

IMPACTS OF INTRASPECIFIC KLEPTOPARASITISM AND DIET SHIFTS ON RAZORBILL *ALCA TORDA* PRODUCTIVITY AT THE GANNET ISLANDS, LABRADOR

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SUMMARY

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Intraspecific kleptoparasitism, the stealing of food from members of the same species, has received widespread but mostly superficial attention in the scientific literature. However, the effects of such behavior can be significant. Here we report on high rates of intraspecific kleptoparasitism in the Razorbill *Alca torda* at the Gannet Islands, a behavior that appears to be colony-specific. Razorbills carry their prey conspicuously in the bill, making them vulnerable to kleptoparasitic attacks from neighboring birds. We examined the relationship between the frequency of kleptoparasitic attacks and the prey species carried by breeding adults. During 2003–2006, 69% of all Razorbills carrying food to a chick were attacked ($n = 182$) and of these attacks, 18% ($n = 22$) were successful. Group attacks (two or more kleptoparasites) were more successful numerically (27%, $n = 71$), but only one member of the group ever received the reward. The frequency of kleptoparasitism observed by Razorbills at the Gannet Islands is one of the highest reported for any seabird, including many specialist kleptoparasites such as frigatebirds. This finding, combined with the lowest observed Razorbill productivity (overall success = 0.39, $n = 222$) for the Gannet Islands and drastic shifts in diet, may indicate decreased food availability.

Key words: *Alca torda*, diet, kleptoparasitism, Razorbill, reproductive success

INTRODUCTION

The stealing of food (kleptoparasitism) is widespread among many seabird families—most prominently the Laridae, Fregatidae and Stercorariidae (Hopkins & Wiley 1972, Carroll & Cramer 1985, Le Corre and Jouventin 1997, Spear *et al.* 1999, Shealer & Spindelov 2002). Kleptoparasitic behavior is separated into two forms: interspecific (between members of different species) and intraspecific (between members of the same species). In the family Alcidae, interspecific kleptoparasitism is relatively common (Ingold & Tschanz 1970; Rice 1985, 1987; Emms & Verbeek 1991; St. Clair *et al.* 2001), but few cases of intraspecific kleptoparasitism have been reported (Ainley *et al.* 2002).

Razorbills *Alca torda* are colonial seabirds that provision their chicks with small fish, which they carry conspicuously in the bill (Hipfner & Chapdelaine 2002). Upon returning to the colony with fish, Razorbills typically land on one of a few roosting rocks adjacent to the breeding colony. Individuals must then walk from the roosting rock to the nest, which can be more than 6 m away. During this time, individuals are vulnerable to kleptoparasitic attacks.

The frequency of kleptoparasitic interactions in many seabirds has been shown to respond to local conditions, including decreasing prey availability (Uttley *et al.* 1994, Oro 1996, Ainley *et al.* 2002), and high rates of kleptoparasitism have been linked to decreased feeding rates and low productivity (Hulsman 1976, Sydeman *et al.* 1991, Barrett 1996, Tuckwell and Nol 1997, Triplet *et al.* 1999, St. Clair *et al.* 2001). Here, we present the first record of high rates of intraspecific kleptoparasitism and discuss its potential relationship with Razorbill productivity and prey availability.

METHODS

Study site

Our study was conducted at the Gannet Islands, Labrador (Newfoundland and Labrador, Canada, 53°56'N, 56°30'W), which include six islands (GC1–GC6) located in the Atlantic Ocean, approximately 440 km northeast of Cartwright, Newfoundland and Labrador. The Gannet Islands support the largest colony of Razorbills in North America, with approximately 9800 breeding pairs (Chapdelaine *et al.* 2001). In the 1980s, the climate at the Gannet Islands was typical of the sub-Arctic region, with heavy pack ice remaining around the islands until late June (Birkhead & Nettleship 1983). The area has experienced significant warming in recent years however, and the waters surrounding the islands are now completely clear of ice as early as the first week of May (Canada 2006).

