Is an increase in gull numbers responsible for limiting Atlantic Puffin *Fratercula arctica* numbers on Burhou, Channel Islands?

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Abstract
This study investigated whether increased numbers of *Larus* gulls on the English Channel Island of Burhou restrict or endanger the island's Atlantic Puffin *Fratercula arctica* population. About 120 breeding pairs of Atlantic Puffins in 2005–07 indicated little change in numbers since 1980, although a large decline occurred between 1950 and 1980. Numbers of Great Black-backed Gulls *Larus marinus* have changed little since 1969 but their direct predation on the reduced population of Atlantic Puffins was a considerable addition to adult mortality rates. Kleptoparasitic attacks by a greatly increased population of Lesser Black-backed Gulls *L. fuscus*, and by Herring Gulls *L. argentatus*, were probably too infrequent and too unsuccessful to affect Atlantic Puffin breeding success. When a large Atlantic Puffin population is reduced, predation by Great Black-backed Gulls and reduced recruitment caused by high breeding densities of gulls may prevent recovery of that population.

Introduction

The most southerly breeding populations of Atlantic Puffins *Fratercula arctica* in the east Atlantic, on Les Sept Iles (Brittany) and Burhou (Channel Islands), have been reduced from tens of thousands to 200–300 pairs over the last 60 years, the main declines having occurred by 1980 (Cramp *et al.* 1974; Danchin & Cordonnier 1980; Harris 1984; Lloyd *et al.* 1991).

Two likely factors contributing to this decline have been oil spills in the region and human disturbance. Oil spills from the grounding of the tankers *Torrey Canyon* in 1967 and *Amoco Cadiz* in 1978 were followed by substantial declines in the Atlantic Puffin (hereafter 'Puffin') population in Brittany (Pericaud 1979; Harris

1984), and it is likely that the Burhou population was similarly affected. More recently, oil spills from the tankers *Erika* off Brittany in 1999 (Cadiou *et al*. 2004) and *Prestige* off northwest Spain in 2002 (García *et al*. 2003) affected wintering seabirds in the Bay af Biscay, including Puffins. Human disturbance may also have contributed to the decline on Burhou, as between 1950 and the early 1980s fishermen and private individuals were permitted on the island at any time and a tourist boat landed daily during the breeding season (Pierce *et al*. 1986; Carney *et al*. 1999). A prohibition on visitors to the island during the Puffin breeding season was introduced in the mid 1980s and although the population has not declined any further (Mitchell *et al*. 2004) it shows no signs of recovery.

The failure of the Burhou Puffin colony to recover between 1980 and 2000, when many in the UK were increasing (Harris & Wanless 2004), suggests factors other than oil and disturbance may now be limiting numbers there, perhaps including climatic effects on food supply (Harris *et al*. 2005; Sandvik *et al*. 2005). However, the quality and quantity of the fish loads carried by Burhou Puffins in 2007 were at least as good as those seen at other UK Puffin colonies in recent years (M. Harris & S. Wanless pers. comm.), and a separate study on Burhou in 2006 and 2007 found Puffins carried mainly Gadidae and sandeels (Ammodytidae) of good-sized loads, indicating food supply during the breeding season was not then an issue (Sanders 2008).

Another factor that could be preventing any recovery of Burhou's Puffins is the increased population of nesting gulls. Between 1969 and 2000 breeding numbers of Lesser Black-backed Gulls *Larus fuscus* in the Channel Islands rose dramatically, with smaller increases reported for Herring Gulls *L. argentatus* and Great Black-backed Gulls *L. marinus* (Mitchell *et al*. 2004). Gulls can kill Puffins and steal their food (Taylor 1985; Russell & Montevecchi 1996; Finney *et al*. 2001; St Clair *et al*. 2001). Kleptoparasitism may affect Puffin breeding success and chick survival directly, or indirectly by increasing energetic costs to adults undertaking avoidance and escape behaviours (Rice 1987), while the presence of large numbers of gulls at a Puffin colony can reduce recruitment (Finney *et al*. 2003). Here we examine the effects *Larus* gulls may have in preventing the recovery of Burhou's Puffin population.

