'E), situated on the west coast of the island of Gotland in the Baltic Sea. Great Cormorants are piscivorous and build nests in the scree-slope, in trees and on cliff ledges. For the first three years after colonization, Great Cormorants bred only on cliff ledges, but more recently they have started to nest on the scree-slopes to a greater extent, with a few nests also in trees; for example, in 2001 approximately 60 % of the Great Cormorants bred on scree-slopes, 35% on cliff ledges, and 5% in trees (unpublished data). The Common Guillemot *Uria aalge*, also a piscivorous seabird, has bred on the cliff ledges on Lilla Karlsö since at least the 18th century (von Linné 1741). Using breeding distribution data of Common Guillemots gathered before and after Great Cormorants colonized the study island, we analysed how nest site niches utilized by Common Guillemots changed in response to cormorant colonization, allowing us to test predictions of competitive exclusion and niche differentiation. Long-term population data for both species were used to assess potential population effects following the colonization.

METHODS

Study site and populations The only seabird cliffs in the Baltic Sea are situated on the island of Lilla Karlsö and on its sister island Stora Karlsö. On Lilla Karlsö, there are two large seabird cliffs where birds nest on cliff ledges, in cavities and on the ground. The cliff ledges on Lilla Karlsö are cavernous, with sufficient width and depth to be suitable breeding places for both Common Guillemots and Great Cormorants. However, they vary in roof height ranging from less than 1m to several metres, or no roof at all. Most Great Cormorants nest on ledges where Common Guillemots also breed. Public access to the breeding colonies (both from land and sea) is prohibited.

Population data For both species, population data from 1988 until 2004 was obtained from an annual nature monitoring report for Lilla Karlsö (Hjernquist 2004).

Cliff ledge data In 1974 (before the Great Cormorant colonized the study island), 1997 and 2001 (after the Great Cormorant colonized the study-island) ledges with auks were surveyed from a boat outside the restricted water-zone. The great majority of auks breeding on cliff ledges on Lilla Karlsö are Common Guillemots, and we therefore assumed all auks to be Common Guillemots. At the same time these ledges were categorised as either having high roof heights (approximately 2 m high and including ledges without a roof) or low roof heights (approximately lower than 2 m) and we used this to categorise the niches utilized by the Common Guillemot before or after the colonization event. Thus, we compared one year of data, gathered 18 years before the colonization event, with two years of data, gathered five and nine years after the colonization. Breeding birds are monitored annually on Lilla Karlsö and no apparent shift in breeding sites was observed until after the Great Cormorants colonized the island (personal observations); the years 1974, 1997 and 2001 are therefore assumed to be representative of the breeding distribution before and after the colonization.

RESULTS

Population data Since 1988, Common Guillemot population size has fluctuated around 1100 pairs (mean = 1072.1). The last major population decrease was between 1992 and 1993, with a decline of about 600 pairs, followed by an immediate and rapid increase between 1995 and 1997 to the earlier levels of about 1100 pairs (Figure 1). The Great Cormorant population size has increased since initial colonization and peaked in 2000 (2268 pairs) followed by a slight decrease (Figure 1).

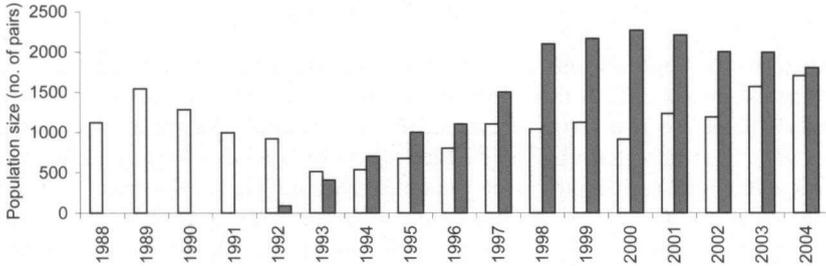


Figure 1. Number of breeding pairs of Great Cormorants (filled bars) and Common Guillemots (open bars) on the island of Lilla Karlsö in the Baltic Sea, 1998-2004 (Hjernquist 2004).

Figure 1. Aantal broedpaar van Aalscholver (grijze staafjes) en Zeekoet (witte staafjes) op het eiland Lilla Karlsö in de Baltische Zee, 1998-2004 (Hjernquist 2004).

Cliff ledge data In 1974, 73% of the 155 cliff ledges with breeding Common Guillemots observed had high roof height. In 1997 and 2001, i.e. after the Great Cormorant colonized the island, 122 and 94 cliff ledges were observed with breeding Common Guillemots, with 31.1% and 29.8% respectively, having high roof heights. This suggests that Common Guillemots shifted from breeding mainly on cliff ledges with high roof heights before Great Cormorants bred on Lilla Karlsö, to breeding on cliff ledges with low roof heights (G-test on merged data, $G_{adj} = 58.0$, $df = 1$, $P < 0.01$; Figure 2). This pattern of change is as evident when analysing the two years after the colonization event separately (1997: $G_{adj} = 44.5$, $df = 1$, $P < 0.01$; and 2001: $G_{adj} = 41.4$, $df = 1$, $P < 0.01$).

