Impacts of poor food availability on positive density dependence in a highly colonial seabird

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For species with positive density dependence, costs and benefits of increasing density may depend on environmental conditions, but this has seldom been tested. By examining a colonial seabird (common guillemot) over a period of unprecedented poor food availability, we test two contrasting hypotheses suggesting that birds breeding at high density have: (i) greater leeway to increase foraging effort owing to more effective defence of unattended chicks against predators; and (ii) less leeway, owing to more attacks on unattended chicks by neighbouring adults. Supporting hypothesis 1, birds at high density increased provisioning rates and hence survival of chicks by foraging simultaneously with their partners, whereas at low density, unattended chicks were liable to be killed by predatory gulls and, unexpectedly, razorbills. Simultaneously, supporting hypothesis 2, heightened aggression towards unattended chicks at high density frequently resulted in infanticide, undermining benefits from collective defence against predators. Consequently, over 25 years, the magnitude of positive density dependence was independent of mean breeding success. These data indicate previously unsuspected trade-offs between costs and benefits of increasing density under changing environments. Previous generalizations about the importance of high density for reproductive success have so far remained robust, but such trade-offs could have unpredictable consequences for future population dynamics.

Keywords: chick neglect; colonial breeding; environmental change; *Uria aalge*; interference competition; social dynamics

1. INTRODUCTION

Vertebrate populations are typically viewed as being regulated by negative density dependence at one or more life-history stages, for instance, because higher densities can lead to increased competition for resources or easier detection by predators (Newton 1998; Rotella *et al.* 2009). In some cases, however, the form of density dependence may be positive. This is a well-known phenomenon in small populations (the Allee effect; e.g. Ferrer & Penteriani 2008; Kramer *et al.* 2009), but can also occur within larger populations when higher local density leads to an increase in individual fitness, notably through collective defence against predators (Clode 1993; Côté 2000). Where such positive density dependence occurs, it is likely that individuals in dense aggregations are still competing with each other for resources (Lewis *et al.* 2001; Elliott *et al.* 2009) or otherwise interacting negatively (Ashbrook *et al.* 2008). Hence, the net balance between such positive and negative effects of increasing density is likely to vary depending on environmental conditions (Kitaysky *et al.* 2000; Lewis *et al.* 2009). However, this prediction has seldom been tested (Wang *et al.* 2006).

Common guillemots *Uria aalge* (hereafter guillemots) have a single-egg clutch and breed on cliff ledges, where they attain very high local densities (up to 30 breeding

pairs per square metre with neighbouring birds in physical contact). Under favourable conditions, higher local density leads to enhanced breeding success through more effective defence of eggs and chicks against predators (Birkhead 1977; Murphy & Schauer 1996). In recent years, populations of guillemots bordering the North Sea have experienced low breeding success (Mavor *et al.* 2006) owing to declines in the abundance and quality of their main prey (Wanless *et al.* 2005), allowing us to reassess the relationship between breeding density and breeding success under unfavourable conditions. Chicks are typically guarded by at least one adult at the breeding site, but poor foraging conditions are increasingly forcing parents to forage simultaneously, leaving their chick unattended (Wanless *et al.* 2005; Ashbrook *et al.* 2008). Such parental non-attendance has also been recorded under adverse conditions at other colonies (Boekelheide *et al.* 1990). Unattended chicks may gain protection from a high density of neighbouring birds (Birkhead & Nettleship 1984; Burger & Piatt 1990), giving parents greater leeway to increase their foraging effort. However, unattended chicks are also at increased risk of being attacked and killed by neighbouring adults (Ashbrook *et al.* 2008). Hence, it is unclear whether the net benefit of breeding at higher density is enhanced or diminished under unfavourable conditions. Here, we combine standardized data on breeding success and chick survival over 25 years with direct observations and video recordings over two recent years, to compare parental attendance

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and food provisioning, together with attacks on chicks and chick survival to fledging, at high- (HDP) and low-density plots (LDP). We use long-term data for the period 1984–2008 to examine whether or not the magnitude of positive density dependence is related to average breeding success each year. We then use detailed data for 2007–2008 to test two contrasting hypotheses: (i) birds breeding at higher density have greater leeway to increase their foraging effort in response to poor foraging conditions, owing to more effective collective defence of unattended chicks at high density; and (ii) birds breeding at higher density have less leeway to respond to poor foraging conditions, owing to more attacks on unattended chicks by neighbouring adults at high density.

