Kleptoparasitism in Common Guillemots *Uria aalge* at two colonies during a period of poor food availability

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Abstract

Kleptoparasitism, the stealing of food items from other animals, is an important foraging strategy for many taxa. In many cases the kleptoparasites and hosts are different species but less commonly, prey items are stolen from conspecifics. Recent studies have highlighted the potential importance of intra-specific kleptoparasitism in food-stressed populations, and here we show facultative kleptoparasitism at two North Sea colonies of Common Guillemots *Uria aalge* during one year of poor breeding success and one year of near average breeding success. The frequency of kleptoparasitism differed between colonies and years, reflecting variation in the magnitude of the benefits from kleptoparasitism, which was probably associated with variation in prey availability at sea. Specialised foraging strategies such as kleptoparasitism may allow individuals to buffer adverse conditions more effectively than those foraging only at sea.

Introduction

Kleptoparasitism, the stealing of food items from other animals, is a common behaviour recorded in many seabird species (Furness 1987). It can sometimes involve high energy expenditure and risk of injury (Furness 1987; Sirot 2000), and so may be beneficial to individuals only during food shortages (Oro 1996; Sirot 2000). Facultative kleptoparasitism occurs in many groups of birds and is an important feeding technique in several families of seabirds (Lavers & Jones 2007), although in some cases it may be a specialised behaviour shown in only a small proportion of individuals (Steele & Hockey 1995; Shealer & Spendelow 2002).

Common Guillemots *Uria aalge* (hereafter 'Guillemots') are not kleptoparasitic under normal feeding conditions but during periods of food-stress (e.g. during El Niño events), adults have been recorded stealing prey from small or satiated chicks (Ainley *et al*. 2002) and from other adults (Furness 1987). Recently, breeding success at Guillemot colonies bordering the North Sea has been poor (Mavor *et al*. 2005; Wanless *et al*. 2005; Heubeck 2009) and under these circumstances, kleptoparasites may profit from stealing food for their chicks. Changes in the social behaviour of this species have already been observed in response to poor food availability, with parents able to increase chick-provisioning rate by leaving their chick unattended at the colony and foraging simultaneously (Ashbrook *et al*. 2010). Here, we quantify the occurrence of kleptoparasitism under such conditions in two widely separated populations.

Methods

This study was carried out at the Isle of May, SE Scotland, UK (56°11'N 2°34'W) and Sumburgh Head, Shetland, UK (59°51'N 1°16'W; distance between colonies ≈ 420 km), where standardised data on Guillemot breeding success have been collected since 1982 (Newell *et al*. 2008) and 1989 (Heubeck 2009), respectively. The foraging areas of these two colonies do not overlap, with Guillemots typically foraging within 20 km of the Isle of May (Thaxter *et al*. 2009) and within 10 km of Sumburgh Head (Monaghan *et al*. 1994). Both colonies experienced very low breeding success in one of the two study years (2007 at the Isle of May, with an average of 0.37 chicks fledged per breeding pair; 2008 at Sumburgh Head, with 0.28 fledged per pair), and only slightly below average breeding success in the other year studied (2008 at the Isle of May, with 0.77 chicks fledged per breeding pair (1982–2006 average = 0.89 ± 0.02 SE); 2007 at Sumburgh Head, with 0.56 (1989–2006 average = 0.61 ± 0.04 SE)).

We observed prey deliveries at study plots containing 97 chick-rearing pairs in 2007 and 82 pairs in 2008 at the Isle of May, and 88 pairs in 2007 and 48 pairs in 2008 at Sumburgh Head. At the Isle of May, plots were observed between 27 May and 6 July 2007 (n = 37 days with observations) and between 5 June and 9 July 2008 (n = 35 days). Observations lasted for one hour and commenced at 05:00, 11:00 and 17:00 one day and at 08:00, 14:00 and 20:00 the next (201 hours of observation in total). At Sumburgh Head, plots were observed between 13 June and 10 July 2007 (n = 15 days) and between 15 June and 5 July 2008 (n = 15 days). Observations lasted one or two hours each, between 09:00 and 17:15 (54 observation hours in total). Observations were made using binoculars from c. 10 m above the study plot at the Isle of May and using a telescope from c. 30 m above the study plot at Sumburgh Head.

Within a season, we classified pairs into categories based on kleptoparasitic status: kleptoparasitic pairs (those recorded stealing at least one prey item from another Guillemot; n = 23), kleptoparasitised pairs (those where at least one prey item brought in for the chick was stolen; n = 22), kleptoparasitic and kleptoparasitised pairs (those recorded to kleptoparasitise other pairs and be kleptoparasitised themselves; n = 5), and control pairs (those that were not recorded to kleptoparasitise or be kleptoparasitised; n = 265). However, as observations were not continuous, some pairs may have been misclassified and the frequency of kleptoparasitism underestimated. Parents returning with prey normally landed close to, or on, the breeding site at the Isle of May. At Sumburgh Head, however, ~ 75% of birds landed outside the study plot and walked from there to the breeding site (<