Chick diet and kleptoparasitism

Observations of chick feedings were conducted from mid-July to late August in 1996 and 2003–2006 from blinds located on islands GC2 and GC4. Kleptoparasitic interactions were recorded during feeding watches in 2003–2006. The following information was recorded for each observed feeding or kleptoparasitic interaction:

- Band numbers (when available) of the target (bird carrying the fish) and the kleptoparasite
- Number, size and species of fish involved
- Number of birds involved in the attack
- Total number of times the target was attacked

In a successful attack, either the pursuer managed to grab the fish or part of it from the target's beak, or the target dropped the fish and the pursuer grabbed it just before or after it reached the ground. The success rate was defined as the number of attacks in which the kleptoparasite obtained food against the total number of attacks. We conducted binomial logistic regression analyses to determine if a particular fish species was preferred and thus whether a bird carrying that species was more likely to be attacked.

Productivity

We used methods identical to those published by Birkhead and Nettleship (1983) for monitoring Razorbills at the Gannet Islands. Most Razorbills occupy crevices in low-lying boulder scree (<10 m above sea level), and so the presence of an egg or chick can be detected only by entering the colony and visiting individual nests. However, regular disturbance of Razorbill breeding sites has been shown to reduce breeding success (Birkhead & Nettleship 1983, Lyngs 1994), and such breeding sites may not provide a reliable estimate of Razorbill breeding success. A small proportion of the population breed on narrow cliff ledges, and such sites can be monitored without disturbance because the occupant or occupants

can be observed from a distance with a spotting scope or the naked eye. However, even this approach may not provide a good measure of breeding success, because open sites are not typical of Razorbill nests on the Gannet Islands and are more vulnerable to gull predation (Birkhead & Nettleship 1983, Rowe & Jones 2000).

To accurately estimate Razorbill productivity and to maintain methods comparable to those used by Birkhead & Nettleship (1983), we established three plot types that were subject to varying levels of disturbance. "Undisturbed plots" were cliff sites that could be monitored without entering the colony. "Low disturbance plots" were checked only three times during the breeding season: once upon arrival on the islands in late June when all eggs had been laid, a second time when approximately 90% of eggs had hatched and 15 days later when most chicks were near fledging. "Moderately disturbed plots" were checked every four days beginning approximately four days before peak hatching and continuing until all chicks had fledged. Moderately disturbed sites were not checked during incubation because Lloyd (1979) showed that, in Razorbills, most nest failure occurs during the incubation period.

Hatching success was defined as the proportion of eggs laid that produced chicks. Fledging success was defined as the proportion of chicks that survived to nest departure. Overall success is the proportion of eggs laid that produced chicks that survived to 15 days of age.

RESULTS

Chick diet

Sand Lance *Ammodytes* spp. was consistently the dominant prey species, representing more than 50% of the overall chick diet in all years of the present study (Table 1). From 1996 to 2006, the proportion of adult Capelin *Mallotus villosus* increased from 3% to 14% of the overall diet. Young of the year (YOY) Capelin, an age class not previously reported in the diet of Razorbills at the Gannet Islands, accounted for 3% of the diet in 2005 and 2006.

Productivity

Razorbill reproductive success at the Gannet Islands was significantly lower in 2004–2006 than in any other year studied ($G = 64.17$, $df = 6$, $p < 0.001$; Table 2). Hatching success for 2004–2006 averaged 62%, with nests in the low-disturbance plot having the lowest value (55%, Tables 2 and 3). Fledging success averaged

TABLE 1
Diet^a of Razorbills at the
Gannet Islands, Labrador, 1981–2006

Prey type	Years of study		
	1981/82 ^b	1996 ^c	2003–2006 ^d
Sand Lance <i>Ammodytes</i> spp.	0.62	0.90	0.80
Capelin <i>Mallotus villosus</i>			
Adult	0.38	0.03	0.14
Young of the year	0.00	0.00	0.03
Daubed Shanny <i>Leptoclinius maculatus</i>	<0.01	0.01	0.03
Other	0.00	0.06 ^e	0.00

^a Proportional composition based on number of items delivered.

