A STUDY OF THE FACTORS INFLUENCING BREEDING SITE SELECTION AND ATTENDANCE OF ATLANTIC PUFFINS *FRATERCULA ARCTICA* ON LUNDY

by

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ABSTRACT

A remnant population of Atlantic Puffins *Fratercula arctica* occupies Lundy. This study set out to describe the decline in Puffin numbers on Lundy and conduct an initial investigation into the factors mediating colony attendance and breeding site selection. Counts took place at St. Philip's Stone over 19 days from 2 July to 4 August 2008. Wind speed (knots), rainfall (mm), air temperature (ºC), mean numbers of Herring Gulls and time of day were analysed as predictors of the mean number of Puffins in a stepwise regression. Attendance was significantly higher in the evening than at midday, but numbers were not significantly higher in the morning compared to numbers at midday. A novel finding showed that attendance decreased as temperature increased. Effects of wind speed and rainfall approached significance, and gull numbers had no effect on attendance, but observations suggest that Puffins benefited from their presence. In a within-site analysis of St. Philip's Stone, non-parametric tests indicated pairs which bred successfully were located close to a cliff edge and in areas occupied by other auks. In a between-site analysis of the site register data, presence of Puffins was more likely when Guillemots and Razorbills occupied the area. Puffins were mainly present on the west side of the island. This study signifies that ecological variables influence Puffin breeding site selection and attendance, but future work is needed for increased reliability.

Key Words: *Atlantic Puffins, Lundy, population evolution, colony attendance, breeding site selection, conservation.*

INTRODUCTION

Lundy harbours a population of Atlantic Puffins *Fratercula arctica* which has suffered a dramatic decline in numbers since the mid-twentieth century (Davis & Jones, 2007). One important factor in this decline has been predation by rats, which were eradicated between 2002 and 2004 in order to facilitate the reproduction of Manx Shearwaters (*Puffinus puffinus*) and other seabirds (Appleton *et al.*, 2004; Appleton *et al.*, 2006).

However, other factors (e.g. climate change, industrial fisheries) are at the origin of the decline of Atlantic Puffins in the UK (Cocherel & Mahusier, 2008). Whereas thousands of Puffins once bred on Lundy's cliffs, only six breeding pairs are estimated to be present today. Although annual surveys have become more intensive to monitor the impact of the rat eradication, extensive investigations into factors that affect Puffin behaviour are lacking on Lundy. Thus, this study aims to contribute to the current annual survey[1] with a more detailed analysis of this remnant population.

Objectives of the study and background information

One of the objectives of this study was to examine the patterns and mediating factors of colony attendance. Research on other islands has demonstrated cyclical patterns of colony attendance, defined here as the visible presence of individuals at the colony. Numbers peak in the evening, are lowest at midday with a smaller peak in the morning (e.g. Harris, 1984; Calvert and Robertson, 2002). There is a gradual increase in numbers over the breeding season as more non-breeding birds frequent the colony, with a dramatic decline over 2-3 days as birds synchronously migrate at the end of the season (Ashcroft, 1979). The function of these patterns remains largely unknown, and they may just be an outcome of ecological influences. For example, light intensity and food availability fluctuate during the day, so that Puffins may tend to stay at the colony when foraging efficiency is compromised (Harris, 1984). Attendance may also be positively related to gull numbers to reduce the risk of kleptoparasitism (Merkel *et al.*, 1998). On the other hand, it has been found that harsh weather conditions, such as high wind speeds and heavy cloud cover, reduce attendance in other auks (e.g. the common Guillemot *Uria aalge,* Finney *et al.*, 1999). Conversely, in extreme weather conditions, birds could also stay at the colony because the energy expending whilst foraging is too vital for survival. However, there is little direct evidence implicating the role of these factors in patterns of Puffin attendance. In a large colony of Puffins breeding in Newfoundland, wind speed and temperature had respectively little or no effect on colony attendance (Calvert and Robertson, 2002), but we believed that in a multispecies colony like the one observed, weather variables could have a more significant effect.

The study also set out to examine which factors affect the breeding site selection of the Lundy Puffin population. Research on other islands has shown that it is influenced by certain ecological features. Burrow density has been shown to be negatively correlated with distance from the cliff edge (Grant and Nettleship, 1971; Rodway *et al.*, 1998). Additionally, breeding sites were more likely to be selected when conspecifics were resident, and had been resident in previous years (Ashcroft, 1979; Calvert & Robertson, 2002). Puffins have a tendency to seek the presence of their conspecifics. They usually breed in large colonies and can often be seen together floating in rafts on the sea and also with numerous other auk species (Harris, 1984). According to the 'many-eyes' hypothesis, this makes them less vulnerable to predators (Lima, 1995). They are also likely to return to the colony in groups, which is an effective anti-predator strategy (Merkel *et al.*, 1998).