10–15 seconds to several minutes; Heubeck 2009). Once at the breeding site, the transfer of prey from the adult to the chick usually takes a few seconds (Tschanz 1968). Members of a pair and their chick could be identified by their attachment to a particular site. During observations, the species and sizes of prey items delivered were recorded, whether they were stolen, the prey deliverer's and kleptoparasite's breeding site if known (Isle of May: 96% identified; Sumburgh Head: 53%) and the final outcome of the stolen prey (fed to chick, eaten by kleptoparasite, dropped, or torn into fragments). As stolen prey items were not removed from the study areas, we assumed that prey delivered by parents was caught at sea and not stolen from other areas of the colony. Prey items are carried length-ways in the bill and so it was possible to estimate small (< 6 cm), medium (9 cm), and large (> 12 cm) size categories (Harris & Wanless 1985; Thaxter *et al.* 2009) and to identify items to species or Family: sandeels (Ammodytidae), clupeids (*Spattus sprattus* and *Clupea harengus*), gadoids (Gadidae, *Merlangius merlangus* and *Pollachius virens*), Snake Pipefish (*Entelurus aequoreus*) and squid (Teuthida). We calculated the frequency of kleptoparasitism as the number of prey items stolen divided by the total number of prey items delivered, which was corrected for the total duration of observations. Birds stealing prey were classified as breeders, failed breeders or non-breeders (including both site holders and non-site holders) when known. Only prey stolen from breeders (active and failed) were included in the analysis; the few instances (n = 3) when display prey items (Harris & Wanless 1985) were stolen from non-breeders were excluded, as they were not fed to chicks. In cases of hyper-kleptoparasitism (where prey was stolen not only from the deliverer, but also from the kleptoparasite), the kleptoparasite's breeding site was recorded where possible.

We used generalised linear models (GLMs) to test for a difference between colonies and years in the proportions of prey items stolen, controlling for the duration of observations and their timing in relation to stage of season. Model simplification was performed by sequential removal of the least significant terms, using likelihood ratio tests to determine the minimum adequate model (Crawley 2007). To test whether kleptoparasites were targeting certain prey sizes or species, Fisher's exact tests were used to compare the proportions of different sizes and species delivered to the proportions that were stolen. All statistics were performed using R 2.10.1 (R Development Core Team 2007).

Results

Intra-specific kleptoparasitism was uncommon overall (3% of 1,655 prey items delivered), but was significantly more frequent at Sumburgh Head in 2008 than in 2007, and at Sumburgh Head than the Isle of May in both 2007 and 2008 (Sumburgh Head, 2007: 2.1% of 313 prey delivered; 2008: 7.9% of 131 prey; Isle of May, 2007: 1.5% of 464 prey; 2008: 1.7% of 747 prey; GLM with binomial errors; two-way interaction between colony and year: $LR_{1,93} = 4.09$, $P < 0.05$).

Detailed observations indicated that birds at certain sites appeared to specialise in stealing prey, with only 8% of pairs performing kleptoparasitism (n = 315), stealing an average of 0.02 ± 0.001 SE prey items per hour (Isle of May 2007: 10 of 87 pairs

Figure 1. Hyper-kleptoparasitism: three Common Guillemot *Uria aalge* kleptoparasites fighting over a fish stolen from a neighbouring adult. This single fish was fought over by five adults, not including the deliverer, before finally being torn to pieces. Isle of May, 28 June 2007. © Kate Ashbrook.

stole fish; 2008: 11 of 82 pairs; Sumburgh Head 2007: 3 of 88 pairs; 2008: 4 of 48 pairs). All kleptoparasites across both colonies were breeders with chicks (n = 28).

At the Isle of May, kleptoparasites invariably fed the stolen prey to their chick (n = 21). At Sumburgh Head, however, a variety of outcomes was recorded with 37.5% and 55.6% of prey being fed to the chick in 2007 and 2008, respectively. The remaining prey were eaten by the adult, dropped or torn into fragments as they were being stolen. Hyper-kleptoparasitism was recorded on nine occasions at the Isle of May (2007: 0.8% of 464 prey items delivered; 2008: 0.7% of 747) and nine times at Sumburgh Head (2007: 1% of 313; 2008: 4.6% of 131), with up to five birds involved (Figure 1).

On the Isle of May, birds preferentially stole large prey items in both 2007 and 2008 (Fisher's exact test: 2007: P = 0.05; 2008: P = 0.008). There was no difference between the frequencies of different size-classes of prey stolen and the sizes delivered at Sumburgh in 2007 (Fisher's exact test: P = 0.15), but there was a significant bias towards stealing larger prey in 2008 (P < 0.001; Figure 2). There was no significant difference between the proportions of different prey species delivered to chicks and the proportions stolen at both colonies (Fisher's exact test: P > 0.3 in all cases).

