Figure 1. Bridled Common Guillemot *Uria aalge* with a Capelin *Mallotus villosus*, Hornøya, NE Norway, June 2007 (note the running roe). © *Robert T. Barrett.*

No difference in chick-provisioning by bridled and non-bridled Common Guillemots *Uria aalge*

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Abstract
Despite recent evidence that bridled Common Guillemots *Uria aalge* may depend more on cold-water prey species than non-bridled, there was no morph-specific difference in the species composition or size of fish caught for chicks by adults in a North Norwegian colony. This supports the recent suggestion that selection pressure on the morphs acts in the non-breeding season, rather than in summer.

Introduction

Parental investment is a trade-off between the costs or benefits of resource allocation to offspring or to self-maintenance and own survival (Royle *et al*. 2004). An excess effort in either direction will lead to natural selection against the individuals in question. In birds, feeding chicks is costly and in most species both parents contribute to the effort, although not necessarily equally (Lack 1968; Lewis *et al*. 2002 and references therein). Many studies have documented sexual differences in foraging behaviour and food provisioning, even among bird taxa where sexual dimorphism is all but absent (e.g. Table 1 in Lewis *et al*. 2002). Among the auks (*Alcidae*), these include subtle differences in behaviour, time spent in the colony, the time of day spent foraging, dive depths or dive lengths but not necessarily in the choice of fish (e.g. Thaxter *et al*. 2009; Elliott *et al*. 2010; Paredes & Insley 2010). Among *Uria* guillemots, the behavioural differences may partly be due to a differential allocation of effort to maintain or enhance body condition in anticipation of the period of post-fledging paternal care and hence future survival (Thaxter *et al*. 2009; Elliott *et al*. 2010).

Whereas sexual dimorphism is minimal among guillemots, the Common Guillemot *U. aalge* is a clear colour-dimorphic species consisting of a bridled morph with a white eye-ring and auricular groove and a non-bridled morph with a black head and no such patterning. There are otherwise no differences in morphology and body measurements (e.g. wing, culmen, gonys, head+bill) of the two morphs (Table 1: 2-sample t-test, P > 0.05 for all measurements). The frequency of the bridled form, however, increases with latitude, suggesting a higher tolerance for cold than non-bridled birds (Birkhead 1984 and references therein). This was supported by Reiertsen *et al*. (2012) whose models clearly showed a differential survival between the two morphs at a breeding colony in North Norway, with that of the bridled morph being negatively correlated to the winter sea-surface temperature in the Barents Sea while that of the non-bridled morph was slightly positively correlated to the same parameter. They also suggested that there was no differential selection on the two morphs during the breeding season, but rather during the winter. This is in contrast to Birkhead (1984) who suggested the opposite pattern. Reiertsen *et al*.'s (2012) study also suggested that the bridled morph was more dependent on cold-water species such as Capelin *Mallotus villosus* as prey whereas the non-bridled birds foraged more on warm-water species such as young age-classes of Cod *Gadus morhua* and the Norwegian spring-spawning Herring *Clupea harengus*.

In North Norway, Common Guillemots feed their chicks on small, energy-rich pelagic fish such as Capelin, Herring and sandeels *Ammodytes* sp. (Barrett 2002). Capelin is a cold-water species that lives its entire life-cycle in arctic, subarctic and cool-temperate seas (Stergiou 1991). Reaching a maximum length of ~20 cm, it is an important prey for seabirds throughout its life cycle. Capelin is one of the dominant pelagic fish of the Barents Sea and in spring approaches the coast of North Norway where it spawns on the sea bed at depths of 20–75 m (but sometimes deeper) and temperatures of < 7 °C (Stergiou 1991; Gjøsæter 2009). Herring, on the other hand, is a warmer-water species, belonging to the Norwegian Sea ecosystem and entering the Barents Sea as 0- and I-group fish having drifted northeastwards as larvae. These prey remain in the Barents Sea

Table 1. Mean measurements (mm ± SE; sample size in brackets) of bridled and non-bridled Common Guillemots *Uria aalge* taken during the breeding season (1980–2011) at Hornøya, NE Norway.

