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Breeding performance of the Imperial Shag (*Phalacrocorax atriceps*) in relation to year, laying date and nest location

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Abstract. The breeding productivity of seabirds usually declines over the course of a breeding season. Breeding productivity in colonial birds has also been found to be affected by the distance from a nest to the edge of a colony, with peripheral nests usually having lower productivity than centrally located nests. We evaluated the influence of laying date and nest location (distance from the edge of the colony) on clutch-size and breeding success of the Imperial Shag (*Phalacrocorax atriceps*) during three breeding seasons (2004–06) at Punta León, Argentina. There was no relationship between year, laying date or nest location and variation in clutch-size. Further, whereas breeding success did not differ between years, breeding success consistently decreased with laying date. We also found an interactive effect between laying date and nest location. Distance from the edge of the colony was not related to breeding success of Shags that laid either early or at the peak of the season, but the breeding success of late breeders increased with distance from the edge of the colony. Our findings of a seasonal decline in breeding success are consistent with the typical pattern exhibited by seabirds. Our results suggest that low-quality (young or less-capable) pairs that breed late in the season may benefit from nesting away from the edge of the colony, reducing levels of disturbance and risk of nest-predation.

Additional keywords: central–peripherial distribution, distance from the edge, parental quality, seabirds, seasonal decline.

Introduction

For birds breeding in seasonal environments, the timing of breeding and placement of nests are two key factors often strongly associated with fitness. In temperate zones, a seasonal decline in components of fecundity and productivity is a common pattern in seabirds (Lack 1968; Moreno 1998; Schreiber and Burger 2002). One of the main hypotheses explaining the seasonal decline in breeding performance is the parental quality hypothesis (Coulson and White 1956), proposing that young or low-quality breeders tend to lay late in the season and suffer impaired success. Accordingly, several studies have shown that older birds lay eggs earlier and have higher breeding success than young birds (Coulson and White 1958; Sydeman *et al*. 1991; see also Saether 1990; Moreno 1998).

The distance of a nest from the edge of a colony has also been reported to be an important factor affecting breeding success in colonial birds (Coulson 1968; Lack 1968; Siegel-Causey and Hunt 1981). The central–peripheral distribution hypothesis (Coulson 1968) suggests that spatial variation in breeding success arises because centrally located nests are less accessible to predators and are more frequently occupied by higher quality birds than peripheral nests.

Although several studies have analysed seasonal and spatial variation in the breeding parameters of seabirds, few studies simultaneously analysed the interactive effects of these factors.

The Imperial Shag (*Phalacrocorax atriceps*) is a medium-sized colonial seabird of southern South America coastlines (Nelson 2005). Preliminary analysis of data on Imperial Shags banded and re-sighted at Punta León during the last 7 years suggest strongly that older birds breed earlier in the season than younger birds and that Shags first breed at 2 years old, with first-time breeders reproducing exclusively late in the season at the edge of colonies (W. S. Svagelj and F. Quintana, unpubl. data). In addition, the Kelp Gull (*Larus dominicanus*) has been reported to depredate Imperial Shag eggs and chicks in Punta León, hunting almost exclusively from the ground by walking up to Imperial Shag nests located at the edge of colonies (Quintana and Yorio 1998). The system studied here therefore appears appropriate for examining seasonal and spatial variation in breeding performance.

In this paper, we examine the influence of the timing of breeding (laying date) and nest location (distance from the edge of a colony) on the reproductive performance of the Imperial Shag breeding at Punta León, Argentina. Assuming that parental quality is related to laying date (Saether 1990; Moreno 1998), we predict a decline in clutch-size and breeding success of the Imperial Shag over the breeding season. Also, based on the central–peripheral distribution model of nest dispersion likely apply to colonial seabirds nesting in homogeneous habitats with a low level of protection (see Velando and Freire 2001), we predict

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that clutch-size and breeding success should increase with the distance of the nest from the edge of the colony.

Materials and methods

We conducted the study from October to December over three consecutive breeding seasons (2004–06) at a colony of Imperial Shags at Punta León (43°05′S, 64°30′W), Chubut, Argentina. The site of the colony at Punta León is a flat and elliptical area ~130 m long × 15 m wide, without vegetation inside. The colony comprises ~3200–3400 breeding pairs, with nests at a homogeneous density of ~2 nests m^{-2} (Svagelj 2009; W. S. Svagelj and F. Quintana, unpubl. data).