[1] The Lundy wardens, N. Saunders and S. Wheatley, conduct annual surveys of the Puffin population on Lundy, in which they estimate the maximum number of individuals observed, the number of breeding individuals, and productivity (Saunders & Wheatley, 2008).

These aspects of Puffin behaviour remain largely unstudied on Lundy and the factors that affect their attendance seem little understood. Thus, our aim was to increase understanding to benefit the conservation of this locally rare population, by conducting the first investigation into breeding site selection and colony attendance in Lundy Puffins.

Hypotheses and predictions

Our first hypothesis is that colony attendance will vary according to breeding stage, time of day, weather conditions and gull numbers (*Hypothesis One*). Specifically, *Prediction One* is that Puffin numbers will gradually increase over the observation period to a peak, and then decline abruptly over 2-3 days as the breeding season ends. We also predict that highest numbers will be found in the evening and lowest numbers at midday, with a smaller peak in the morning (*Prediction Two*). Moreover, we expect that lower numbers will be found when weather conditions are unfavourable for foraging, such as high wind speeds, as the birds will spend more time finding food (*Prediction Three*). The effect of gull numbers on colony attendance will also be tested. However, as there is a lack of evidence about their effect on Puffin attendance, this prediction remains unidirectional (*Prediction Four*).

Our second hypothesis is that ecological variables will influence whether Puffins are observed and breeding in an area (*Hypothesis Two*). Specifically, within the same colony, we expect that successful breeding Puffin pairs will have a burrow located nearer to the cliff edge and closer to other auk species in comparison to unoccupied burrows or unsuccessful breeding pairs (*Prediction One*). We also expect that between different sites, more Puffins will be present when other auks are counted on the same area (*Prediction Two*). This is because Puffins might benefit from the high level of vigilance granted by the large numbers of alcids, providing warnings about possible dangers and protecting the Puffins against predation by Greater Black-backed Gulls *Larus marinus.* Finally, we predict that active sites will be on the west side of the island (*Prediction Three*) because this side has steeper slopes and as a result, may support higher numbers of other auk species and provide preferable breeding sites. Moreover, the west side might be closer to richer foraging areas in the Atlantic Ocean.

METHODS

The study was conducted on Lundy from 2 July to 4 August 2008 during the chick provisioning and fledging breeding cycle stages, after obtaining permission from the warden (N. Saunders). Authors' observations of provisioning behaviour to separate burrows indicated that there were two breeding pairs at Jenny's Cove and four at St. Philip's Stone. The colony at St. Philip's Stone was used as the study plot because observations could be made at a closer distance to the colony, thus enabling more accurate observations using field binoculars. The observation point was a flat projection of headland approximately 90m away from the breeding site, as measured by a rangefinder (Yardage Pro®, Bushnell®). As fly offs were never observed following our arrival at the observation point, we believe that our presence did not have any impact on the behaviour of the birds.

The population decline and the rat eradication

A review of the annual Puffin censuses on Lundy from 1939 to 2008 was conducted (Annual Report of the Lundy Field Society, 1947-2008; Perry, 1940). The maximum number of Puffins and number of breeding pairs observed per year was recorded.

Patterns and influencing factors of colony attendance

During the study period, 19 days were used for data collection. A maximum of two three-hour observation sessions took place on each day, with each observer conducting one session. Observation sessions were carried out at three different time periods: Morning (06:00-09:00), Midday (12:00-15:00) and Evening (18:00-21:00). During each session, counts of the total number of Puffins visible on the study plot were made every five minutes using field binoculars and a timer. Simultaneously, counts of the total number of gulls around the Puffins' breeding burrows (defined as the number of Herring *L. argentatus* and Lesser Black- backed Gulls *L. fuscus* visible with the binoculars centred on the burrows) were also made every five minutes. Birds were counted if any of their body parts were visible at the exact beginning of the count, but not if they flew in while the other birds were counted. Opportunistic events (e.g. panic flights, inter- and intra-specific interactions) were also recorded.

Two tests of inter-observer reliability were carried out: one prior to commencing the research (1 July 2008) and one during the study period (16 July 2008). Each test consisted of a three-hour observation session in which both observers (CBC & KM) carried out the planned data collection separately and simultaneously. These data were then compared to calculate inter-observer reliability. The two inter-observer reliability tests showed that our observations were consistently highly compatible at 92% and 95% reliability, which enabled us to carry out observation sessions separately.