^b Birkhead & Nettleship (1983).

^c Source: I.L. Jones, unpubl. data.

^d Current study.

^e Other species include Stout Eelblenny *Anisarchus medius*, Snake Blenny *Eumesogrammus praecisus*, and squid.

TABLE 2
Razorbill productivity at the Gannet Islands, Labrador, 1980–2006

Component	Years of study					
	1980–1983 ^a		1997 ^b		2004–2006 ^c	
	(n/N)	(Prop.)	(n/N)	(Prop.)	(n/N)	(Prop.)
Hatching success	492/775	0.63	38/51	0.75	196/314	0.62
Fledging success	377/492	0.77	37/38	0.97	125/197	0.63
Overall success	377/775	0.49	37/51	0.73	125/314	0.39

^a Birkhead & Nettleship (1983).

^b Hipfner & Bryant (1999).

^c Current study. Nests from each of the three plot types (low disturbance, moderate disturbance and undisturbed) are combined. Prop. = proportion.

63%, with nests in the low-disturbance plot having the lowest value of 60%. Moderate-disturbance and undisturbed plots had 68% and 61% fledging success respectively. Of all chicks that died ($n = 72$), 57% did so within the first 7 days of life.

Intraspecific kleptoparasitism

Intraspecific kleptoparasitism in Razorbills at the Gannet Islands appears to be a recent phenomenon, because no observations of this behavior have been reported since monitoring began in the early 1980s. This behavior was not observed at other colonies in Labrador or on Gull Island (Newfoundland and Labrador, 47°15'N, 52°46'W; J. Lavers, pers. obs.) and occurs only in about 1 of every 60 feedings on Machias Seal Island [New Brunswick, 44°30'N, 67°06'W; $n = 221$ (University of New Brunswick, Atlantic Co-operative Wildlife Ecology Research Network, unpub. data)].

A total of 182 observations of Razorbills carrying fish on the Gannet Islands were recorded from 2003 to 2006 (Table 4). Of these, 125 observations involved kleptoparasitic interactions in which the bird carrying the fish was attacked one or more times (attack rate = 0.69, Table 4). Sand Lance, which accounted for more than 77% of all kleptoparasitic interactions, were significantly more likely to be the target of an attack than were adult Capelin and Daubed Shanny *Leptoclinus maculatus* ($G = 8.17$, $df = 1$, $p = 0.004$). Overall, 18% of attacks were successful ($n = 22$).

In 71 kleptoparasitic interactions, two or more Razorbills attempted to steal fish from a single individual (hereafter referred to as "mobbing"). Mean group size was 4.3 birds ($n = 71$, $SE = 0.30$), but in six cases, 10 or more aggressors converged on the target bird

from multiple directions. Of the 71 mobbings, 19 were successful (success rate = 0.27).

Twelve banded Razorbills were identified as the aggressor in kleptoparasitic interactions (Table 5). Eight of these birds were banded as chicks (that is, they were of known age). Mean age of the attacker was 4.8 years (range: 3–8 years; $SE = 0.74$). The remaining four birds were banded as adults, and so their exact ages were unknown. However, previous studies have shown that the first bill groove does not develop until a Razorbill's third summer and that the number of grooves increases by a maximum of one groove annually (Hipfner & Chapdelaine 2002, Hope Jones 1988). On that basis, the birds observed were four or more years of age.

Eleven banded birds were identified as the target of kleptoparasitic attacks (Table 6), all of those birds were at least five years of age when the attack occurred. Because the number of Razorbills banded on the Gannet Islands was small, a determination whether certain banded birds were specializing in kleptoparasitic behavior or were repeatedly being victimized was not possible. All birds listed in Tables 5 and 6 (except 895-13523, which was both an aggressor and a target) were observed in kleptoparasitic interactions on a single occasion.