	Wing	Culmen	Gonys	Head+bill
Non-bridled	213.5 ± 0.4 (171)	48.0 ± 0.2 (168)	14.4 ± 0.1 (169)	116.9 ± 0.3 (173)
Bridled	213.8 ± 0.6 (82)	48.5 ± 0.3 (79)	14.5 ± 0.1 (80)	117.6 ± 0.4 (82)

for 3–4 years and then depart at a length of 20–23 cm (Holst *et al*. 2004; Olsen *et al*. 2010). Common Guillemots prey on the youngest age classes (0- and I-group, < 20 cm; Husebø *et al*. 2007) of Herring (Barrett 2002). Where Herring and Capelin overlap in distribution, the former tend to be distributed in shallower water than the latter, sometimes in the uppermost 20 m in the Atlantic Water that, by mid-summer has begun to stratify forming a warmer, upper layer (Toresen & de Baros 1995; Huse & Toresen 1996; Ingvaldsen & Loeng 2009). In the Arctic summer, there is little vertical migration of either species (Huse & Toresen 1996). Sandeels are also warm-water species living in temperate and boreal marine shelf ecosystems and may constitute up to 40% of the chicks' diet at Hornøya in some years. Unfortunately little is known about its biology in the Barents Sea as it is not a commercial species and therefore not a focus of resource surveys and research in the northern regions (Bergstad *et al*. 2013).

Whereas there is no evidence of sex-specific differences in the choice or size of fish caught by the adults to be fed to the chicks in North Norway (Barrett *et al*. 2010), Reiertsen *et al*.'s (2012) results suggest that the bridled and non-bridled morphs depend more on cold- and warm-water species respectively as a food resource. Although this suggestion focused on their winter diet, it is not unreasonable to suggest that it may also carry over to the breeding season and that there may be a differential preference for prey types in summer that does not (always) affect survival. Whereas a field study of adult diet is relatively complex, the documentation of food brought to chicks is relatively simple (e.g. Harris & Wanless 1985; Barrett *et al*. 1997), thus lending itself well to testing differences between bridled and non-bridled morphs in prey species delivered to the chicks. This study tests the prediction that bridled Common Guillemots breeding in a North Norwegian colony feed their chicks more on a cold-water species (Capelin) than non-bridled birds. The latter were predicted to catch more of the warmer-water species (Herring and/or sandeel).

Material and methods
The study was carried out during the hatching and main chick-rearing period in a colony of 8–10,000 pairs of Common Guillemots (in 2012, own unpubl. data) on Hornøya (70°23′N 31°10′E), a small island in NE Norway during the chick-rearing periods of 2008, 2010, 2011 and 2012. On Hornøya the frequency of bridled Common Guillemots is high compared to colonies further south (> 30%; Reiertsen *et al*. 2012) facilitating good sample sizes of both morphs. Chick food data were collected either by catching adults bringing fish into the colony (in 2008; see Bugge *et al*. (2011) for details) or by direct observation of food items carried by adults into a sub-colony of 1,000–1,500 individuals using 10x50 binoculars at distances of 5–20 m (2010–12). Daily observations lasting about

one hour were made 11–19 times during the main chick-rearing period. On arrival of a bird carrying a fish in the colony, the morph was noted and, when possible, the food item was identified to species. Being very characteristic in their shape, colour and presence or absence of visible scales, the three main fish prey (Capelin, Herring and sandeel) were easy to recognize, whereas fish within the Gadidae were more difficult to distinguish in the time available and were lumped as 'gadid'. Very few fish could not be identified at all and these were included in the category 'other' in Table 2. When only observed, each fish was, when possible, categorized as small, medium, large and very large, through comparisons with the length of the adult bird's bill (Barrett *et al*. 1997).

The frequency of bridling of birds in the colony was determined three times (in 2008, 2010 and 2011) during the period of the study through counts of birds in the colony with or without bridling from digital photographs of the sub-colony used for feeding observations. Differences in diet composition between the two morphs were tested using Chi-square (χ^2) in Minitab 15 (Minitab Inc., Pennsylvania). To test if one of the morphs fed the chick more often than the other, the numbers of each morph recorded with fish was tested against frequency of bridling recorded in the sub-colony, again using Chi-square.

Results

Seventy-six fish were collected in 2008. There was no apparent difference in the choice between the two morphs ($\chi^2 = 0.382$, df = 1, P > 0.05, combining Herring, sandeel and gadids in one category due to small sample sizes - see Table 2). Between 988 and 1,408 fish were recorded annually in 2010–12 and the chick diet was dominated by Herring, Capelin and sandeel although the relative composition varied between years (Table 2). Again no difference was found in the overall diet composition between the morphs in any of the three years ($\chi^2 = 4.624$ (2010), 3.578 (2011), 1.286 (2012), df = 3 (having combined categories 'gadid' and 'other' due to small numbers of the latter), P > 0.05 in all years). This held true when all but two of the 41 daily sets of diet composition were compared between the morphs and when combined Herring and sandeel was tested against Capelin. In one of the two exceptions, bridled adults caught more Capelin than expected, and in the other less Capelin than expected. Nor were there differences in the mean

Table 2. Numbers (% in brackets) of fish brought to chicks by bridled and non-bridled Common Guillemots *Uria aalge* at Hornøya, North Norway in 2008 (sampled) and 2010–2012 (observed); no. of observation days per year in brackets.