A total of 87 hours of observation were carried out (29 Sessions: 10 x Morning, 10 x Midday and 9 x Evening). Hourly records of air temperature (°C), wind speed (Kts) and rainfall (mm) were made using the island's weather station and accompanying software (WeatherLink 5.7™). Session number and date were also recorded to reflect breeding cycle stage.

For the first hypothesis, predictions Two, Three and Four were analyzed using a hierarchical, stepwise linear regression with mean number of Puffins per count as the dependent variable and three blocks of regressors (Table 1). For the purpose of the analysis, the nominal regressor 'time of day' was transformed into a dummy variable. Mean number of Lesser Black-backed Gulls per count was also excluded from the analysis due to lack of data; very few were seen after the first week of the study period.

Table 1: Blocks of regressors in the hierarchical stepwise linear regression used to test Predictions Two, Three and Four of Hypothesis One

	Block		
	1 (Time of day)	**2 (Gull number)**	**3 (Weather conditions)**
Regressors	Morning Midday Evening	Mean Number of herring gulls per count	Wind speed (Kts) Air temperature (°C) Rainfall (mm)

Factors affecting Puffin's presence and burrow location

In order to compare the factors affecting selection of a burrow within a colony, we analyzed the position of the Puffin burrows at St Philip's stone. A picture of the study zone was divided into equal squares, similarly to the division used in the yearly survey. The relative distance from the cliff edge, the number of Guillemots and Razorbills observed and the presence or absence of a successful breeding pair of Puffins in each area was recorded. An estimation of the number of auks in each square was provided by one author (GS) and two other observers (S. Wheatley & N. Saunders, pers. comm.) and a mean of these numbers was computed.

In order to compare the factors determining the presence or absence of Puffins on a slope, data were extracted from the Island's site register (Price, 2004) and analyzed. For each division of the island, we compiled the number of Guillemots and Razorbills counted in 2004, the orientation of the division and if the presence of one or more Puffins was detected there in the past 23 years (1981-2004). As the variation in the number of Guillemots and Razorbills was minor during the last 24 years (Price, 2004), the number of auks counted in 2004 could be used to compare the general presence of Puffins for this whole period.

Due to the small sample size, a non-parametric Mann Whitney *U* test was used to test Prediction One. The presence or absence of a successful breeding pair of Puffins (i.e. observed provisioning of a chick) was the dependent variable, and the independent variables were the number of Guillemots and Razorbills and the distance from the cliff edge of the zone in the same square.

A Mann-Whitney *U* test was also used to analyze Predictions Two and Three, because one of the test variables was unordered and the other two were not normally distributed. The presence or absence of Puffins on a slope during the past 27 years was treated as the dependent variable. The test variables were the number of Guillemots and Razorbills present in the same area in 2004 and the orientation of the area (North, South, East or West).

RESULTS

As Figure 1 shows, there has been a consistent decline in the maximum number of Puffins observed each year from 1939 to 2008, although there appeared to be some recovery in the periods 1971-1973 and 1980-1982. The number has declined from at least 7000 birds in 1939 (3500 pairs counted by Perry in 1939) to 16 in 2008. The number was lowest in 2004, with a maximum of 5 Puffins observed.

The number of breeding pairs has increased from zero to six in the last six years. The lowest number ever recorded since 1939 occurred in the period 2002-2004, in which no breeding pairs were observed during three consecutive years. Most of the increase happened during the period 2006-2008 with numbers rising from 1 to 6 breeding pairs (Figure 2).

Hypothesis One

As Figure 3 illustrates, the mean number of Puffins counted every five minutes increased and decreased in an apparently random fashion during most of the study period, with the highest mean number occurring on 7 July 2008 (session 7; M=6.4) and the lowest

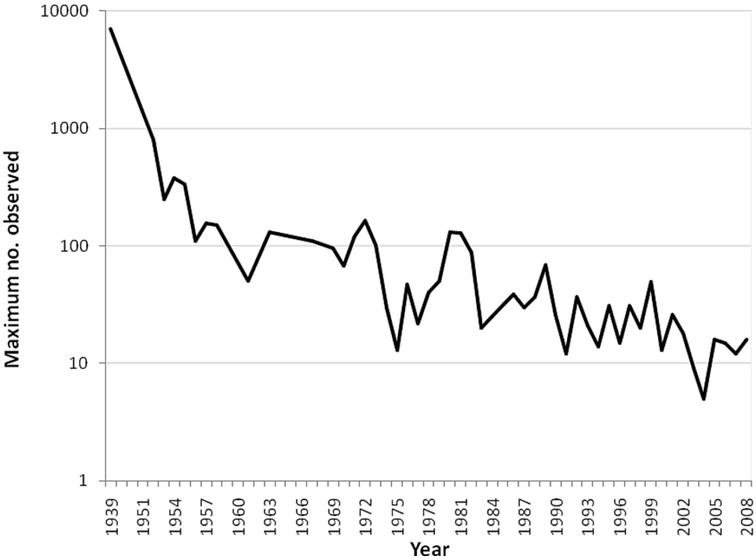

Figure 1: Trend in the known maximum number of puffins observed from 1939 to 2008 (Logarithmic scale)