In Razorbills, more than one nest can occupy space under a single boulder; determining the nest that an adult occupies once it has disappeared into a crevice is therefore difficult. Thus, determining feeding rates and quantifying the direct effects of kleptoparasitism (that is, chick growth) was not possible in this study.

TABLE 3
Breeding success of Razorbills at the Gannet Islands in two disturbed and one undisturbed plot, 2004–2006

Plot type	Hatch success		Fledge success		Overall	
	(n/N)	(Prop.)	(n/N)	(Prop.)	(n/N)	(Prop.)
Undisturbed	46/61	0.75	28/46	0.61	28/61	0.45
Low disturbance	72/130	0.55	43/72	0.60	43/130	0.33
Moderate disturbance	79/123	0.64	54/79	0.68	54/123	0.44
Total	196/314	0.62	125/197	0.63	125/314	0.39

Prop. = proportion.

TABLE 4
Fish species involved in kleptoparasitic interactions between Razorbills on the Gannet Islands, 2003–2006

Prey type	Birds carrying fish		Birds attacked		Successful attacks ^a	
	(n)	(Prop.)	(n)	(Prop.)	(n)	(Prop.)
Sand Lance <i>Ammodytes</i> spp.	127		91	0.72	17	0.19
Capelin <i>Mallotus villosus</i>						
Adult	23		11	0.48	4	0.36
Young of the year	6		4	0.67	0	0.00
Daubed Shanny <i>Leptoclinus maculatus</i>	10		3	0.30	0	0.00
Unidentified	16		15	0.94	1	0.07

^a Fish stolen by kleptoparasite.

Prop. = proportion.

DISCUSSION

Razorbill diet at the Gannet Islands has shifted dramatically since the early 1980s, with once-dominant fish species such as Capelin decreasing substantially in representation. In the early 1980s, Capelin accounted for almost 40% of Razorbill chick diet at the Gannet Islands (Birkhead & Nettleship 1983, Table 1). By the mid-1990s, Capelin were observed in only 3% of feedings, indicating that a major shift had occurred. At the same time, Common Murres

Uria aalge, Thick-billed Murres *U. lomvia* and Atlantic Puffins *Fratercula arctica* at the Gannet Islands were all observed feeding their chicks up to 75% fewer Capelin than in previous years (Bryant *et al.* 1999, Baillie & Jones 2004). It has been suggested that few alternatives to Capelin exist in the prey base in Labrador and that, without Capelin, breeding failure of many seabirds is inevitable (Brown & Nettleship 1984). In the present study, the proportion of Capelin in Razorbill chick diets increased slightly to 14%; however, the appearance of previously unrecorded prey items such as YOY

TABLE 5
Razorbills identified as aggressors in kleptoparasitic interactions on the Gannet Islands

Band number	Year banded	Year involved in kleptoparasitic interaction	Minimum age at time of attack	Bill grooves (n) ^a	Attack successful
895-13523	1997	2006	11	N/A	Unknown
895-13851	1997	2006	11	N/A	No
895-13999	1997	2005	8	N/A	Yes
895-14436	2000	2006	6	N/A	No
895-14439	2000	2003	3	N/A	Yes
895-15780	1998	2005	7	N/A	No
895-15831	2000	2006	6	N/A	Yes
895-18412	2003	2006	3	N/A	Yes
895-18429	2003	2006	3	N/A	Yes
895-18436	2003	2006	3	N/A	No
895-19726	2005	2005	4	2 ^b	No
895-19729	2005	2005	5	3 ^b	No

^a Provided for birds banded as adults.

^b See text for explanation.

TABLE 6
Razorbills identified as victims of kleptoparasitic attacks on the Gannet Islands

Band number	Year banded	Year involved in kleptoparasitic interaction	Minimum age at time of attack	Bill grooves (n) ^a	Fish stolen
895-13168 ^b	1996	2004	8	1.5	No
895-13266	1996	2004	8	N/A	Yes
895-13412	1996	2005	9	N/A	No
895-13526	1997	2005	8	2	No
895-13523	1997	2006	9 ^c	N/A	No
895-13856	1997	2006	9 ^b	2	Yes
895-15978	2002	2003	3 ^c	1	No
895-16559	2001	2003	4 ^c	2	No
895-17921	2004	2006	5 ^c	2	Unknown
895-19418	2004	2006	5 ^c	2.5	Yes
895-19725	2005	2005	4 ^c	2	No

^a Provided for birds banded as adults.