2. MATERIAL AND METHODS

The study was carried out on the Isle of May, UK (56°11' N, 2°34' W), where standardized data on guillemot breeding success and chick age at death have been collected since 1984 at two study plots differing markedly in breeding density (Harris & Wanless 1988). At the HDP (approx. 32 sites per square metre; 99 chicks in 2007; 98 chicks in 2008), most breeding birds were in physical contact with two or more neighbours (Ashbrook *et al.* 2008). By contrast, at the LDP (less than five sites per square metre; 31 chicks in 2007; 29 chicks in 2008), birds bred singly, or in small groups. Chicks were potentially able to move throughout most of the HDP, but chick movement was typically limited to a few tens of centimetres in the LDP owing to the small size and limited connectivity of ledges. Only guillemots bred in the HDP, but razorbills *Alca torda* (2007, 26 pairs; 2008, 19 pairs) and black-legged kittiwakes *Rissa tridactyla* (2007, eight pairs; 2008, nine pairs) bred among the guillemots in the LDP. Neither razorbills nor kittiwakes are traditionally viewed as being predators of chicks, although aggression between adults of all three species is common (Walsh *et al.* 2001). Elsewhere on the island, there were approximately 3000 breeding pairs of herring gulls *Larus argentatus*, approximately 2000 pairs of lesser black-backed gulls *L. fuscus* and approximately 30 pairs of great black-backed gulls *L. marinus* (Alampo & Lamont 2007), all of which species are known to prey on guillemot chicks (Birkhead 1977).

Birds were observed daily from 27 May to 6 July ($n = 41$ days) in 2007 and from 5 June to 9 July ($n = 35$ days) in 2008. Median hatch date did not differ significantly between plots in either year (χ^2 test using days from start of June: 2007: $\chi^2 = 0.9$, $p = 0.4$; 2008: $\chi^2 = 0.2$, $p = 0.7$) and the plots were less than 100 m apart, so that parents at high- and low-density sites experienced similar conditions in terms of weather and marine environment. Observations were made for 1 h, three times per day at each plot: in the morning (05.00–06.00 or 08.00–09.00), around midday (11.00–12.00 or 14.00–15.00) and in the evening (17.00–18.00 or 20.00–21.00). Observation periods were alternated between days and plots (i.e. high density, observations commenced at 05.00, 11.00 and 17.00; low density, at 08.00, 14.00 and 20.00; times then switched the following day). During observation periods, we recorded departures and arrivals of parents, food delivery to chicks, instances of aggression directed towards chicks and causes of any chick fatalities onto a dictaphone. We also recorded the breeding status of individuals displaying aggression, including breeding site if known.

From these data, provisioning rate was calculated for each chick as the total number of feeds the chick received divided by the total time (h) for which it was observed. Parental attendance data were used to calculate the proportion of time throughout hours of daylight for which each chick was left unattended in each of the 2 years. To avoid any possible biases owing to unattended chicks being easier to spot within the LDP, this parental non-attendance measure was calculated as the number of observation periods during which the chick was observed with neither parent present at any stage during the hour divided by the total number of observation periods for that chick. This pair-specific measure was used to investigate relationships among parental non-attendance, provisioning rates and survival of chicks to fledging. In addition, the numbers of attended and unattended chicks were counted each midday at a separate medium-density plot each year from 2004 (the year when chicks were first left unattended; Wanless *et al.* 2005) onwards, to investigate how the ages at which chicks died each year were related to a standardized measure of parental attendance at the colony. These counts were also taken at both study plots in 2007–2008 to examine how changes in non-attendance across the chick-rearing period each year were related to breeding density.

In addition to direct observations in 2007–2008, we used a video camera system (<http://www.tracksys.co.uk>) to record both study plots from 04.45 to 21.00 every day (outside these hours, light intensity was too low for reliable video analysis). Video footage was used to determine the causes of chick death outside periods of direct observation and from a total of 82 chick deaths, 61 per cent were observed either directly or via video footage. Unobserved deaths ($n = 32$) were either during hours of darkness (52%) or during the daytime, but outside the area covered by the video camera because chicks had moved away from their breeding site before being killed. Chicks were determined to have died from starvation if they were poorly fed, appeared emaciated and died on their breeding site without being attacked beforehand. We also recorded breeding success (the proportion of eggs resulting in a fledged chick, for comparison with previous years) and fledging success (the proportion of chicks that departed to sea) at each site. Following Harris & Wanless (1988), a chick was assumed to have fledged successfully if it disappeared when aged at least 14 days post-hatching and fully feathered.