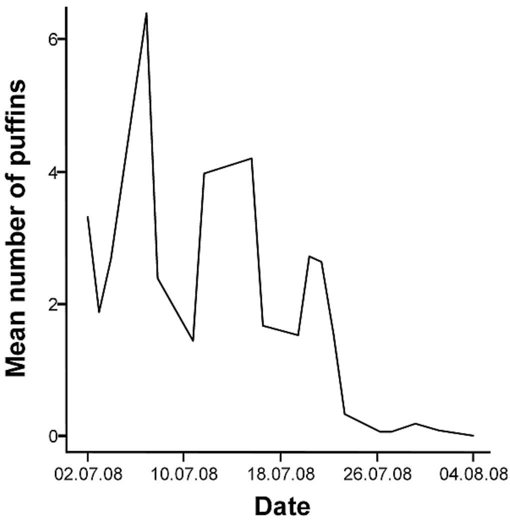

Figure 2: Trend in the number of breeding pairs observed from the rat eradication in 2002 to 2008

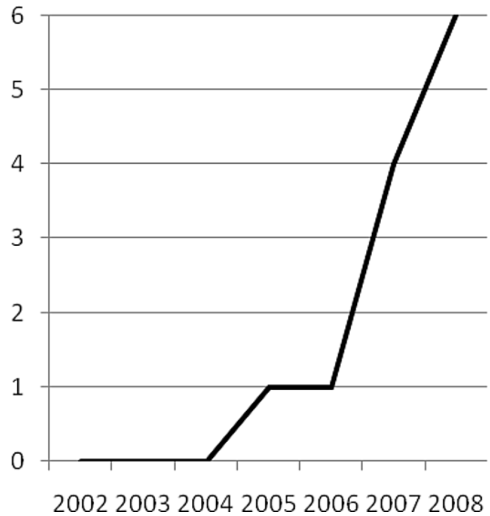

Figure 3: Mean number of puffins observed per 5-minute count over the study period 2 July-4 August 2008

Table 2: Results of the stepwise linear regression showing the coefficient, the sample size, the t-statistic and its level of significance (p-value) for each regressor

Test variable	B	t	N	Significance (p)
Morning	0.037	0.261	65	0.795
Evening	1.495	3.389	65	0.001*
Temperature	-0.393	-2.643	65	0.010**
Wind Speed	-0.188	-1.827	65	0.072
Mean Number of H. Gulls	-0.121	-1.037	65	0.304
Rainfall	0.204	1.929	65	0.058

Key. * significant at the 5% level ** significant at the 1% level.

occurring on 4 August 2008 (session 29; M=0). Towards the end of the study period, Puffin numbers declined to a very low mean on 24 July (session 24; M=0.08) which was unusually low compared to the data collected throughout sessions 1-23. Numbers continued to decline in the period 24-27 July. No Puffins were observed in the final session of the study period.

As the mean number of Puffins per count decreased to an unusually low number after session 23 (24 July; see Figure 3), any data collected after session 23 was excluded from the analysis.

The regression model significantly described 29.1% (R^2_{adj} = 26.9%) of the variance in the data, $F_{2,65}$ = 13.341, p<0.001. As the data was drawn from field work, we consider this model to be a good fit. Table 2 shows the results of the analysis for each regressor.

As Figure 4 shows, the mean number of Puffins per count was highest in the evening, lowest at midday with a smaller peak in the morning. The analysis showed that the number of Puffins counted in the evening was significantly higher than during the rest of the day (Table 2), increasing by a mean of 1.5 Puffins per count. No statistical significance was found for the observed morning peak. The mean number of Puffins was negatively related to wind speed, as fewer Puffins were seen when higher wind speed were recorded (Figure 5). However, this difference was not statistically significant (Table 2). Figure 5 also shows a weak inverted U-shaped curve. The mean number of Puffins per count was shown to be significantly negatively related to air temperature (Table 2), decreasing by a mean of 0.4 Puffins with every increase in degrees Celsius (Figure 6). A positive relationship was found between the mean number of Puffins and rainfall, which was approaching significance. The negative relationship with the number of Herring Gulls did not reach significance (Table 2). Additionally, a Spearman's correlation analysis showed that there was a significant negative correlation between the two significant regressors (ρ_{69}=-0.331; p=0.005).

