Rockhopper Penguin–Imperial Cormorant mixed colonies in the Falkland Islands: a stroke of luck for late breeders

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Abstract. Mixed-species colonies occur frequently, especially among seabirds, and may provide mutual benefits among associated species including antipredator advantages. The “protector” species in such associations may provide early warning signals or by aggressively defending their own nests, may expel predators from the area. We explored costs and benefits to Rockhopper Penguins (Eudyptes chrysocome) in relation to offspring production in both monospecific colonies and those mixed with Imperial Cormorants (Phalacrocorax atriceps) at Saunders Island (Falkland Islands), emphasizing differences in predation pressure. We considered behavioral responses of chicks (in crèches), as well as differences in their nutritional condition, morphometric measurements, and survival compared among different breeding colonies. Our study revealed a paradox: High-quality adult penguins, those arriving early and occupying lower-elevation sites closer to the coast, produced better-nourished chicks earlier in the season. However, they averaged half the number of chicks fledged, compared to breeders that arrived later in the season. Late breeders were forced by unavailability of optimal habitat to nest in more elevated areas, forming mixed colonies with cormorants, which, in turn, provided them with protection from nest predators. This study provides an example of the role of luck in nature, and how it may compensate for differences in individual fitness.

Key words: Eudyptes chrysocome; individual quality; luck; mixed colony benefits; nutritional conditions; Phalacrocorax atriceps; Phalacrocorax australis; predation; productivity.

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INTRODUCTION

The most commonly proposed hypotheses for the evolution of colonial breeding in birds focus on advantages related to reducing nest predation and enhancing resource acquisition (Lack 1968, Hoogland and Sherman 1976). Predator swamping occurs when predators can eat only a small proportion of the available prey (Ainley et al. 2005, Pöysä et al. 2019). Thus, colonial birds may breed synchronously so that most chicks are present at the same time and place to thereby overcome the predator’s ability to prey on every chick. In turn, that increases the probability of survival for any individual chick. Even if breeding colonies attract predators (Brown 1967), this swamping effect, together with the collective antipredator behavior of colony members, such as early warning calls, mobbing, and attacks, leads to a decrease in net predation rates. Birds
breeding in colonies, however, especially with a high degree of synchrony, must cope with ancillary factors such as increased competition for space, nest materials, food, and other resources (Pöysä et al. 2019).

Mixed-species colonies occur frequently, especially among seabirds (Burger 1984, Gaglio et al. 2018). One potential explanation for this phenomenon is the low availability of nesting habitat, especially for large populations that breed on small, remote islands adjacent to waters that are especially rich in food resources (Murphy 1925, Belopolski 1957, Ainley and Boekelheide 1990). Additionally, mixed colonies might benefit individuals of each of the co-occurring species (Krebs 1974) through predator swamping, sharing of early warning signals, or information transfer (Cullen 1960, Smith 1975, Nuechterlein 1981). In some cases, mixed-species colonies provide predator protection not available in monospecific colonies (Fuchs 1977, Götmark and Andersson 1980). The “protector” species in such associations may provide early warning signals (Nuechterlein 1981), or by aggressively defending their own nests, they may expel predators from the area, offering additional protection to the less-aggressive or “protected” species (Erwin 1979, Dyrzc et al. 1981). In the protector-species hypothesis, the less-aggressive species will benefit from the association and may actively choose to nest in the company of the “protector” species (Burger 1984).

The protector-species hypothesis explains mixed-species colonies on the basis of benefits for both species, with the “protector” species decreasing predation rates through increased aggressiveness and both species contributing to the predator swamping effect. Protective nesting associations are recognized as important for bird conservation (Haemig 2001). In such associations, where the dependence is not obligate, the disappearance of the protector species may increase nest predation rates on the associated species, with ensuing demographic consequences (e.g., Kuussaari et al. 2009, Hylander and Ehrén 2013, Brodie et al. 2014).