Data were collected from a total of 632 Shag nests (143 nests in the 2004 season, 195 in 2005, 294 in 2006). We checked nests every 1–3 days from the start of laying until completion of clutches in the colony. During the chick-rearing period, we visited nests every 3–5 days to determine the fate of chicks. Chicks were considered to have fledged if they reached 30 days of age. Clutch-size was determined for 632 nests and the number of chicks fledged per nest was determined for 471 nests. The differences in sample size between clutch-size and the number of chicks fledged per nest are the result of 161 nests from the 2006 season that were used in manipulative experimental treatments; consequently, we excluded these nests in our breeding success analysis.

To test the effects of year, laying date and nest location (distance from the edge of the colony) – the explanatory variables – on clutch-size (number of eggs laid) and breeding success (number of chicks fledged per nest), we employed generalised linear models (GLM) with Poisson family distribution and log-link function (McCullagh and Nelder 1989; Crawley 2007). Year was included in the analyses as a three-level fixed factor. Laying date was included as a four-level ordered factor, where breeding attempts in each season were assigned to one of four quartiles (1st, 2nd, 3rd and 4th quartiles, representing early, medium–early, medium–late and late breeders respectively). Distance from the edge of the colony (measured to the nearest 5 cm; median 95 cm, range 5–260 cm, $n=632$) was included as a continuous variable.

Model selection was based on information–theoretic procedures (Burnham and Anderson 2002). Models with all possible combinations of explanatory variables were considered. This resulted in 19 candidate models, with 18 models corresponding to all possible combinations of three explanatory variables and their interactions, and a base model without explanatory variables (null model). A null model was useful for assessing the relative explanatory power of models and explanatory variables of interest. Because models relating to clutch-size and breeding success did not exhibit overdispersion ($\hat{c} \leq 1$), model selection was based on Akaike's information criterion corrected for small sample size (AIC_c) (Burnham and Anderson 2002). Conclusions were based on the best models. Continuous and categorical explanatory variables included in the best models were evaluated using the z statistic and the likelihood ratio test respectively. Statistical analyses were carried out using R software, Version 2.10.1 (R Development Core Team 2009). Values are reported as means ± s.e. except where noted. All tests were two-tailed, and differences were considered significant at $P<0.05$.

Results

Laying and laying date

First eggs were found on 3, 22 and 8 October in 2004, 2005 and 2006 respectively. Laying continued for ~6 weeks, up until the third week of November. The median date of laying (i.e. date when 50% of the sampled breeding pairs laid the first egg of the clutch) was 14 October in 2004, 31 October in 2005, and 21 October in 2006. The duration of the laying period, as the number of days between the completion of the first and last clutches in the colony each season, was 42 days in 2004, 31 days in 2005 and 42 days in 2006.

Clutch-size

Mean clutch-size was 2.79 eggs per nest (s.d. = 0.51, $n=632$), with a range of 1–4 eggs. The modal clutch-size was three eggs (75% of clutches, $n=475$), and clutches of two and three represented 95% of clutches ($n=602$). Of the 18 clutches of four eggs, in only six (33%) were all four eggs simultaneously in the nest; in the remaining 12 (67%) at least one egg was lost before the fourth egg was laid. In 11 (92%) of these clutches, the first-laid egg was lost before the second egg was laid. Only four pairs attempted breeding twice in a season, all of them after early breeding failures during laying or early incubation.

The model that best described variation in clutch-size was the null model. Neither year (2004: 2.79 ± 0.04 eggs, $n=143$; 2005: 2.82 ± 0.03 eggs, $n=195$; 2006: 2.77 ± 0.03 eggs, $n=294$; $\chi^2_2=0.1$, $P=0.96$) nor laying date ($\chi^2_3=4.8$, $P=0.19$; Fig. 1) were related to variation in clutch-size. Distance from the edge of the colony was not related to variation in clutch-size ($\beta=0.0004 \pm 0.0004$, $z=0.96$, $P=0.34$).