Methods

Burhou lies 1.6 km north of Alderney, at 49°44' N 2°14' W, has an area of 23 ha, and supports breeding Puffins, Herring Gulls, Lesser Black-backed Gulls, Great Black-backed Gulls, European Shags *Phalacrocorax aristotelis,* Great Cormorants *Ph. carbo* and European Storm-petrels *Hydrobates pelagicus*.

Census of Puffin and gull populations: During late April and early May 2005–07 burrows visited regularly by Puffins or showing signs of regular use (freshly disturbed soil, or faeces) were counted and marked, and observed throughout the season for further activity and recording provisioning of chicks. These observations were used to estimate the number of apparently occupied burrows (AOB) as the season progressed, and to estimate breeding success (Walsh *et al*. 1995). In 2005, breeding success was recorded for the entire island population, but in 2006 and

2007 was calculated only for the main colony (38% of the island population each year), as this area could be monitored more regularly and intensively. Previous estimates of Burhou's Puffin population were made by counting birds rafting on the sea between April and June, therefore whole island rafting counts were also made several times each season for comparison.

Individual Great Black-backed Gull territories and nest locations were indentified and mapped. For Herring and Lesser Black-backed Gulls, which breed in mixed colonies, two people walked systematically through defined sections of the island placing a raffle ticket in each nest they found; a third observer then followed immediately after and assessed counting efficiency for each section by recording unticketed nests (Wanless *et al*. 1996). The proportions of nests of the two species were determined by applying counts of each species in the defined sections prior to nest counting, to the number of nests counted.

Gull predation on Puffins: To determine the proportion of seabird predator specialists in each species of gull, and identify individuals responsible, all pellets and prey remains were collected on weekly visits to each Great Black-backed Gull territory in 2005, and any Puffin remains/pellets were searched for and collected from Great Black-backed Gull territories in 2006 and 2007. A sample of 25 nests of both Herring and Lesser Black-backed Gulls was selected at random in the main colony areas and visited weekly to collect prey remains throughout the 2005 breeding season. Club sites, where non-breeding gulls congregated, were cleared of prey remains at the start of each season, and visited weekly to identify and collect any Puffin remains. Pellets were dissected and all animal remains identified to family, or when possible to species. Premaxillae and vertebrae of bony fish were identified by reference to Watt *et al*. (1997) and otoliths to Härkönen (1986).

Provisioning by Puffins and kleptoparasitism by gulls: Puffins returning with fish (loads delivered) to a sample of 30–40 burrows containing young in the main colony were logged during continuous dawn to dusk watches on between one and four days each year. In addition to these watches, provisioning was recorded on an *ad hoc* basis each year during chick-rearing, with one to seven hours spent observing parts of the colony at different times of the day on each visit to the island. Puffins carrying fish were observed as they approached the island and the fate of each feeding attempt was recorded as either successful (bird entered a burrow with fish) or unsuccessful (fish stolen by a gull, noting the species responsible). Other interactions between gulls and Puffins were also recorded, such as gulls chasing Puffins as they returned on provisioning flights, and Puffins being inhibited from entering their burrows by the presence of loafing gulls. Puffins scared away by gulls on their first attempt to land were watched, and their subsequent behaviour recorded. In total, 103.5 hours of observation for provisioning and kleptoparasitism were conducted in 2005, 76.5 hours in 2006 and 33.5 hours in 2007.

Analytical methods: Provisioning rate (fish loads delivered per burrow per hour) was modelled using a generalised linear model (GLM), in which the number of loads successfully delivered to chicks was the response variable and the natural log of the number of burrow-hours under observation was the offset, specified with a log link and Poisson error distribution. Model selection was conducted using a backward stepwise approach, with F ratio tests being used to examine the increase in deviance caused by removal of the year effect in order to accommodate over-dispersion. Daily provisioning rates were calculated by multiplying the hourly delivery rate by 18, assuming an 18-hour feeding day during the study period. Parameter estimates and their 95% confidence limits were calculated from the minimum adequate model.