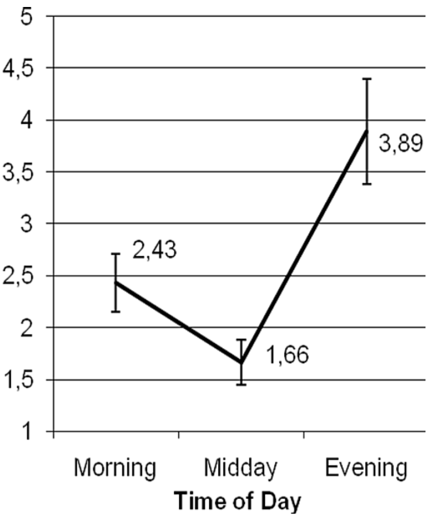

Figure 4: Mean number of puffins per five-minute count as a function of the time of day (error bars represent mean standard error)

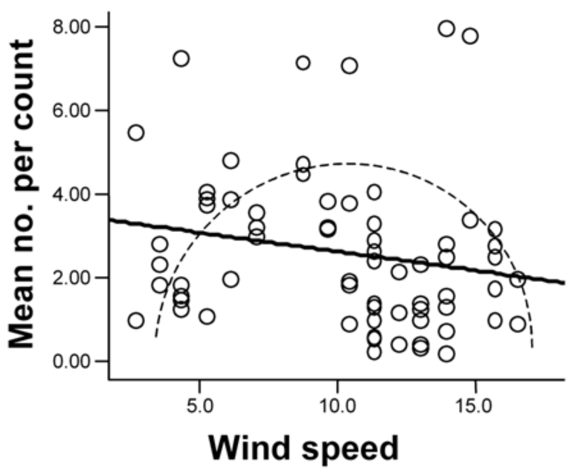

Figure 5: Mean number of puffins per five-minute count as a function of wind speed (Kts)

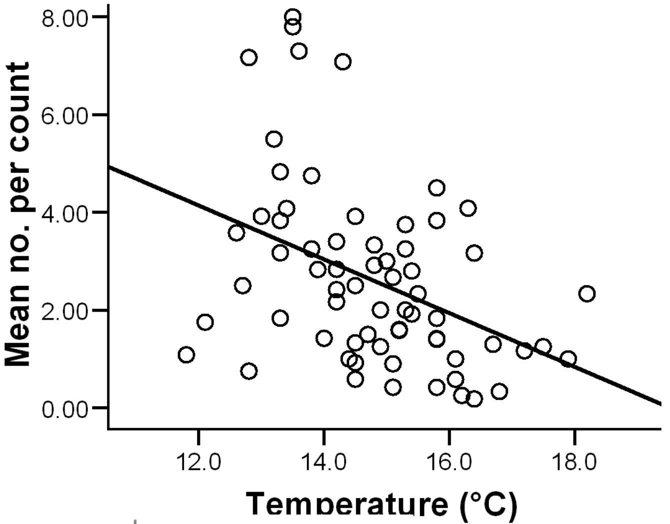

Figure 6: Mean number of puffins per five-minute count as a function of temperature (°C)

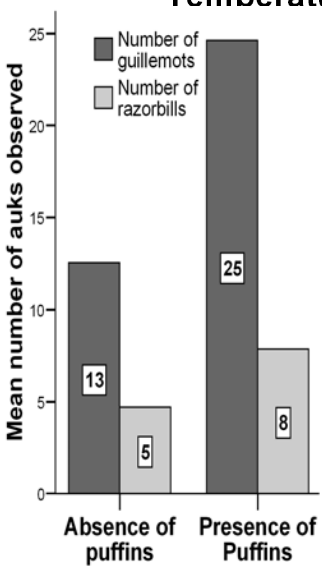

Figure 7: Number of auks in island areas as a function of the presence or absence of puffins

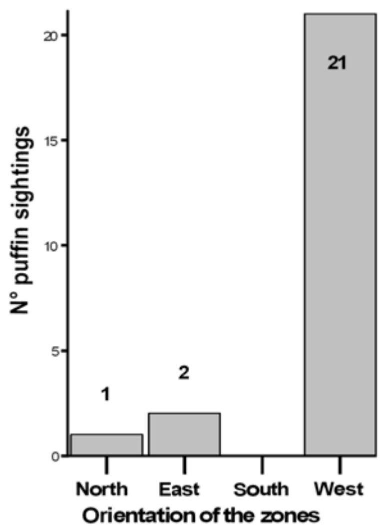

Figure 8: Number of puffin sightings at each orientation (north, south, east and west) on Lundy