^b Recaptured as an adult in 2000.

^c See text for explanation.

Capelin and an increase in Daubed Shanny suggest that Razorbills are having difficulty locating Capelin and are turning to alternative (and possibly less nutritious) prey.

Razorbill productivity at the Gannet Islands during 2004–2006 was the lowest recorded since monitoring began (Table 2). Hatching success was especially low, being only 62% as compared with 87% and 74% for Razorbills monitored on Machias Seal Island in the same years (Bond *et al.* 2007). Razorbill fledging success typically ranges between 85% and 95% (Lloyd 1979, Harris and Wanless 1989, Lyngs 1994, Hipfner and Bryant 1999), but on the Gannet Islands, it was only 63%. Chick mortality is typically greater in the first few days of life because of an inability to thermoregulate (Barrett 1984). However, in our study, 43% of chick mortalities were of late-stage chicks (8–12 days old) with no obvious cause of death other than emaciation. It appeared that prey alternatives to Capelin were available to Razorbills at the Gannet Islands, but that these prey may not have been sufficiently abundant or energetically equivalent. These findings provide partial support for Brown and Nettleship's (1984) hypothesis that prolonged absence of Capelin leads to reduced reproductive performance of seabirds in Labrador.

Poor productivity in Razorbills at the Gannet Islands did not appear to be associated with human disturbance in 2004–2006. This conflicts with Birkhead & Nettleship's (1983) study of Razorbill productivity at the Gannet Islands, which found that regular researcher visits to breeding sites significantly reduced hatching success. In both years of our study, productivity in sites checked only a few times throughout the breeding season (low-disturbance) was significantly lower than in plots checked at four-day intervals (moderate-disturbance). The low-disturbance plot was changed from 2004 to 2005, which reduced the possibility of having chosen a particularly poor site in both years. Cliff nesting Razorbills (undisturbed plot) had the highest success rate, despite increased exposure to gull predation and weather.

The level of kleptoparasitism observed in Razorbills at the Gannet Islands was among the highest reported for seabirds, including many specialist or habitual kleptoparasites such as frigatebirds, gulls and terns (Osorno *et al.* 1992, Steele & Hockey 1995, Shealer & Spindel 2002, Martinez-Abrain *et al.* 2003). Overall, attacks performed by single Razorbills were less successful than those carried out by groups. The greater success rate of group attacks appeared to result from an enhanced ability to harass and overwhelm the target, as has been reported for Arctic Skuas *Stercorarius parasiticus* (Arnason & Grant 1978). However, only one individual in the group ever received the stolen fish; thus the success rate per individual decreased as the number of participants in the group increased (see also Hatch 1975, Caldwell & Furness 2001). In Razorbills, an average group size of fewer than two individuals was required to make the per capita rate of success from group attacks equal to that of individual chases. Mean group size in Razorbills is 4.3 individuals; therefore there were very few circumstances in which individuals could increase their chance of success by joining a group. The fact that we observed as many as 15 individuals competing for a single fish adds further support to the idea that food availability was low during this study.

In many seabird species, immature birds are more likely than adults to kleptoparasitize (Carroll & Cramer 1985, Steele & Hockey 1995, Tuckwell & Nol 1997). Breeding adults are typically more experienced foragers, and so juveniles are able to use intraspecific kleptoparasitism to exploit the greater hunting capabilities of adults

(Steele & Hockey 1995). However, this factor did not pertain for Razorbills, because all but three banded birds ($n = 23$) involved in kleptoparasitic interactions were of breeding age at the time of the attack. The fact that experienced breeders are attempting to steal food from other breeders rather than to forage on their own may further indicate that food availability was low.