The likelihood of a gull attempting to steal fish from a Puffin and the likelihood of it succeeding were modelled using a GLM with the number of attacks/successes as the response variable and the number of provisioning attempts as the binomial denominator, specified with a logit link and a quasi-binomial error distribution. Model selection was conducted as described above.

Modelling the Puffin population: To predict the effects of gull predation upon Puffin numbers, a simple population model was developed. As *Larus* gulls on Burhou were found to be dietary generalists (from analysis of their pellets), it was assumed that variation in the numbers of Puffins did not affect the number of gulls. The model was one for an age-structured population of breeding Puffins. The recruits were assumed to be the survivors of chicks fledged five years earlier (Appendix 1), and the annual age-independent mortality of breeding Puffins was taken initially as 8%, the highest value of those estimated for breeding Puffins from five colonies in the northeast

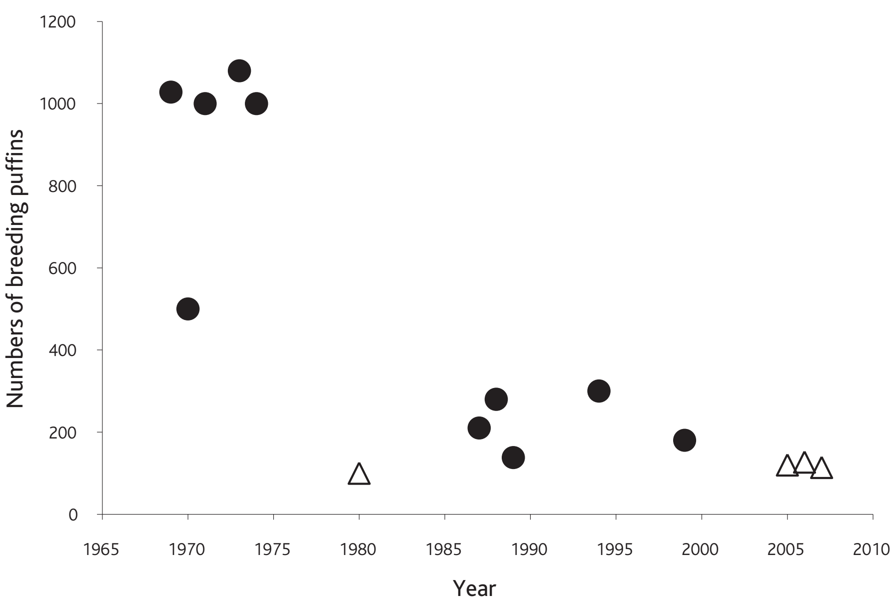

Figure 1. Estimates of the number of breeding pairs of Atlantic Puffins *Fratercula arctica* on Burhou, based on counts of rafting birds (solid circles) and apparently occupied burrows (open triangles).

Atlantic (Harris *et al*. 2005). The effects on Puffin numbers of eliminating gull predation was then explored by reducing this 8% mortality by a value based on estimates made of gull predation in this study.

Results

Puffin numbers and breeding success: Censuses of Puffins on Burhou indicated a large decline from the early 1970s (Figure 1). All previous population estimates were based on raft counts, except in 1980 when 'more than 50 but less than 100' occupied burrows were estimated (Danchin & Cordonnier 1980). Counts of AOB in 2005–07 ranged from 114–127, suggesting numbers had not declined since 1980, while the first raft counts for each of the years 2005–07 ranged from 92–139 birds (Table 1). Most burrows were located on the southeast section of the island (c. 85% of the population) with smaller colonies at the west and east ends and on Little Burhou.

In each year, counts of rafting Puffins increased through the season, with a positive correlation between date and rafting numbers, expressed as a proportion of the AOBs recorded in April and May each year (Pearson's $r = 0.824$, $df = 14$, $P < 0.001$;

Table 1. The number of Atlantic Puffin *Fratercula arctica* apparently occupied burrows in April and early May, and counts of rafting birds in the same period.