We used generalized linear models (GLMs) to examine annual variation in the breeding success of guillemots at the HDP and the LDP from 1984 to 2008 and differences between plots in parental non-attendance and fledging success of chicks in 2007 and 2008. GLMs were also used to assess how the extent of parental non-attendance affected the average age of a chick at death at the two study plots between 1984 and 2008. We then used generalized linear mixed-effects models (GLMMs) to examine the relationship between parental non-attendance and chick provisioning rate at high- and low-density sites. To investigate how the total number of attacks experienced by chicks was affected by breeding density in 2007 and 2008, we used linear mixed-effects models (LMMs) with overall plot density (high or low) included as a fixed effect and the number of neighbouring chick-rearing pairs included as a covariate. We also included the number of days for which data were collected for each chick as a covariate, to control for individual differences in chick lifespan or, for surviving chicks, age at fledging. We included both overall plot density and the

Figure 1. Annual variation in (a) breeding success (the proportion of eggs resulting in a fledged chick) and (b) mean ages of failed chicks at time of death. Filled circles, high-density plot; open circles, low-density plot. In (b), where values for mean age at death are missing, all study chicks fledged successfully. Error bars in (b) are ± 1 s.e.

number of neighbouring pairs in this analysis to account for local variation in breeding density within each plot. Neighbouring chick-rearing pairs were classed as those within a radius of 20 cm of a breeding site using scaled photographs of the study plots.

To control for potential confounding influences in these analyses, year and days from median hatch date (as a standardized measure of stage-of-season) were included as fixed effects, plus time of day in the analysis of provisioning rates. Where data were collected at the same breeding sites in the same or different years, we also included site identity as a random effect to account for repeated measures. For all models, empirical scale parameters (residual scaled deviance divided by the degrees of freedom) were calculated to check models were not overdispersed, and plots of residuals were checked to ensure homoscedasticity, normality of errors and negligible influence of outliers in the data. Models were simplified by sequential removal of the least significant term (Crawley 2007). Taking an information theoretical approach, we then used Akaike's information criterion to select the most parsimonious model in each case (Crawley 2007; Bolker *et al.* 2008). All statistics were performed in R 2.8.0 (R Development Core Team 2007).

3. RESULTS

From 1984 to 1999, breeding success of guillemots on the Isle of May was generally high (figure 1a; 0.79 ± 0.01 chicks fledged per breeding pair) and was consistently

higher (13 of 16 years) at the HDP than at the LDP (sign test; $p < 0.05$; HDP $5.3 \pm 2.1\%$ higher on average). After 1999, breeding success declined markedly at both the HDP (1984–1999, 0.80 ± 0.02 ; 2000–2008, 0.59 ± 0.06 ; GLM with quasi-binomial errors; $F_{1,25} = 27.2$, $p < 0.001$) and the LDP (1984–1999, 0.76 ± 0.02 ; 2000–2008, 0.54 ± 0.06 ; $F_{1,25} = 25.8$, $p < 0.001$), but continued to be higher at the HDP (figure 1a; sign test; $p < 0.05$; HDP $9.3 \pm 4.3\%$ higher on average). Over 25 years, there was no significant relationship between average breeding success and the difference in breeding success at the HDP and the LDP (Spearman correlation; $r = -0.14$, $p = 0.3$).

Chicks in 2007–2008 were significantly more likely to be left unattended at the HDP (proportion of chicks left unattended at midday = 0.13 ± 0.02) than at the LDP (0.05 ± 0.015 ; GLM with quasi-binomial errors; $F_{3,97} = 10.9$, $p = 0.001$). Non-attendance was also higher in 2007 (0.14 ± 0.03) than in 2008 (0.04 ± 0.01 ; $F_{3,97} = 97.0$, $p < 0.001$). In addition, parental non-attendance of chicks at both plots increased as chicks grew ($F_{3,97} = 241.0$, $p < 0.001$).