Here, we present results from a study of the association between the Imperial Cormorant (Phalacrocorax atriceps) and the Rockhopper Penguin (Eudyptes chrysocome) breeding in mixed colonies at the Falkland Islands. These islands present an interesting situation due to the presence of a rich community of predators potentially conditioning the formation of mixed colonies. Despite an apparently high level of breeding success in the Falkland Islands, the Southern Rockhopper Penguin (E. c. chrysocome) population is in severe decline (Bingham 2002). During the 1930s, what was thought to be one of the largest populations of the species, with ca. 1,800,000 breeding pairs occurred on the Falkland Islands. The total population, however, has since decreased to ca. 280,000 breeding pairs (Baylis et al. 2013). A possible cause of the perceived decrease is the change in population size of a predatory raptor, the Striated Caracara (Phalcoboenus australis), which once was considered a threat to livestock and consequently, was widely persecuted, thus severely reducing its numbers (Catry et al. 2008). Conservation measures in recent decades have led to an increase in the caracara population, from 206 pairs during the 1960s to 605 pairs in 2014 (Reeves et al. 2018). Thus, the trajectories of penguin and caracara populations appear to be inversely associated, but the dynamics of a protector species, the Imperial Cormorant, may also be involved.

As far as we know, the breeding biology of seabirds in mixed colonies at the Falkland Islands has not been studied, although increased understanding of the interspecific dynamics would be helpful in developing appropriate conservation measures. We analyzed costs and benefits to Rockhopper Penguins in relation to offspring production in both monospecific and mixed (penguin-cormorant) colonies, emphasizing predatory pressure. We considered behavioral responses of chicks (in crèches), as well as differences in their nutritional condition and morphometric measurements among different breeding colonies. Ultimately, we discuss the consequences of population changes in protector, protected, and predator species for species’ resilience.

**Material and Methods**

**Study species and colonies**

We conducted this study on Saunders Island (51.37° S, 60.09° W) from 20 January to 4 February 2017. Saunders Island is 12,500 ha in size and located among the northern Falkland Islands. This island is home to King (Aptenodytes patagonicus), Gentoo (Pygoscelis papua), Rockhopper, and Magellanic (Spheniscus magellanicus) penguins, as
well as Rock Shags (*Phalacrocorax magellanicus*), Imperial Cormorants, and Black-browed Albatrosses (*Thalassarche melanophrys*).

The Rockhopper Penguin is the smallest crested penguin, having a mass of 2.0–3.5 kg. The southern subspecies has a global population of ~1 million birds, with one of the largest populations (~280,000 pairs) breeding in the Falkland Islands (Baylis et al. 2013). This subspecies breeds only in the Falklands and islands of Chile and Argentina, occurring in large colonies located from sea level to cliff- tops at 36 sites around the Falklands. Rockhopper Penguin life history is reviewed in Williams (1995). In summary, a pair usually lays two eggs in early November and incubation takes ~33 days. Chicks enter crèches at 4 weeks of age, and fledge at ~10 weeks of age in early February. Adults generally remain close to the colony during the breeding season, feeding on small fish, squid, and crustaceans, after which breeding sites are abandoned between April and October. Sexes are similar in appearance but can be distinguished by body measurements with females being significantly smaller than males in all cases; bill length and flipper length are the most dimorphic physical metrics (Poisbleau et al. 2010, Morandini et al. 2018). The Southern Rockhopper Penguin is classified as vulnerable by the IUCN because the global population has decreased by ~33% in the last 30 yr; however, increasing population trends from 2005 to 2010 have been reported in several locations (Baylis et al. 2013).

Imperial Cormorants breed in dense colonies on gentle cliff-top slopes. There are over 100 breeding locations for this species around the Falkland Islands, totaling 38,000–84,000 breeding pairs (Woods and Woods 1997). Many of these colonies are mixed with breeding Rockhopper Penguins and/or Black-browed Albatrosses. The cormorant’s natural history is reviewed in Nelson (2005). In summary, sexes are similar in appearance and adults build nests from mud and vegetation, laying 2–4 eggs during mid-November. Eggs hatch in December, and chicks remain in the nest until they fledge in late February. Imperial Cormorants breeding at the Falklands remain throughout the year, traveling long distances in search of small fish and crustaceans, which they catch in foraging flocks during shallow dives.