Year	AOB	Raft counts (dates)
2005	120	139 (17 May)
		126 (26 May)
		195 (7 June)
		200 (10 June)
		252 (7 July)
		247 (20 July)
2006	127	92 (7 April)
		152 (4 June)
		132 (10 June)
		167 (29 June)
		219 (13 July)
		235 (18 July)
2007	114	127 (7 April)
		115 (15 May)
		158 (22 June)
		213 (7 July)

Table 2. Breeding success of Atlantic Puffins *Fratercula arctica* on Burhou, 2005–07, based on the proportion of apparently occupied burrows being provisioned in mid June.

Year	AOB (April/early May)	Sample	% AOB	AOB mid June	Overall Productivity
2005	120	120	100	77	0.64
2006	127	49	38.6	30	0.61
2007	114	44	38.6	32	0.73

Table 3. Numbers of pairs of breeding Great Black-backed *Larus marinus*, Lesser Black-backed *L. fuscus* and Herring *L. argentatus* Gulls (apparently occupied nests, AON) recorded on Burhou in the three national censuses, and in 2005–07 (this study). * The 1969, 1987 and 2000 counts included AON on Little Burhou, whilst counts for 2005–07 were for Burhou only, except in 2005 when 10 AON were also recorded on Little Burhou.

Year (date)	Great Black-backed Gull	Lesser Black-backed Gull	Herring Gull
1969 (24–26 May)	37*	100	112
1987 (12 June)	22*	105	70
1999 (July)	27*	313	125
2005 (30–31 May)	18 (+10 AON on Little Burhou)	1103	202
2006 (25–26 May)	18	937	109
2007 (28–29 May)	16	994	148

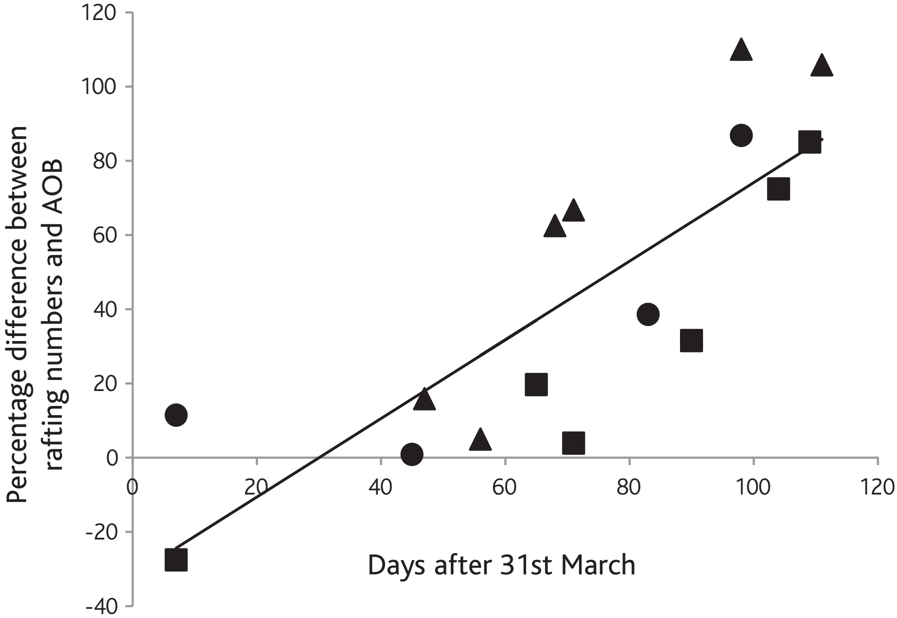

Figure 2. The difference between population estimates based on rafting numbers of Atlantic Puffins *Fratercula arctica* and the AOB on different days during the breeding season. The first day of the season, 31 March, was chosen arbitrarily and the differences between population estimates have been expressed as percentages of the AOB for the year in question so that data from different years can be compared; ▲ = 2005, ■ = 2006, ● = 2007.