In some seabird species, behavioral shifts such as an increase in kleptoparasitic activity have been linked to low prey availability (Steele & Hockey 1995, Triplet *et al.* 1999, Ainley *et al.* 2002). For Razorbills, this case also appears to hold. The appearance of YOY Capelin in the diet of Razorbills and the high rate of kleptoparasitism may be a result of increasing sea surface temperatures (Petrie *et al.* 2003, Petrie *et al.* 2004) and decreased food availability. Capelin and Sand Lance are coldwater species (Carscadden *et al.* 2001) and, independent of their actual abundance, may become less available to Razorbills when they migrate down the water column away from warmer surface waters (Methven & Piatt 1991).

Furness (1987) found that the proportion of birds successfully attacked by kleptoparasites was always less than 5% in a number of seabird species and suggested that relatively low impact is a necessary condition for the interaction of kleptoparasites and targets to be evolutionarily stable. The success rate for individual Razorbill kleptoparasites (not including mobbings) was almost three times the level that might be considered sustainable. If the same individuals are consistently delayed in feeding their chicks, the survival of the young will be reduced (Hulsman 1976). Thus, the level of kleptoparasitism that we observed is potentially detrimental and may explain the low rate of productivity in Razorbills. Future studies should attempt to directly quantify the effects of kleptoparasitism on chick feeding and growth rates, because consistently low productivity resulting from kleptoparasitism could lead to population declines in the long term.

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REFERENCES

- AINLEY, D.G., NETTLESHIP, D.N., CARTER, H.R. & STOREY, A.E. 2002. Common Murre (*Uria aalge*). In: Poole, A. & Gill, F. (Eds). The birds of North America. No. 666. Philadelphia: The Birds of North America, Inc. 44 pp.
- ARNASON, E. & GRANT, P.R. 1978. The significance of kleptoparasitism during the breeding season in a colony of Arctic Skuas *Stercorarius parasiticus* in Iceland. *Ibis* 120: 38–54.
- BAILLIE, S.M. & JONES, I.L. 2004. Responses of Atlantic Puffins to a decline in Capelin abundance at the Gannet Islands, Labrador. *Waterbirds* 27: 102–111.
- BARRETT, R.T. 1996. Prey harvest, chick growth, and production of three seabird species on Bleiksoy, north Norway, during years of variable food availability. Canadian Wildlife Service Occasional Paper No. 91. pp. 20–26.