We studied seven different colonies of Rockhopper Penguins at Saunders Island, three at an area locally called “The Rookery,” and four at “The Neck,” separated from each other by 8.6 km. At the time of our investigation, penguin chicks were in crèches, with crèche size ranging from 72 to 535 chicks. At these seven penguin colonies the number of Imperial Cormorant pairs ranged from 0 to 285, representing a cormorant/penguin chick ratio that ranged from 0.0 to 1.7. We measured elevation and distance between the colony and the sea for each colony using Google Earth, with the GPS location fixed for each colony. Penguins must walk from the ocean to their nests and walking is energetically costly (Pinshow et al. 1997, Dewasmes et al. 1980, Griffin and Kram 2000). In order to index the relative energy expended by adult penguins to get from the beach to their breeding colonies (RE) we used the formula: \( \text{RE} = \text{mgH} \), where \( m \) is the mean mass of a Rockhopper Penguin, \( g \) is gravity, and \( H \) is the vertical height above sea level of the colony.

We used the ratio of penguin chicks to adult penguins present at the colony as an index to population level productivity. We took pictures at the end of the crèche phase, ~1 h before sunset when the number of adult birds is the highest and the activity of predators is the lowest (MF and VM, personal observations) counting both chicks and adults, 10 times at each colony over the study period.

**Predatory pressure, breeding cormorants, and chick crèches**

To investigate the behavior of penguins in crèches, we made 5-min focal observations of randomly chosen chicks (\( n = 331 \), total observation time 1655 min) left unguarded by their parents and within crèches of different sizes, from locations randomly selected in different areas of the seven study colonies (between 44 and 76 observations per colony) across the entire crèche period. For each individual, we recorded crèche size and individual chick movements and interactions. We considered a chick to be part of a specific crèche if the distance to its nearest neighbor was <1 m. The mean size of penguin crèches within a breeding colony depended on the total number of chicks present in the colony (Penteriani et al. 2003b), so we standardized size of crèche as the percent of the total number of...
chicks present at the colony. Therefore, a crèche of 3.4 means that 3.4% of the chicks present at the colony are in the same crèche. To quantify chick movement, we counted the number of individual footsteps made by chicks during the observation period. Chick interactions were quantified by counting the number of times a chick interacted with another chick (“chick-chick interactions”) and the number of times a chick interacted with an adult penguin (generally aggressive pecking; “adult-chick interactions”).

For each study colony, we also conducted surveys of predator presence as an estimate of predation pressure. We made 15-min observations in all the colonies (n = 44, total observation time 660 min, between 5 and 7 observations per colony), and during that time recorded every predator flying over, perching in, or walking through the colony. We considered several potential predators: Striated Caracara, Turkey Vulture (Cathartes aura), Falkland Skua (Stercorarius antarctica), and Southern Giant Petrel (Macronectes giganteus). After each 15-min observation, we conducted a census of the study colony, recording the total number of penguin chicks present, the number of crèches in each colony, and the size of each crèche (i.e., number of chicks) standardized as the percent of the total number of chicks present at the colony. In addition, we standardized predatory pressure as the ratio of the number of predators observed divided by the number of Rockhopper Penguin chicks present at the colony. Finally, at each study colony we recorded the number of cormorant breeding pairs standardized, again, by the number of penguin chicks.

Body measurements, sex determination, and nutritional condition

We captured 80 Rockhopper Penguin chicks in crèches. Each was randomly selected from among the seven study colonies (between 10 and 14 chicks per colony). We weighed each chick and recorded body mass to the nearest 0.1 g using a spring balance. We used calipers and a ruler to measure bill length (exposed culmen; see Aguilera et al. 1993), bill depth (to the nearest 0.1 mm), and flipper length (to the nearest mm). To reduce variability, most of the measurements were made by the same observer (>90%). We selected bill length to estimate chick age because it is the structural measure having the best linear relationship with chick age in this species (Poisbleau et al. 2010).

To evaluate nutritional condition of penguin chicks (Alonso-Alvarez et al. 2003, Morandini et al. 2018), blood samples from 80 chicks were collected between 11:00 and 15:00, thus avoiding variations in blood parameters due to circadian rhythms (Garcia-Rodriguez et al. 1987, Ferrer 1990, Ferrer 1994). Up to 2 mL of blood was extracted from the foot vein using a 23-gauge needle and a 5-mL heparinized syringe. Blood samples were stored in a portable refrigerator at 6°C and then carried to the field laboratory within 8 h, at which time they were centrifuged at 3000 rpm for 10 min. We kept plasma stored frozen at −24°C until analysis. Handling time including blood collection was <3 min per bird, and all birds were released at the capture point.