Discussion

During periods of low prey availability, individuals using a combined strategy of foraging at sea and stealing prey from conspecifics may gain an energetic advantage over those foraging only at sea, allowing them to buffer the reproductive consequences of food shortage more effectively (Oro 1996; Sirot 2000; Shealer *et al.* 2005). Only very rarely has intra-specific kleptoparasitism been recorded at the Isle of May and Sumburgh Head colonies in previous years; this behavioural change has occurred at a time when breeding success has declined and colonies have become a more hostile environment for chicks (Ashbrook *et al.* 2008; Heubeck 2009). Single-prey loaders should seek to maximise the sizes of prey items delivered to chicks (Orians & Pearson 1979), and Guillemots preferentially

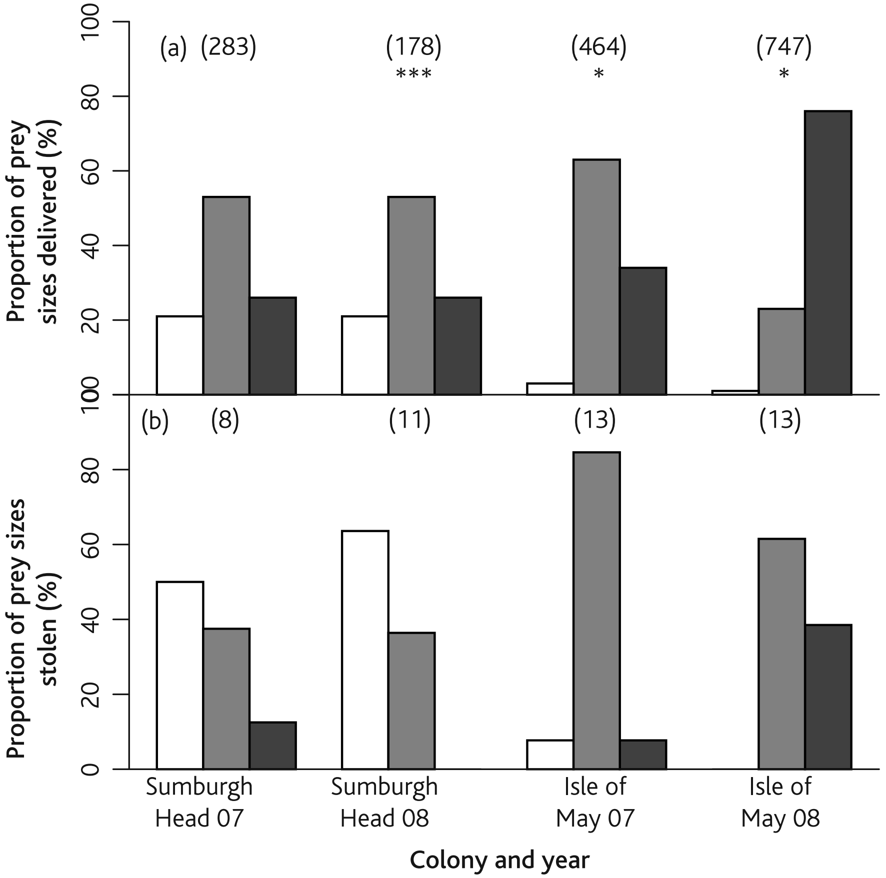

Figure 2. Percentage of prey in different size classes (a) delivered by and (b) stolen from breeding Common Guillemots *Uria aalge* with chicks at Sumburgh Head and Isle of May in 2007 and 2008. Open bars represent large prey; light grey bars, medium prey; dark grey bars, small prey. Statistical significance of differences between percentage size class delivered and percentage size class stolen are shown by asterisks (*P < 0.05, **P < 0.01, ***P < 0.001). Sample sizes are given in brackets.

stole prey that were on average, larger than the prey captured by foraging. Targeting such prey maximises the energetic benefit gained but larger prey items are also more conspicuous and thus may be easier to steal. This suggests that even occasional kleptoparasitism may be costly to Guillemot hosts.

Given the accessibility of this alternative food resource, it is surprising that only a small proportion of individuals became kleptoparasites, suggesting that kleptoparasitism is a specialist foraging strategy such as those seen in other seabird species (Woo *et al*. 2008). Within a population, intra-specific kleptoparasitism may be shown either frequently by a small proportion of individuals or infrequently by many individuals (Steele & Hockey 1995; Shealer & Spendelow 2002). A low frequency of habitual kleptoparasitism performed by a small number of individuals may be a consequence of a high cost or phenotypic constraint preventing more individuals adopting the behaviour (Shealer *et al*. 2005).

The benefits of kleptoparasitism may vary in magnitude according to environmental conditions (Oro 1996), and the frequency of kleptoparasitism was significantly higher at Sumburgh Head in 2008 than in 2007 or in either year at the Isle of May. These differences may reflect the especially poor conditions experienced by birds at Sumburgh Head in 2008, compared to the less severe conditions at this colony in 2007. In addition, the topography of the two study sites may have contributed to variation in the frequency of kleptoparasitism; birds returning with prey made a less direct approach to the breeding site at Sumburgh Head, which probably increased the visibility of prey items to potential kleptoparasites and allowed additional time for scanning for kleptoparasitism opportunities at this site.

In conclusion, we show that Common Guillemots can exploit a combined strategy of foraging at sea augmented by kleptoparasitism during adverse conditions. These data suggest that investigating changes in individual behavioural strategies in response to localised conditions may help to improve predictions of population-level responses to low food availability under future environmental change.

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