- BARRETT, R.T. 1984. Adult body temperatures and the development of endothermy in the Puffin *Fratercula arctica*, Razorbill *Alca torda*, and Guillemot *Uria aalge*. *Fauna Norvegica Series C, Cinclus* 7: 119–123.
- BIRKHEAD, T.R. & NETTLESHIP, D.N. 1983. Studies of alcids breeding at the Gannet Clusters, Labrador, 1980–1983. Canadian Wildlife Service Report No. 125. 144 pp.
- BOND, A.L., MCNUTT, M.P.F., CLARKE, T.C. & DIAMOND, A.W. 2007. Machias Seal Island progress report, 1995–2006 (unpublished report). Fredericton, NB: Atlantic Cooperative Wildlife Ecology Research Network, University of New Brunswick. 86 pp.
- BROWN, R.G.B. & NETTLESHIP, D.N. 1984. Capelin and seabirds in the northwest Atlantic. In: Nettleship, D.N., Sanger, G.A. & Springer, P.F. (Eds). *Marine birds: their feeding ecology and commercial fisheries relationships*. Ottawa: Canadian Wildlife Service Special Publication. pp. 184–195.
- BRYANT, R., JONES, I.L. & HIPFNER, J.M. 1999. Responses of Common and Thick-billed Murres to changes in prey availability at the Gannet Islands, Labrador. *Canadian Journal of Zoology* 77: 1278–1287.
- CALDOW, R.W.G. & FURNESS, R.W. 2001. Does Holling's disc equation explain the functional response of a kleptoparasite? *Journal of Animal Ecology* 70: 650–662.
- CANADA, CANADIAN ICE SERVICE. 2006. Seasonal summary for Eastern Canadian waters, winter 2005–2006. Ottawa: Canadian Ice Service. 38 pp.
- CARROLL, S.P. & CRAMER, K.L. 1985. Age differences in kleptoparasitism by Laughing Gulls (*Larus atricilla*) on adult and juvenile Brown Pelicans (*Pelecanus occidentalis*). *Animal Behaviour* 33: 201–205.
- CARSCADDEN, J.E., FRANK, K.T. & LEGGETT, W.C. 2001. Ecosystem changes and the effects on Capelin (*Mallotus villosus*), a major forage species. *Canadian Journal of Fisheries and Aquatic Sciences* 58: 73–85.
- CHAPDELAIN, G., DIAMOND, A.W., ELLIOT, R.D. & ROBERTSON, G.J. 2001. Status and population trends of the Razorbill in eastern North America. Canadian Wildlife Service Occasional Paper No. 105. Ottawa: Canadian Wildlife Service. 21 pp.
- EMMS, S.K. & VERBEEK, N.A.M. 1991. Kleptoparasite avoidance tactics of Pigeon Guillemots, *Cephus columba*. *Animal Behaviour* 41: 907–909.
- FURNESS, R.W. 1987. Kleptoparasitism in seabirds. In: Croxall, J.P. (Ed). *Seabirds: feeding ecology and role in marine systems*. Cambridge, UK: Cambridge University Press. pp. 77–100.
- HARRIS, M.P. & WANLESS, S. 1989. The breeding biology of Razorbills *Alca torda* on the Isle of May. *Bird Study* 36: 105–114.
- HATCH, J.J. 1975. Piracy in Laughing Gulls *Larus atricilla*: an example of the selfish group. *Ibis* 117: 357–365.
- HIPFNER, J.M. & BRYANT, R. 1999. Comparative breeding biology of Guillemots *Uria* spp. and Razorbills *Alca torda* at a colony in the northwest Atlantic. *Atlantic Seabirds* 1: 121–134.
- HIPFNER, J.M. & CHAPDELAIN, G. 2002. Razorbill (*Alca torda*). In: Poole, A. & Gill, F. (Eds). *The birds of North America*. No. 635. Philadelphia: The Birds of North America, Inc. 36 pp.
- HOPE JONES, P. 1988. Post-fledging wing and bill development in the Razorbill *Alca torda islandica*. *Ring and Migration* 11: 105–110.
- HOPKINS, C.D. & WILEY, R.H. 1972. Food parasitism and competition in two terns. *Auk* 89: 583–594.
- HULSMAN, K. 1976. The robbing behaviour of terns and gulls. *Emu* 76: 143–149.
- INGOLD, P. & TSCHANZ, B. 1970. Tordalken, *Alca torda*, als Nahrungsschmarotzer [Razorbills *Alca torda*, as kleptoparasites]. *Sterna* 9: 201–206.
- LE CORRE, M. & JOUVENTIN, P. 1997. Kleptoparasitism in tropical seabirds: vulnerability and avoidance responses of a host species, the Red-footed Booby. *Condor* 99: 162–168.