Figure 2). Whereas counts of rafting birds before mid May (during incubation) approximated to the number of AOB (± c. 30%), those in late June and early July overestimated the number of breeding pairs by up to 100%.

Based on the numbers of AOB being provisioned by adults beyond mid June, mean breeding success in 2005–07 was 0.66 chicks per pair (Table 2).

Gull census: Counting efficiency of nests of Herring and Lesser Black-backed Gulls was always > 80% for each area surveyed, but there was considerable variation in numbers, with 46% and 15% fewer in 2006 than in 2005, respectively. Great Black-backed Gull numbers were stable at 18 pairs (two individuals known to be Puffin predators in 2005 and 2006 were culled in 2007 before the census count), with similar totals for Burhou and Little Burhou (a small islet only accessible from Burhou at low tide) in 2000 and 2005 (Table 3).

Gull diet and predation rates: Relatively few pellets were recovered in the vicinity of the nests in Lesser Black-backed and Herring Gull colonies, suggesting either that adult birds cast pellets away from the colony, or that their food was completely digestible. The 16 pellets and prey remains found at Lesser Black-backed Gull nests all consisted of fish, with 56% composed of Horse Mackerel *Trachurus trachurus*, 25% Garfish *Belone belone* and 19% unidentified fish species. Prey remains at Herring Gull nests were much more varied, with only 5% consisting of fish (Table 4). A total of 97 pellets were collected from 11 Great Black-backed Gull territories in 2005 (the remaining seven identified territories either failed at the egg stage or had their eggs removed by the Burhou warden, so pellets and prey remains were not collected from them). Of the pellets collected four contained Puffin remains in both 2005 and 2006, and two contained Puffin in 2007. In addition to these, the remains of one Puffin was also found in a Great Black-backed Gull club site in 2005. The ten pellets collected from Great Black-backed Gull territories came from just five pairs, all breeding next to the main Puffin colony; each contained a Puffin bill with at least two grooves, thus potentially from a breeding adult (Harris 1984).

We used a simple model of the Burhou Puffin population (Appendix 1) to estimate the future effects of reducing this level of predation to zero. It was assumed that in the presence of predation during the breeding season, age independent mortality of Puffins is 8.0% and that removal of predation by Great Black-backed Gulls would reduce the overall mortality to 6%. Figure 3 shows the predictions of the model for Puffin numbers if the predatory gulls are removed, with the number of breeding pairs of Puffins increasing slowly but progressively.

Interactions between gulls and Puffins: Kleptoparasitism rates (successful attacks) were low in all years, affecting less than 0.5% of all provisioning flights (Table 5). Whilst attacks were carried out by both species, 69% were made by Herring Gulls, but all the successful attacks observed were made by Lesser Black-backed Gulls. The gulls involved all appeared to have nested or attempted to nest within 50 m of the Puffin colony, except for one attack which was carried out at