Provisioning rate was higher in 2008 than in 2007 (GLMM with binomial errors: $\chi^2 = 10.0$, $p < 0.01$) and across both years, there was a significant positive relationship between provisioning rate and parental non-attendance ($\chi^2 = 116.7$, $p < 0.001$), showing that chicks left unattended more frequently were fed more often. However, unattended chicks were also liable to be

Figure 2. Proportion of daylight hours during which fledged and failed chicks were left unattended in 2007 and 2008 in relation to plot density. Open bars, fledged chicks; filled bars, failed chicks.

attacked by neighbouring breeders (78% of 492 attacks in 2007; 90% of 475 attacks in 2008), and these attacks were three times more frequent at the HDP (proportion of unattended chicks attacked, 0.18 ± 0.03) than at the LDP (0.06 ± 0.02 ; ANOVA using square-root arcsine-transformed data; $F_{2,94} = 12.7$, $p < 0.001$). There was no difference between years in this respect ($F_{2,94} = 0.002$, $p = 0.9$). Within each study plot, the frequency of attacks on individual chicks increased with the number of chick-rearing neighbouring pairs (LMM using log-transformed data; $F_{4,138} = 38.2$, $p < 0.0001$), particularly at the HDP (interaction between density and number of neighbouring pairs; $F_{4,138} = 10.2$, $p < 0.01$).

The proportion of time chicks were left unattended throughout the hours of daylight had contrasting effects on chick survival to fledging at the different densities. The most parsimonious model explaining chick survival included a three-way interaction between the proportion of time spent unattended, year and density (GLMM with binomial errors; three-way interaction, $\chi^2 = 6.5$, $p = 0.01$). This interaction showed that at the HDP in 2007, chicks that were attended less had a higher probability of fledging than those with higher levels of parental attendance (proportion of time chicks spent unattended: fledged, 0.47 ± 0.04 ; failed, 0.22 ± 0.03), contrasting with the LDP where chicks that survived were attended more frequently (proportion of time chicks spent unattended: fledged, 0.33 ± 0.06 ; failed, 0.43 ± 0.14 ; figure 2). At the lower levels of parental non-attendance in 2008, there was no relationship between attendance and chick survival at either density.

The main cause of chick mortality at the HDP was attacks by adult guillemots, with no recorded deaths at this study plot owing to predation by gulls or attacks by razorbills (table 1). By contrast, chick mortality at the LDP was owing mainly to predation by herring gulls and lesser black-backed gulls and to attacks by razorbills. Across the 25 years from 1984 to 2008, the average ages at which chicks died were significantly positively related to

Table 1. Causes of chick death at high- and low-density plots in 2007–2008. (Accidental deaths occurred when chicks were knocked from the cliff apparently without intent, either during feeding or in fights between adults.)

	density	
	low	high
number of observed deaths	13	37
% owing to		
guillemots	23.1	70.3
gulls	46.1	0
razorbills	30.8	0
starvation	0	24.3
accident	0	5.4

both year (i.e. older in later years; figure 1b) and colony-wide parental non-attendance (i.e. older for years of lower attendance) and significantly negatively related to breeding success (i.e. older in years of poor success; three-way interaction; $F_{1,42} = 7.60$, $p < 0.01$). There was no effect of density on average age at death ($F_{1,42} = 0.02$, $p = 0.8$).

4. DISCUSSION

Under favourable conditions, most pre-fledging mortality of guillemots occurs during the first few days post-hatching when chicks are most vulnerable to adverse weather conditions (Harris & Wanless 1988). In recent years, however, the mean age at which chicks are lost has increased at both high and low densities (figure 1b), reflecting increasing numbers of older unattended chicks and heightened intraspecific aggression towards chicks, in addition to increased mortality owing to starvation and predation.

In 2007, breeding success was the lowest recorded over 25 years, presumably owing to a low quantity and quality of prey in waters surrounding the colony (Ashbrook et al. 2008). Under these circumstances, not only was there an unprecedented level of parental non-attendance owing to both parents foraging simultaneously, but birds breeding at high density were almost three times more likely than birds at low density to leave their chick unattended at midday. This contrasts with responses of closely-related Brünnich's guillemots *Uria lomvia*, where food shortages have resulted in greatly reduced chick growth rates but with relatively little effect on parental foraging effort at either large or small colonies (Gaston et al. 1983; Kitaysky et al. 2000). In this study, as expected, simultaneous foraging by parents resulted in a higher rate of food delivery to the chick, and at high density, where almost one-quarter of chick deaths were apparently owing to starvation, parental non-attendance increased the likelihood of a chick surviving to fledging (figure 2). Apparently, no chicks were killed by predators at the HDP, which suggests that parents benefited from a high density of neighbours in terms of increased communal protection of chicks. This contrasts with the LDP, where leaving chicks unattended reduced their likelihood of survival to fledging, and predation by gulls was the most frequent cause of chick mortality (table 1). As parents at the HDP left their chick unattended more frequently than

those at the LDP, this suggests that parents correctly assessed the level of threat against the benefits of increasing their foraging effort. There were no recorded deaths owing to starvation at the LDP, probably because as soon as chicks at this site were left unattended, they were rapidly taken by predators. Hence, the proximate cause of mortality was predation, even though chicks left unattended at this site were very poorly fed and probably in imminent threat of starvation.