DISCUSSION

Our results imply that the Common Guillemot has switched from nesting on cliff ledges with high roof heights to nesting on cliff ledges with lower roof heights after Great Cormorants started to breed on the island. Common Guillemots and Great Cormorants have overlapping niches on the island of Lilla Karlsö and the observed pattern of change in the Common Guillemot's realized nest site choice implies that interspecific competition over nest sites occurs between the two species. Thus, Common Guillemots have probably altered their realized niche in order to coexist with the colonizing Great Cormorant, in accordance with the competitive exclusion principle, where species may coexist if they differentiate their realized niche(s).

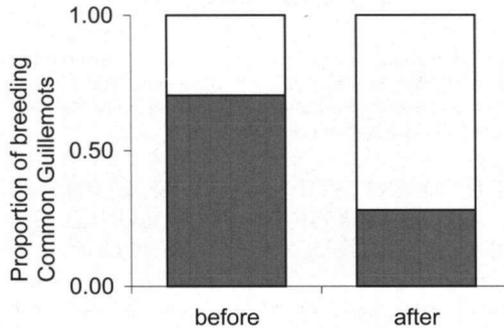


Figure 2. The proportion of Common Guillemot breeding on cliff ledges with either high (filled area) or low (open area) roof heights before and after colonization by Great Cormorants (G-test on merged data, $G_{adj} = 58.0$, $df = 1$, $P < 0.01$).

Figuur 2. Het aandeel Zeekoeten dat broedt op klifrichels met een hoog (gearceerd) of laag 'dak' voor en na kolonisatie door Aalscholvers (G-test op samengevoegde data, $G_{adj} = 58.0$, $df = 1$, $P < 0.01$).

The large Common Guillemot population decline between 1992 and 1993 could have been caused by, for example, food shortage or intra- or interspecific competition. However, Common Guillemot food resources such as clupeids (herring *Clupea harengus* and sprat *Sprattus sprattus*) increased during this period (Casini 2003). Furthermore, Razorbills *Alca torda* breeding in different sites on Lilla Karlsö, using the same food resources as Common Guillemots, did not decline during this period (Hjernquist 2004), and neither did the Common Guillemot population breeding on the sister island Stor Karlsö (S. Hedgren pers. comm.). The temporary decline in the Common Guillemot population coincided with the colonization of Great Cormorants and could possibly be a result of interspecific competition over breeding sites. A recent study of intraspecific nest site competition among Common Guillemots on the Isle of May, Scotland, showed that Common Guillemots exhibited strong nest site fidelity, and if an individual is evicted from its previous nest site it can spend several years as a non-breeder (Kokko *et al.* 2004). However, there was a slight decrease in the Common Guillemots population size before the colonization and it is therefore possible that the decrease was not a response to Great Cormorant colonization. So Great Cormorants might not have evicted Common Guillemots from ledges with high roof heights. Instead, when the Common Guillemot population increased (1995-97) the only available ledges were of low roof heights as Great Cormorants occupied most ledges with high roof heights.

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NICHE DIFFERENTIATIE VAN ZEEKOETEN *URIA AALGE*
ALS AANPASSING AAN KOLONISATIE
DOOR AALSCHOLVERS *PHALACROCORAX CARBO*

*Kolonisatie door een nieuwe soort resulteert in veel gevallen in competitie om beschikbare bronnen tussen de koloniserende en reeds aanwezige soorten. Competitie tussen soorten wordt gezien als een factor die uitstervingsnelheid, populatie dynamiek, samenstelling van de (broedvogel)gemeenschap, niche differentiatie en evolutie beïnvloedt. We vonden dat competitie tussen Aalscholver *Phalacrocorax carbo* en de Zeekoet *Uria aalge* in een zeeklifkolonie om broedplaatsen resulteert in niche differentiatie en coëxistentie. In Zweden is het aantal Aalscholwers de laatste twee decennia op een natuurlijke wijze toegenomen en heeft het verspreidingsgebied zich uitgebreid. We laten zien, dat Zeekoeten voor de expansie van de Aalscholver met name op klifrichels met een hoog 'dak' broedden, en dat hun broedplaatsen zich hebben verplaatst naar richels met een lager 'dak'. De kolonisatie van de Aalscholver valt samen met een tijdelijke afname van het aantal Zeekoeten op de studielocatie. Deze tijdelijke afname zou veroorzaakt kunnen zijn door toegenomen competitie om broedplaatsen in combinatie met een sterke neiging van Zeekoeten om jaarlijks terug te keren naar dezelfde broedplaats.*

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