We also included a body condition index as an estimate of nutritional condition. We regressed bill length on the cube root of mass, retaining residuals of this regression (body condition index) as a proxy for body condition (Ferrer et al. 2017, Morandini et al. 2018, Morandini and Ferrer 2019). This approach should be interpreted carefully due to high variability in body mass of penguin chicks, depending on elapsed time since last feeding; however, it is an additional estimate of nutritional condition among chicks that is independent of blood parameters. We did not select chicks that we saw being fed, but we cannot completely disregard the possibility that some very recently fed chicks were included in our measurements.

We performed biochemical analyses of blood plasma on a computer process-controlled multi-channel auto analyzer (Cobas-Integra 400, Roche Diagnostic). Due to the small quantity of blood collected per bird, it was not possible to conduct all the analyses in all 80 birds from which we drew blood, but rather we analyzed blood samples from 71 to 80 birds for each of the 11 physiological parameters measured. These included glucose (GOD-PAP method; n = 79), urea (urease method; n = 80), uric acid (uricase method; n = 80), cholesterol (CHOHPAP method; n = 80), triglycerides (enzymatic method; n = 80), creatine kinase (CK, enzymatic method; n = 80), alkaline phosphatase (ALP, cresolphthalein phosphate hydrolysis; n = 76), total protein (biuret reaction; n = 80).
statistical variables on (1) chick behavior (ln link function) to evaluate the effect of a variety of explanatory variables on (2) chick behavior (ln link function) to evaluate the effect of a variety of explanatory variables on colony productivity (no. chicks/adult). We used Pearson correlation coefficients to investigate potential correlations among explanatory variables in each analysis. If explanatory variables were correlated with r ≥ 0.70, we did not include both parameters in the same model. Breeding cormorants start the breeding season slightly later than Rockhoppers, preferentially selecting areas further from the beach, with higher elevation and lower densities of Rockhopper Penguins (Pole-Evans, personal communication). We found that distance to the sea and elevation of the colonies were highly correlated (r > 0.80). And because of the differences in chronology and cormorant preferences, both were highly correlated with the proportion of breeding cormorants (r > 0.80). Thus, the proportion of breeding cormorants also reflected elevation and distance from the sea because nesting cormorants were more abundant at higher-elevation sites that were farther from the sea (Fig. 1). For this reason, we chose to retain only the proportion of breeding cormorants as a covariate in our modeling exercise. We investigated three relationships. For (1) chick behavior, we explored the association between the proportion of breeding cormorants per penguin chicks present at the colony, the crèche size where penguin chicks occurred, and the interactions of penguin chicks with adults. For (2) mean crèche size, we investigated the association between predation pressure and the proportion of breeding cormorants per penguin chick. Finally, (3) for penguin productivity, we investigated the association between predation pressure and the proportion of breeding cormorants. We included location (The Rookery vs. The Neck) and colony (n = 7; 3 at “The Rookery” and 4 at “The Neck”) as nested random factors in all the models.

We used an information-theoretic approach to develop three a priori model sets for chick behavior, mean crèche size, and productivity. We ranked models using Akaike’s information criterion adjusted for small sample sizes (AICc), ∆AICc (the difference in AICc between each candidate model and the model with the lowest AICc value), and Akaike weights (AICc weights; Burnham and Anderson 2002). Models within 2 ∆AICc values of the top model were considered
competitive. We used the “lme4” package (Bates et al. 2015) in R version 1.1.423 (R Core Team 2013) to estimate general mixed model coefficients and model selection statistics.

**RESULTS**

**Differences among colonies**

There were no differences in chick sex ratio between colonies with and without cormorants (GLM binomial, logit link function; presence cormorants, \( \beta = 0.29, SE = 0.25, 95\% CI = -0.20 \) to 0.79, \( P = 0.2445 \)). Comparing morphometric measurements between colonies with and without breeding cormorants, significant differences were found only in bill length (ANOVA, \( F_{5,87} = 2.89, R^2 = 0.073, P = 0.0183 \)), with shorter bill lengths (reflecting younger age) in chicks from colonies mixed with cormorants (mean ± SD bill length in colonies with cormorants = 38.39 ± 1.38, and without cormorants = 39.15 ± 1.04).