Breeding success

Of 471 nests monitored through the breeding cycle and whose outcome was known (see Materials and methods section), average breeding success was 1.24 fledglings per nest (s.d. = 0.78, $n=471$), ranging from 0 to 3 fledglings. Modal brood size at independence was 2 fledglings (43% of breeding

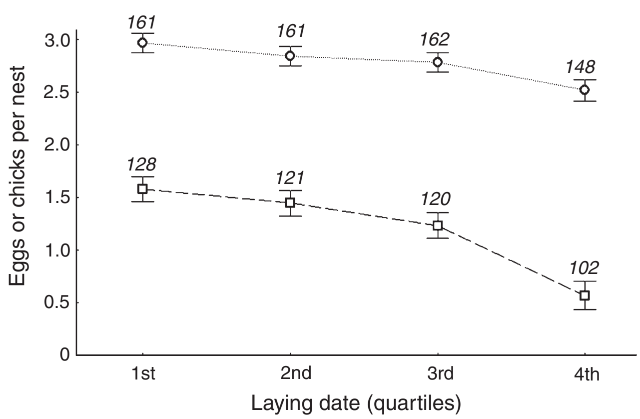

Fig. 1. Mean clutch-size (circles) and breeding success (number of chicks fledged; squares) of Imperial Shags reproducing early, medium-early, medium-late and late in the breeding season (1st, 2nd, 3rd and 4th quartiles respectively). Numbers indicate sample size; whiskers show standard error.

attempts, $n = 202$ of 471). Of the 471 clutches 96 (20%) failed to produce fledglings.

The model that best explained the variation in breeding success included laying date, distance from the edge of the colony and their interaction (likelihood ratio test, comparison with null model: $\chi^2_7 = 77.2$, $P < 0.0001$); this model accounted for 23% of variation. Breeding success decreased with laying date ($\chi^2_3 = 61.3$, $P < 0.0001$; Fig. 1). Most of the failed breeding attempts corresponded to pairs reproducing late in the season, with the proportion of failed attempts 5% (7/128), 10% (12/121), 18% (21/120) and 55% (56/102) for 1st, 2nd, 3rd and 4th quartile respectively. The effect of the distance of a nest from the edge of the colony on breeding success differed with laying date (interaction term laying date × distance from the edge: $\chi^2_3 = 11.6$, $P < 0.01$). Although breeding success was unrelated to the distance of a nest from the edge of the colony for birds reproducing in the first three quartiles of the season (1st: $\beta = -0.0011 \pm 0.0013$, $z = -0.8$, $P = 0.40$; 2nd: $\beta = 0.0022 \pm 0.0014$, $z = 1.6$, $P = 0.11$; 3rd: $\beta = 0.0015 \pm 0.0015$, $z = 1.0$, $P = 0.32$), the breeding success of late breeders increased with the distance of a nest from the edge of the colony (4th: $\beta = 0.0074 \pm 0.0021$, $z = 3.5$, $P < 0.0005$; Fig. 2). Finally, year was not related to variation in breeding success (2004: 1.14 ± 0.07 chicks, $n = 143$; 2005: 1.25 ± 0.05 chicks, $n = 195$; 2006: 1.33 ± 0.07 chicks, $n = 133$; $\chi^2_2 = 1.8$, $P = 0.41$).

Discussion

Imperial Shags at Punta León showed consistent breeding productivity across years, with neither clutch-size nor breeding success differing between years. The consistency in key breeding parameters is likely to be a consequence of the availability of a highly predictable food resource in a fairly stable marine ecosystem. The Patagonian Shelf in general, and the area exploited by Imperial Shags from Punta León in particular, are characterised by a moderately high productivity and stability (Acha *et al.* 2004; Rivas *et al.* 2006). Moreover, during the 2004–09 breeding seasons, Imperial Shags of Punta León fed in the same geographically small area of high productivity (Quintana *et al.* 2011; F. Quintana, unpubl. data) associated with a seasonal marine tidal front at the south-east of the Valdés Peninsula (Rivas *et al.* 2006).

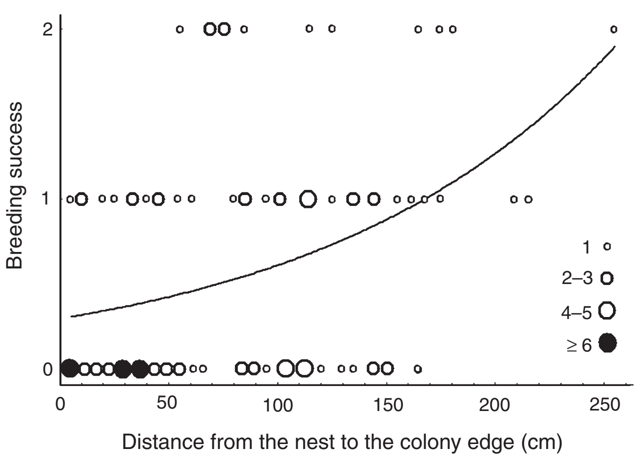

Fig. 2. The relationship between breeding success and the distance of a nest from the edge of the colony for Imperial Shags breeding late in the season (4th quartile; $n = 102$). Circles represent the absolute frequency of breeding attempts for each 5-cm interval in distance from the edge. The adjusted function $y = e^{(-1.24 + 0.0074x)}$ was obtained from a generalised linear model with Poisson family distribution and log-link function (see Methods).