- LLOYD, C.S. 1979. Factors affecting breeding of Razorbills (*Alca torda*) on Skokholm. *Ibis* 121: 165–176.
- LYNGS, P. 1994. The effects of disturbance on growth rate and survival of young Razorbills *Alca torda*. *Seabird* 16: 46–49.
- MARTINEZ-ABRAIN, A., GONZALEZ-SOLIS, J., PEDROCCHI, V., GENOVART, M., ABELLA, J.C., RUIZ, X., JIMENEZ, J. & ORO, D. 2003. Kleptoparasitism, disturbance, and predation of Yellow-legged Gulls on Audouin's Gull in three colonies of the western Mediterranean. *Scientia Marina* 67: 89–94.
- METHVEN, D.A. & PIATT, J.F. 1991. Seasonal abundance and vertical distribution of Capelin (*Mallotus villosus*) in relation to water temperature at a coastal site off eastern Newfoundland. *ICES Journal of Marine Science* 48: 187–193.
- ORO, D. 1996. Interspecific kleptoparasitism in Audouin's Gull *Larus audouinii* at the Ebro Delta, northeast Spain: a behavioural response to low food availability. *Ibis* 138: 218–221.
- OSORNO, J.L., TORRES, R. & GARCIA, C.M. 1992. Kleptoparasitic behavior of the Magnificent Frigatebird: sex bias and success. *Condor* 94: 692–698.
- PETRIE, B., PETTIPAS, R.G., PETRIE, W.M. & DRINKWATER, K.F. 2003. An overview of meteorological, sea ice, and sea-surface temperature conditions off eastern Canada during 2003. Research document 2004/047. Ottawa: Department of Fisheries and Oceans, Canadian Science Advisory Secretariat. 36 pp.
- PETRIE, B., PETTIPAS, R.G. & PETRIE, W.M. 2004. An overview of meteorological, sea ice, and sea-surface temperature conditions off eastern Canada during 2004. Research document 2005/020. Ottawa: Department of Fisheries and Oceans, Canadian Science Advisory Secretariat. 37 pp.
- RICE, J. 1985. Interactions of variation in food supply and kleptoparasitism levels on the reproductive success of Common Puffins (*Fratercula arctica*). *Canadian Journal of Zoology* 63: 2743–2747.
- RICE, J. 1987. Behavioural responses of Common Puffins to kleptoparasitism by Herring Gulls. *Canadian Journal of Zoology* 65: 339–347.
- ROWE, S. & JONES I.L. 2000. The enigma of Razorbill *Alca torda* breeding site selection: adaptation to a variable environment? *Ibis* 142: 324–327.
- SHEALER, D.A. & SPENDELOW, J.A. 2002. Individual foraging strategies of kleptoparasitic Roseate Terns. *Waterbirds* 25: 436–441.
- SPEAR, L.B., HOWELL, S.N.G., OEDEKOVEN, C.S., LEGAY, D. & BRIED, J. 1999. Kleptoparasitism by Brown Skuas on albatross and giant-petrels in the Indian Ocean. *Auk* 116: 545–548.
- ST. CLAIR, C.C., ST. CLAIR, R.C. & WILLIAMS, T.D. 2001. Does kleptoparasitism by Glaucous-winged Gulls limit the reproductive success of Tufted Puffins? *Auk* 118: 934–943.
- STEELE, W.K. & HOCKEY, P.A.R. 1995. Factors influencing rate and success of intraspecific kleptoparasitism among Kelp Gulls (*Larus dominicanus*). *Auk* 112: 847–859.

SYDEMAN, W.J., PENNIMAN, J.F., PENNIMAN, T.M., PYLE, P. & AINLEY, D.G. 1991. Breeding performance in the Western Gull: effects of parental age, timing of breeding, and year in relation to food availability. *Journal of Animal Ecology* 60: 135–149.

TRIPLET, P., STILLMAN, R.A. & GOSS-CUSTARD, J.D. 1999. Prey abundance and the strength on interference in a foraging shorebird. *Journal of Animal Ecology* 68: 254–265.

TUCKWELL, J. & NOL, E. 1997. Intra- and inter-specific interactions of foraging American Oystercatchers on an oyster bed. *Canadian Journal of Zoology* 75: 182–187.

UTTLEY, J.D., WALTON, P., MONAGHAN, P. & AUSTIN, G. 1994. The effects of food abundance on breeding performance and adult time budgets of Guillemots *Uria aalge*. *Ibis* 136: 205–233.



Fig. 1. Razorbill 895-18436 attempting to kleptoparasitize another unbanded Razorbill on the Gannet Islands, Labrador, in July 2006. (Photo courtesy of Jennifer Lavers.)