Hypothesis Two

A Mann-Whitney *U* analysis showed that the presence or absence of a breeding pair of Puffins in a particular zone of St. Philip's Stone was significantly related to the number of Guillemots present in the same zone, U=2.0, p<0.01 and the zone's relative distance from the cliff edge, U=3.0, p=0.22, but not to the number of Razorbills in the same zone. Moreover, a Spearman's test did not reveal any correlation between the two significant variables (ρ(15)=-0.34;p=n.s).

The presence or absence of Puffins at island areas was positively related to the number of Guillemots and Razorbills at the same area (Figure 7) and the orientation of the area was shown to affect the presence or absence of Puffins, with sightings highest on the west (Figure 8). A Mann-Whitney *U* analysis showed that these relationships were significant (Table 3).

Table 3: Results of the Mann-Whitney U test for Hypothesis Two, Prediction Two

	Number of Razorbills	**Number of Guillemots**	**Orientation**
Mann Whitney U	1119	1311	1314
Significance (2-tailed)	0.009**	0.030*	0.035*
N	N_0 = 138; N_1= 24	N_0 = 140; N_1= 24	N_0 = 141; N_1= 24

Key: * significant at the 5% level ** significant at the 1% level. N_0: Number of areas where no puffins were sighted; N_1: Number of areas where puffins were sighted.

DISCUSSION

This is the first study to investigate the factors affecting colony attendance and breeding site selection of Puffins on Lundy, and describe the decline in the population size since 1939 to the present.

Population decline and the rat eradication

After the rat eradication which was completed in 2004, the breeding population appears to be recovering. The relatively quick recovery from one to six breeding pairs in the last 2 years is a trend that indicates a continued increase in future breeding seasons. However, as the quality and quantity of observations carried out during the previous years are unknown, we cannot guarantee the accuracy of the collected data and can only give a global interpretation of the fluctuations in population size. More successful pairs might have been observed this year because of the more intensive observations that have been carried out.

Although rats were identified as the main factor affecting burrow-nesting seabirds on Lundy (Appleton *et al.*, 2004), they are certainly not the only reason why Puffins are presently rare on Lundy. Global warming and fisheries are affecting Puffins' survival (Frederiksen *et al.,* 2004; Harris *et al.,* 1997) as well as pollution (oil spills), fishing nets, predators and species competing for burrow sites (e.g.: Manx Shearwater) (Cocherel and Mahusier, 2008). Although further studies would be needed to investigate the real effect of these factors on the Lundy Puffin population, all of them are susceptible to affect it, as they are occurring worldwide.

Thus, the temporary extinction of Lundy Puffins was probably caused by a combination of several factors rather than the sole effect of rat invasion. Now that the rats have been ostensibly eradicated from the island, the Puffin population will probably increase in the next decades but it is doubtful that Lundy will ever again harbour thousands of breeding pairs, as it did in 1939.

Patterns and influencing factors of colony attendance

The findings indicate that attendance does not increase gradually over the breeding season, but rather increases and decreases randomly, which does not support Prediction One. This may be because of the small number of breeding pairs observed during the study, which might not be adequate to determine a general pattern. Indeed, the trend was previously observed in a larger population on Skömer Island, Wales (Ashcroft, 1979). Also, it is possible that there was an insufficient amount of non-breeding Puffins visiting the site. This is certainly probable considering that populations have been relatively small on Lundy for decades (Davis & Jones, 2007); low productivity may have resulted in low numbers returning to the natal colony.

Conversely, in support of Prediction One, numbers decreased to an unusually low mean within 2-3 days towards the end of the breeding season (24-27 July). Such an abrupt decrease in numbers at the end of the breeding season may reflect their migration to wintering areas, as observed by Ashcroft (1979). Indeed, the only remaining Puffins at the site after 24 July were observed provisioning chicks, suggesting that these individuals delayed migration until their chicks had fledged (authors' pers. obs; Harris, 1984).