In addition to the predictable and productive food resources, the absence of any interannual variation in breeding success is probably mediated by brood reduction. At Punta León, Imperial Shags exhibit brood reduction, with broods of three fledglings extremely rare (<1% of breeding attempts; Svagelj 2009; W. S. Svagelj and F. Quintana, unpubl. data). Last-hatched chicks in three-hatchling broods usually starve to death within the first 2 weeks of life (Svagelj 2009; W. S. Svagelj and F. Quintana, unpubl. data). Such strong brood reduction can reduce interannual differences in breeding parameters at intermediate stages of the breeding cycle, evening out breeding success across years (W. S. Svagelj and F. Quintana, unpubl. data).

Laying date and seasonal decline in breeding performance

In our study, the breeding success of the Imperial Shag was strongly related to the timing of breeding. Our findings of a seasonal decline in breeding success are consistent with the typical pattern shown by seabirds (Moreno 1998) in general, and cormorants and shags in particular (Snow 1960; Shaw 1986; McNeil and Léger 1987).

By manipulating the breeding time of European Shags (*Phalacrocorax aristotelis*) of known age, Daunt *et al.* (1999, 2007) provided strong experimental support for the parental quality hypothesis. These studies showed that experienced (old) European Shags delivered more food to chicks and produced more fledglings than naive (young) parents, irrespective of the time of season (Daunt *et al.* 1999, 2007). Although parental quality appears to be primarily responsible for the seasonal variation in the breeding success of Imperial Shags, we cannot rule out an effect of a seasonal decline in the availability of food (food-supply hypothesis; Lack 1968; Perrins 1970). Further experimental studies manipulating the breeding time of birds of known age are needed to disentangle the effects of these different factors.

Distance of nests from the edge of the colony

Siegel-Causey and Hunt (1981) found that Double-crested Cormorants (*Phalacrocorax auritus*) nesting in the centre of colonies were more successful than pairs breeding at the periphery. In that study, peripheral pairs suffered a disproportionately high number of depredations relative to the number of predator visits they received, whereas centre-nesting pairs received fewer depredations than expected, indicating a differential parental quality between central (high quality) and peripheral (low quality) breeders (Siegel-Causey and Hunt 1981). Recently, Staverees *et al.* (2008) found that breeding success of Cape Gannets (*Morus capensis*) was positively related to the distance from the colony edge. In our study, we found an interactive effect between laying date and nest location on breeding success. Distance from the edge of the colony was not related to breeding success of pairs nesting early or during the peak of the season, but the breeding success of late breeders increased with the distance of their nest from the edge of the colony. Our results suggest that low-quality (young or less-capable) pairs that breed late in the season might benefit from nesting away from the edge of the colony, reducing disturbance and nest-predation risks.

Our results provide partial support for the central–peripheral hypothesis, because the distance of a nest from the edge of the colony was related to breeding success, but only for late breeders. The central–peripheral distribution is the generally accepted model for nest-dispersion patterns in seabird colonies (Furness and Monaghan 1987; Schreiber and Burger 2002; but see Velando and Freire 2001). Velando and Freire (2001) suggest that homogeneous colonial habitats having a low level of protection are likely to fit the central–peripheral model, whereas in heterogeneous habitats where high-quality nesting sites are scarce, the quality of neighbouring nests may be inversely related, with high-quality individuals occupying the best nesting sites and low-quality individuals surrounding high-quality breeders (i.e. central–satellite model). Although the physical characteristics of the Punta León colony would fit the central–peripheral model (see Methods), future studies could evaluate alternative models of nest distribution.

Our study observed consistent breeding productivity across years. However, there was a strong seasonal decline in breeding success, probably as consequence of the temporal segregation in parental quality between old and young birds reproducing early and late in the season respectively.

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