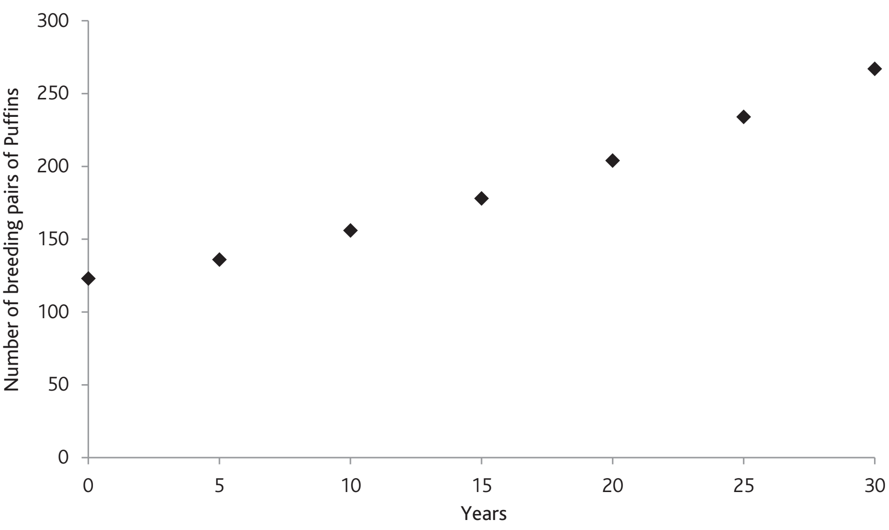

Figure 3. The increase in the numbers of breeding pairs of Atlantic Puffins *Fratercula arctica* on Burhou (given at 5-year intervals) predicted to result from the removal of predatory Great Black-backed Gulls *Larus marinus*.

Table 4. Percentage of different types of prey in pellets found in 2005 in Great Black-backed Gull *Larus marinus* territories (81 pellets collected from 11 territories throughout the breeding season), Lesser Black-backed Gull *L. fuscus* nests (16 pellets or remains from 25 nests), and Herring Gull *L. argentatus* nests (21 pellets or remains from 25 nests).

	Percentageof prey type in diet		
Prey	**Great Black-backed Gull**	**Lesser Black-backed Gull**	**Herring Gull**
Fish[a] (Pisces)	44	100	5
Rabbit *Oryctolagus cuniculus*	23		
Gull (Laridae) chick[b]	14		
Unidentified bird	6		
Cuttlefish *Sepia officinalis*	4		5
Puffin *Fratercula arctica*	5		
European Storm-petrel *Hydrobates pelagicus*	2		5
Gull (Laridae) egg[b]	2		
Shorebird[b] (Charadriiformes)	1		
Feral pigeon *Columba livia*			5
Terrestrial invertebrate[b]			10
Vegetation			48
Human refuse			4
Limpet[b] (Patellogastropoda)			13
Crab[b] (Decapoda)			5

[a] Garfish *Belone belone*; Horse Mackerel *Trachurus trachurus*; and unidentified fish species
[b] species not identified.

Table 5. Total number of recorded provisioning rates of Atlantic Puffins *Fratercula arctica* on Burhou each season, the percentage frequency with which provisioning flights were attacked by gulls and the percentage of flights where the attack was successful derived from minimal adequate models. LCI and UCI are upper and lower 95% confidence intervals respectively.

Year	**2005**	**2006**	**2007**
Hours of observation	103.5	76.5	33.5
Provisioning flights recorded	498	737	256
Provisioning rate (deliveries/day)	4.13 (CI = 3.38–5.05)	5.41 (CI = 4.18–7.01)	3.31 (CI = 2.35–4.67)
Percentage flights attacked	7.24 (CI = 5.81–9.00)	4.48 (CI = 3.23–6.18)	5.47 (CI = 3.58–8.27)
Percentage flights robbed	0.40 (CI = 0.19–0.86)	0.14 (CI = 0.04–0.50)	0.39 (CI = 0.10–1.44)

sea. Most attacks occurred as Puffins were about to land, or at the burrow entrance. Puffins deterred by gulls on their first provisioning attempt were observed to wheel around the colony several times or sit on the sea for a short period, before re-attempting provisioning.

Provisioning rates varied significantly from year to year ($F_{3,163} = 316.9$, $P < 0.001$, scale parameter = 5.12). There were also significant differences from year to year between the likelihood of a provisioning flight being attacked ($F_{3,143} = 255.1$, $P < 0.001$, scale parameter = 1.87) and the success of these attacks ($F_{3,143} = 581.3$, $P < 0.001$, scale parameter = 1.15).

Discussion

During 2005–07 an average of 120 pairs of Puffins attempted to breed on Burhou, and the only other estimate based on AOB counts, of 50–100 pairs in 1980 (Danchin & Cordonnier 1980), suggests the population had not declined since then. We conclude that the higher counts of rafting birds for the Seabird Colony Register (210 on 12 June 1987) and Seabird 2000 (180 in July 1999) censuses are also consistent with approximately 100–120 breeding pairs, since rafting individuals should not be assumed to be equivalent to one breeding pair, and the error of estimating breeding numbers from raft counts increases approximately linearly the later in the season counts are carried out.