The demonstration that mean number of Puffins per count was significantly related to time of day, in which numbers were highest in the evening, lowest at midday with a smaller peak in the morning, supports Prediction Two and replicates previous findings (e.g. Harris, 1984; Calvert and Robertson, 2002). Considering that time of day was a reliable factor, it could explain the random variation in attendance observed throughout the breeding season, as counts were not made at the same time everyday. Moreover, the observed daily cycle may be a consequence of ecological influences affecting Puffin foraging efficiency. Indeed, the smaller peak in numbers in the morning may reflect the fact that during the chick rearing period, Puffins spend the night at sea and return to the colony after using the first hours after dawn to forage for themselves (Cocherel and Mahusier, 2008). Additionally, the presence of fish within Puffins' diving range (60m; Cocherel and Mahusier, 2008) might change according to daily fluctuations in light intensity (Harris, 1984). Yet, fish tend to rise to the sea surface in the evening (Durant *et al.*, 2003)which could indicate that a decreased light intensity in the evening impairs foraging rather than a lack of available prey.

The present study was the first known demonstration that temperature affects Puffin attendance. Fewer Puffins were seen on the slope of their breeding site in warmer temperatures. As Puffins are used to cold temperatures, they might not be able to regulate their body temperature in hot weather conditions and thus prefer to raft in the sea.

Fewer Puffins were observed on the slope of their breeding site when a higher wind speed was recorded and replicates findings from a study on another auk species (i.e. the common Guillemot; Finney *et al.*, 1999), but this difference was not significant. Like Guillemots, Puffins might spend more time foraging and returning to their colony in stormy conditions. In addition, the weak inverted U-shape curve observed on Figure 5 suggested that colony attendance was also lower when wind speed was reduced, which would be consistent, as a lack of wind appears to make flight more difficult for Puffins (Calvert and Robertson, 2002). Puffins have very short wings, making their efficiency in powered flight limited, especially over long distances (Wanless *et al.*, 1990). Thus, it is plausible that moderate wind speeds, which assist with aerodynamics but do not impair flight efficiency, are preferable for foraging. Additionally, on Lundy, the presence of Puffins in an area is dependent on the number of alcids present in the same zone (see later). Consequently, the factors affecting Guillemot's colony attendance (e.g.: wind speed) might have an indirect impact on the Puffin's colony attendance. However, although we found evidence that high wind speeds result in low attendance, the effect of low wind speeds is only illustrated by a very weak inverted U-shaped curve. Thus, further work is required to produce more reliable evidence about the effect of low wind speeds on attendance.

More Puffins were seen on the slope when rainfall was higher, but this relationship did not reach significance. Heavy rain reduces visibility and might make flight and foraging more difficult, causing the foraging activity to be too costly. However, there was not enough variation in the rainfall during the observation sessions (between 0 and 2.2 mm of rain per hour) to enable a good interpretation of the results for this parameter.

Finally, Herring Gull numbers at the colony did not affect mean number of Puffins per count, and thus Prediction Four was not supported. This may be because of the relatively small number of gulls at the colony, compared with the much larger numbers in the study which showed that higher numbers of gulls reduce Puffin recruitment (Finney *et al.*, 2003). However, the presence of Herring and Lesser Black-backed Gulls could also benefit the Puffins, as these species mob one of their common predators, the Great Black backed Gull. A study carried out on Lundy about Guillemots demonstrated that only a few 'specialist' gulls were predating on Guillemots' chicks and eggs (Taylor, 1978, reported by Davis and Jones, 2007). Moreover, the author noticed that Guillemots breeding next to gulls benefited because the latter were defending the area around their nest, thus chasing other potential avian predators (Gulls, Crows). Additionally, the location of the breeding burrows near the cliff edge (see later) might have made the influence of the gulls' presence negligible, as food-carrying adults could fly directly into their burrows without the risk of kleptoparasitism.

Factors affecting Puffin's presence and burrow location

Within the same colony, we found a significant relationship between the locations of the Puffins' burrows where a chick was raised successfully and the distance from the cliff edge. In fact, all the successful Puffin breeding pairs occupied a burrow located close to the cliff edge. This finding concurs with previous studies on larger colonies which also demonstrated a strong negative correlation between burrow density and distance from the shore edge (Rodway *et al.*, 1998; Grant, 1971). Proximity to the cliff edge may allow Puffins to escape to the safety of the sea more rapidly and with greater ease when threatened. Moreover, as previously stated, a burrow close to the cliff edge may allow provisioning adults to return directly to the safety of the burrow, thus reducing the risk of kleptoparasitism (Grant and Nettleship, 1971). A significant relation was also found between the presence of successful breeding Puffins and the number of Guillemots counted in the same zone. Puffins usually breed in large colonies but are only found in small numbers on Lundy. Those could thus benefit from the presence of other auks species much more than Puffins breeding in large colonies. Guillemots and Razorbills are found in large numbers on Lundy and are thus more able to detect the arrival of a predator and warn the whole colony. However, no significant relationship was found with the number of Razorbills present in the same area. This could be because the benefits of breeding close to them is reduced as they are potential competitors for burrows (Harris, 1984), but we believe that this result is only due to the small sample size.