Fish	2008 (19)		2010 (11)		2011 (19)		2012 (11)	
	Non-bridled	Bridled	Non-bridled	Bridled	Non-bridled	Bridled	Non-bridled	Bridled
Herring	2 (4%)	0	215 (29%)	93 (27%)	360 (39%)	190 (39%)	47 (7%)	21 (7%)
Capelin	45 (83%)	17 (77%)	403 (54%)	202 (59%)	357 (39%)	197 (40%)	483 (69%)	201 (70%)
Sandeel	6 (11%)	4 (18%)	119 (16%)	39 (11%)	172 (19%)	81 (16%)	146 (21%)	53 (18%)
Gadid	1 (2%)	1 (5%)	15 (2%)	6 (2%)	25 (3%)	19 (4%)	19 (3%)	9 (3%)
Other	0	0	0	1 (< 1%)	4 (< 1%)	3 (< 1%)	5 (1%)	4 (1%)
Total	54 (71%)	22 (29%)	752 (69%)	341 (31%)	918 (65%)	490 (35%)	700 (71%)	288 (29%)

size of Capelin caught by the two morphs in 2008 (non-bridled 139.3 ± 2.1 (SE) mm, bridled 144.9 ± 3.4 mm, 2-sample t = -1.39, P = 0.2) or in the size categories of the three main diet items brought in to the colony by the two morphs in 2010–2012 (Table 3, χ^2 tests, P > 0.05 in all cases).

There were small but insignificant differences in the frequency counts of the bridled morph in 2008, 2010 and 2011 (range 30.5–33.8%, χ^2 = 1.11, df = 2, P > 0.05; Table 4), and no differences between the proportions of non-bridled/bridled birds with fish each year (Table 2) and those of birds in the colony (χ^2 = 0.08–3.36, df = 1, P > 0.05).

Discussion

This is the first study to address possible differences in choice of fish for chicks between the bridled and non-bridled morphs of Common Guillemot. Although no consistent differences were found, the result is useful in the discussion concerning differential selection on the two morphs. The lack of any differences in chick food supports Reiertsen *et al*.'s (2012) suggestion that selection pressures seem to be acting during the winter and not during the breeding season. One important caveat, however, is the lack of data on foraging ranges, trip durations, diving behaviour and feeding frequencies of the two morphs, but the fact that the morph ratios of fish-carrying birds equalled that of the population as a whole suggests that at least the latter (feeding frequency) did not differ. Such behavioural differences have been found among the sexes of auks (e.g. Thaxter *et al*. 2009; Paredes & Insley 2010). Furthermore, the diet of chick-feeding adults is very

Table 3. Numbers of Herring *Clupea harengus*, Capelin *Mallotus villosus* and sandeels *Ammodytes* sp. in different size categories observed being brought to chicks by bridled and non-bridled Common Guillemots *Uria aalge* at Hornøya, North Norway in 2010–2012.

Fish		2010 Non-bridled	2010 Bridled	2011 Non-bridled	2011 Bridled	2012 Non-bridled	2012 Bridled
Herring	Medium	9	2	14	5	22	9
	Large	186	85	313	166	24	10
	V. large	2	6	33	19	1	2
Capelin	Medium	7	2	11	9	11	3
	Large	387	190	333	179	380	166
	V. large	7	9	12	8	90	32
Sandeel	Small	0	0	6	0	5	1
	Medium	29	70	37	16	63	21
	Large	89	30	127	62	73	30

Table 4. Counts of non-bridled and bridled Common Guillemots *Uria aalge* at Hornøya, 2008–2011 (from Reiertsen *et al*. 2012).

	Non-bridled	Bridled	% bridled
2008	180	86	32.3
2010	270	138	33.8
2011	317	139	30.5

different from that of chicks at Hornøya (Bugge *et al*. 2011) such that morph-related differences in chick-feeding behaviour, attendance patterns and diet of adults should be (and, on Hornøya, are being (T. Reiertsen pers. comm.)) further addressed in the search for selection pressures on the two morphs.

While not finding any morph-related selection of prey, the result is in accordance with the theories of optimal foraging (Orians & Pearson 1979) that predict that single prey-loading species, like the Common Guillemot, will maximise net energy gain through a selectivity of prey caught for the chick. Although Capelin, Herring and sandeels may occur at different depths or distances from the colony, they are all high-energy fish and readily available off Hornøya (Barrett 2002; Barrett *et al*. 2010) such that the adults likely target the species that is easiest to access at the time of their return to the colony, irrespective of depth or temperature. As such, it is unlikely that the two morphs that are of equal size and thus most likely having similar abilities to catch fish (e.g. Halsey *et al*. 2006) would exhibit different foraging strategies when the time available to search for food is constrained by their need to return to the chick.

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