Since the greatest decline in Puffin numbers occurred before the large increase in Herring and Lesser Black-backed Gull numbers, we suggest that this increase was not the primary cause of the Puffin decline. However, the increased gull population may be limiting recovery via predation, or interference with chick provisioning and hence growth or recruitment.

Our data indicated that of the three gull species breeding on Burhou, only Great Black-backed Gulls preyed directly on adult Puffins and that some individuals specialised in doing so. With approximately 120 breeding Puffin pairs, predation by Great Black-backed Gulls accounted for at least 2% of annual mortality in 2005 and 2006; however as part of the island management plan two Great Black-backed Gulls identified as preying on Puffins in 2005 and 2006 were culled early in the 2007 season and annual mortality of Puffins due to predation was reduced that year to a minimum of 0.8% of the population. These are all minimum estimates as it is likely that gulls may have consumed prey away from their territories. Estimates of the overall mortality rate of adult Puffins made over several years on the Isle of May (Harris 1984) and Skomer (Ashcroft 1979) were 4–5% per annum. In a more recent study conducted in five colonies over a 13-year period, Harris *et al.* (2005) concluded that annual adult Puffin mortality was between 7.5% and 8.5% and that most mortality occurred outside the breeding season. If this is so, predation by Great Black-backed Gulls may add significantly to mortality rates of adult Puffins on Burhou. Since the population of Great Black-backed Gulls on Burhou appears to have remained stable since 1969 when the Puffin population was estimated at over 1,000 pairs (raft counts), it seems possible that the number of Puffins killed annually by gulls has remained constant over the intervening period. Whereas this level of predation would be responsible for a 0.2% addition to mortality of Burhou Puffins in 1969 when the population was possibly 1,000 pairs, its addition to Puffin mortality was 2% by 1980 after the Puffin population declined. It seems possible that this additional mortality has been a major factor in the failure of the breeding population of Burhou Puffins to increase between 1980 and 2005.

Both the incidence (5.6%) and success rate (0.3%) of kleptoparasitic attacks by gulls on Burhou can be considered low compared to the proportions of fish loads stolen at seven colonies between 1968–1982, which (apart from zero at St Kilda in 1974–77) ranged from 0.3% on Skomer in 1969 to 18.7% on the Isle of May in 1975, when the

Isle of May colony was increasing rapidly (Harris 1984). Breeding success of Burhou Puffins in 2005–07 averaged 0.66 chicks/burrow, higher than mean values in 2005–06 on Fair Isle (0.57/egg), though lower than values for Skomer (0.79/burrow), the Farne Islands (0.87/egg) and Isle of May (0.74/egg) (Mavor *et al*. 2008).

The large number of Lesser Black-backed Gulls nesting on Burhou in 2005–07 and the encroachment of their territories towards the main Puffin colony raises the possibility of this suppressing recruitment. Puffin recruitment on the Isle of May increased by 25% in areas where gulls had been cleared from within 50 m of the Puffin colony (Finney *et al*. 2003). Although the large increase in numbers of Lesser Black-backed and Herring Gulls on Burhou has occurred since 1980, and Puffin numbers have not declined since then, if the gull populations were to expand any further their presence could adversely affect the recruitment of Puffins to the island.

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Appendix 1.

Model for investigating changes in the population of breeding Puffins.

A simple Leslie matrix was used initially to describe an age-structured model of the Puffin population. It was assumed that all recruits to the colony (first year breeders) were derived from a surviving fraction of the chicks of the colony that had fledged five years earlier. The breeding pairs were assumed to lay one egg each. Breeding success was taken to be 60% for each breeding pair in all age groups and the surviving offspring were assumed to be made up of equal numbers of males and females. Only surviving females were counted with the assumption that one female was equivalent to one breeding pair. Annual mortality of breeding adult Puffins on Burhou in 2005 was taken to be 8.0% (Harris *et al*. 2005), and was assumed to include predation by the Great Black-backed Gulls. When gull predation was eliminated, mortality was reduced to 6%.