As only four breeding pairs of Puffins could be observed this year, further research determining the factors affecting the location of a burrow within a multispecies colony is needed to draw any definitive conclusions. It is also possible that the exact location of gulls' nests might also have had an influence on Puffins' burrow location and breeding success, but due to lack of data this variable could not be included in the analysis.

In the period 1981-2004, Puffins were sighted more often on the sites where other auk species were also sighted. Puffins usually forage in flocks (Harris, 1984) and studies of large colonies demonstrated that they tend to return in groups to their breeding site after a foraging bout (Merkel *et al.*, 1998). However, as Puffins are found in small numbers on Lundy, their foraging efficiency might be improved by breeding close to other auk species which have similar foraging behaviours. Moreover, foraging and arriving in groups on a slope is an effective anti-predator and anti-kleptoparasitism strategy, as it creates a confusion effect that makes it difficult for predators to target an individual (Grant, 1971).

Additionally, Puffin sightings were found to be significantly more numerous on the west side of the island. This finding might just be due to the strong correlation between number of auks and the orientation of the island area. However, Rodway *et al.* (1998) suggested that 'facing prevailing winds may be attractive to Puffins as flight conditions improve with onshore winds and deteriorate with offshore winds' (pp.178). According to this theory, the west cliffs might be preferred to other sides of the island because Lundy's prevailing wind comes from the west. Moreover, a study made on four burrow-nesting alcids demonstrated that preferred breeding sites were associated with cold and saline waters (Kaiser and Forbes, 1992), because fish are more abundant in this kind of water (Thomson, 1981). The east side of the island faces the Bristol Channel whereas the west side faces the Atlantic Ocean. The water might therefore be slightly colder and more saline in this zone, making it richer in fish. Yet, these factors may have had an influence on the breeding site selection of other auk species. Thus, distinguishing between the effects of other auks' presence and breeding site orientation may be impossible. Moreover, the higher number of sightings on the west may be a biased result because there are more vantage points on the west side, making sightings more likely here than elsewhere on the island.

Although Puffins seem to be more numerous on the west where other auks are also present, the factors that have influenced their selection of St Philip's Stone as the main breeding site remain unclear. A speculation is that the density of auks was lower there than on other breeding sites also located on the west coast. Indeed, although Puffins can benefit from the presence of other auks species, it has been demonstrated that their reproductive performance is negatively correlated with population size (Nettleship, 1972), which may also be an outcome of increased competition for burrows (Hunt *et al.*, 1986). In addition, the diversity of species breeding on the slope of St Philip's Stone seems to be greater than on other slopes, especially as the area of the slope is relatively small. Herring Gulls, Lesser Black- backed Gulls, Guillemots and Razorbills all breed at St. Philip's Stone and this great diversity could benefit the Puffins, as they could find several complementary advantages from their neighbours, such as the ability to mob large predators or to detect potential dangers.

CONCLUSION

Small populations of Puffins are rarely studied, but the present study revealed that differences exist between the behaviour of birds breeding in large and small colonies. Indeed, Lundy Atlantic Puffins seem to be more affected by the presence and behaviour of other bird species than Puffins breeding in large colonies, which is probably due to their small number.

Similarly to large breeding populations, colony attendance on Lundy was affected by the period of day, with an evening peak in the number of Puffins observed. In addition, this study was the first to show that air temperature has an effect on the number of Puffins observed at the colony. Puffins were also more present on the west coast, which is closer to foraging patches and more subject to onshore winds. Finally, successful breeding pairs were all located close to a cliff edge.

Further investigations will be needed to determine whether wind speed and rainfall have an effect on colony attendance, as these factors approached significance in this study.

Although methods were in place to obtain a sufficient amount of data (i.e. conducting separate observations) a higher number of observation hours would have been preferable. Larger amounts of data may be able to show a stronger inverted U-shaped trend between mean number of Puffins and wind speed and increase the power of the regression analysis. Additionally, observations that included the entire breeding season, rather than just the chick provisioning and fledging stages, may have provided a better picture of the seasonal attendance patterns. Further studies should also try to compare different breeding sites on the island, as this might also affect the specific behaviours of the birds. Due to bad visibility and to health and safety considerations, data could not be collected in extreme weather conditions. Thus, weatherproof video cameras might be useful to accumulate more data, and in a wider range of weather conditions.

In conclusion, many aspects of the behaviour of the Lundy Puffin population remain unclear. This study should thus be considered as a preliminary study and intends to be a base for further and more developed research.

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