These data strongly suggest that in support of hypothesis 1 above, birds at high density had greater leeway to increase their foraging effort in response to poor foraging conditions owing to more effective collective defence of unattended chicks against predators. Birds breeding at high density may also have had higher intrinsic quality (Lescroel *et al.* 2009), making them more capable of increasing foraging effort on behalf of their offspring under adverse conditions without compromising their own survival (Gaston & Hipfner 2006). This pattern is consistent with data for other species showing increasingly positive local density dependence under increasingly stressful conditions (Goldenheim *et al.* 2008). However, unattended chicks were also much more likely to be attacked and killed by neighbouring breeders at high density, indicating a previously unrecorded negative density dependence in the parental trade-off between chick provisioning and defence against conspecific attack (Ashbrook *et al.* 2008). This provides partial support for hypothesis 2 above, although the trade-off did not result in diminished positive density dependence under adverse conditions so much as undermining the benefits of collective defence against predators, so that the net magnitude of positive density dependence was no greater in years when overall breeding success was low than in years when breeding success was high.

In previous studies of guillemots, parents responded to low prey availability by reducing the time spent together at the nest, but this seldom resulted in chicks being left unattended (Boekelheide *et al.* 1990; Burger & Piatt 1990; Uttley *et al.* 1994). Moreover while chicks are frequently attacked by conspecifics after leaving their breeding sites during fledging (Gilchrist & Gaston 1997), we are not aware of any previous reports of unattended chicks being killed by neighbouring conspecifics prior to departure. In this study, attacks on unattended chicks at the HDP typically followed incursions by chicks into neighbouring breeders' territories (Ashbrook *et al.* 2008), and were probably the result of parents seeking to reduce the risk of adoption or mistaken feeding of unrelated offspring (Ramos 2003) or kleptoparasitism by chicks (Fetterolf 1983). By contrast, at the LDP, chicks were less likely to be attacked by conspecifics, but were attacked by adult razorbills, accounting for about one-third of chick mortality prior to fledging at the LDP in 2007–2008 (table 1). Guillemots and razorbills frequently breed in close proximity, and these attacks on chicks were presumably a form of interference competition, similar to the aggression that commonly occurs between adults early in the season (Birkhead 1978) and to that recorded elsewhere as a result of recent increases in populations of species competing for breeding sites (Oro *et al.* 2009). Surprisingly, however, sites where chicks had been killed by razorbills the previous year in

our study were not frequented by razorbills in either 2008 or 2009. Contemporary theory suggests that in some circumstances, there should be an increasing strength and frequency of positive interactions between species with increasing ambient stress (Bruno *et al.* 2003). There is increasing evidence for such facilitation in plant assemblages (e.g. Goldenheim *et al.* 2008), but our data suggest an opposite effect of increasing ambient stress in interacting species of vertebrates.

In some other species where chicks are typically attended by at least one parent, poor food availability has similarly resulted in parents leaving chicks unattended while both parents foraged simultaneously, with adverse consequences for birds breeding at high local density. For instance, great skua *Catharacta skua* chicks left unattended during periods of food shortage are more vulnerable at higher local density to being killed and eaten by neighbouring adults (Hamer & Furness 1991). A combination of high local density and large colony size may be particularly disadvantageous in this respect. For instance, greater competition for prey within larger colonies of northern gannets *Morus bassana* leads to longer foraging trips by parents (Lewis *et al.* 2001), and in years of low food availability, this can lead at large colonies to parental non-attendance and attacks on unattended chicks by prospecting non-breeders (Hamer *et al.* 2007). Recent authors have emphasized the importance of individual heterogeneity in responses to environmental change (Charmantier *et al.* 2008; Lewis *et al.* 2009). Our data indicate that there may additionally be previously unsuspected trade-offs between costs and benefits of increasing density under changing environments. For guillemots, despite these trade-offs, previous generalizations about the importance of high density for reproductive success have so far remained robust. However, such trade-offs could have unpredictable consequences for future population dynamics.

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