If $n_a(t)$ is the number of Puffins of the age a at time t, $n_a(t)$ is related to the number of the previous year's Puffins who were a year younger (of age a-1) through the relation:

$$n_a(t) = (1 - \mu)\, n_{a-1}(t-1), \quad (1A),$$

where μ is the age-independent mortality. The total number of Puffins in the breeding population, N, can be related to the number of recruits joining the colony (n_0) and the sum of the numbers of Puffins in each of the older age groups, i.e.

$$N = n_0 + \sum_{0}^{\tau} n_a\,(1-\mu) \qquad (2A),$$

where τ is the age of the oldest pair of breeding birds.

It was assumed that between 1980 and 2005 the number of breeding Puffins on Burhou had remained approximately constant at just over 100 pairs and that in 2005 the age structure of the population was stable. If it is also assumed that the mean annual survival of the immature Puffins over the five years between fledging and breeding was constant, that adult mortality was constant and that breeding success was the same for breeding pairs of all ages, the Leslie matrix describing the age structure of the population can be reduced to a simple 2 x 2 matrix by applying the Lefkovitch rule (Case 2000). From this it can be shown that if the population numbers remain unchanged, an adult mortality of 0.08 infers that the product of the survival of the immature Puffins over the five years between fledging and maturity and the reproductive success of each breeding pair is also 0.08 (Case 2000). If reproductive success lies between 0.6 and 0.7, and half of the offspring are females, the mean survival of Puffins from fledging to breeding is between 0.24 and 0.28, values slighter lower than those estimated for the fraction of fledged young Puffins surviving to breeding age on the Isle of May and Skomer (Harris 1984).

Eliminating predatory Great Black-backed Gulls was assumed to reduce adult mortality to 0.06 but leave breeding success and average mortality of immature Puffins unchanged. The dominant eigenvalue of the Lefkovitch matrix, λ, is now

1.02. The numbers of breeding pairs of Puffins in the population, N(*T*), following the reduction in mortality when numbers were N(0) can now be calculated for subsequent years (*T*) from the simple expression:

$N(T) = N(0)\lambda^{T}$ 3A (Case 2000).

The Lefkovitch rule assumes the age structure of the population remains constant. Over the first ten years that follow the fall in mortality from 0.08 to 0.06, changes are expected in the fraction of the total population that each group represents until the new age structure of the increasing population has been established. The magnitude of these small deviations was calculated by setting out the full Leslie matrix as an Excel spread sheet using an initial set of values that could be shown to be compatible with a stable population of 120 breeding pairs and μ = 0.08. A comparison of the results of these calculations with the values predicted by equation 3A indicated the deviations are negligible and the results indistinguishable from those shown in Figure 3.

It should be noted that the model assumes (i) that an increase in population numbers is independent of the size of the population; and (ii) that predation of Puffins has no effect on Puffin numbers other than an increase in the age-independent mortality. Assumption (i) is reasonable if the carrying capacity of the current population is the same as suggested by estimates of its size in the 1950s (10,000–50,000 pairs). If, however, the carrying capacity of the present population is considerably reduced, the rate of increase in Puffin numbers following a 2% reduction in the age dependent mortality would be roughly half that predicted in Figure 3.

Assumption (ii) may underestimate the effects of predation since the victims are breeding birds killed during the breeding season, and their deaths could account for a 5–6% reduction in the survival of the Puffin chicks prior to fledging. Thus removal of predation might increase the numbers of fledging chicks as well as reducing the adult mortality rate.

While relatively small adjustments to the model can accommodate these additional considerations, its usefulness is questionable as neither the carrying capacity of the current population nor the numbers of young Puffins surviving to breeding age are known. We have therefore limited ourselves to this very simple model until more information becomes available.