Blood parameters of penguin chicks were significantly different between colonies with and without cormorants (MANOVA, Wilks = 0.68, \( F_{11,58} = 2.514, P = 0.0115 \)). Differences in urea levels were significant (\( F_{1,78} = 10.36, R^2 = 0.082, P = 0.0019 \); Table 1), with higher levels in colonies with breeding cormorants (mean ± SD urea levels in colonies with cormorants = 2.68 ± 0.63, and without cormorants = 2.15 ± 1.16), reflecting poorer nutritional status of penguin chicks in mixed colonies. In addition, body condition index was different between colonies with and without cormorants (\( F_{1,78} = 5.18, R^2 = 0.062, P = 0.0255 \)), with lighter chicks, on average, observed in colonies with cormorants (mean ± SD body index in colonies with cormorants = −0.03 ± 0.02, and without cormorants = 0.05 ± 0.03).

In total, during 660 min of observations we observed 397 predators, with the Striated Caracara being the most common (37% of the total). Predator presence was significantly different between colonies with and without cormorants (\( F_{1,42} = 11.39, R^2 = 0.213, P = 0.0015 \)), with a mean (±SD) of 12.35 (±6.0) predators/15 min in monospecific colonies vs. 7.83 (±5.28) in mixed colonies. Finally, differences in the estimated index of relative energy expenditure during travel to/from the sea were as much as 3.11 times greater for penguins nesting in colonies at higher elevations.

![Graph showing the relationship between elevation (m) and proportion of breeding cormorants per penguin chick colony, shading indicates 95% CI. As elevation increased, the proportion of breeding cormorants also increased; \( r > 0.80 \).](image-url)
compared to penguins in colonies closer to the beach (see Table 2).

**Cormorants, adult penguins, and crèche behavior**

The proportion of breeding cormorants varied from 0 to 2.9 (mean ± SD = 0.50 ± 0.40). The model relating the number of steps made by a chick during the 5-min observation period with the additive effects of the size of the crèche, the number of aggressive interactions with adult birds, and the proportion of breeding cormorants per penguin chicks at the colony received the most support (99.9% of the AIC weight; Table 3). The main effects indicated that the number of steps increased as crèche size decreased (crèche size, $β = −0.17$, SE = 0.04, 95% CI = −0.25 to −0.09) and adult aggressive interactions became more frequent (adult interactions, $β = 0.18$, SE = 0.03, 95% CI = 0.14 to 0.26). Additionally, penguin chicks moved, shorter distances at mixed colonies (presence cormorants, $β = −0.47$, SE = 0.09, 95% CI = −0.66 to −0.28; Table 3). Thus, mean crèche sizes increased more with increasing predation pressure in colonies without cormorants, than in colonies with a higher proportion of cormorants (Fig. 2).

**Table 1. Results from MANOVA for blood parameters of Rockhopper Penguin chicks between colonies with and without nesting cormorants at Saunders Island, Falkland Islands.**

| Blood parameter          | Multiple R | Multiple $R^2$ | Adjusted $R^2$ | SS  | df | MS  | SS  | df | MS  | F    | P    |
|--------------------------|------------|----------------|----------------|-----|----|-----|-----|----|-----|------|------|
| Log urea                 | 0.363577   | 0.132189       | 0.119427       | 7   | 1  | 7   | 46  | 68 | 1   | 10.35803 | 0.001976 |
| Uric acid (mg/dl)        | 0.071748   | 0.005148       | -0.009482      | 10  | 1  | 10  | 2027| 68 | 30  | 0.35186 | 0.555028 |
| Total protein (g/dl)     | 0.295157   | 0.087118       | 0.073693       | 3   | 1  | 3   | 36  | 68 | 1   | 6.48935 | 0.013119 |
| Triglycerides (mg/dl)    | 0.020324   | 0.000413       | -0.014287      | 386 | 1  | 386 | 934517| 68 | 13743 | 0.02810 | 0.867374 |
| LDH (U/l)                | 0.136414   | 0.018609       | 0.004177       | 80334 | 1 | 80334 | 4236690| 68 | 62304 | 1.28939 | 0.260147 |
| Glucose (mg/dl)          | 0.144174   | 0.020786       | 0.006386       | 3657 | 1 | 3657 | 172280| 68 | 2534 | 1.44347 | 0.233747 |
| Creatinin kinase (U/l)   | 0.141092   | 0.019907       | 0.005494       | 1575259 | 1 | 1575259 | 77555400| 68 | 1140521 | 1.38118 | 0.244000 |
| Cholesterol (md/dl)      | 0.086172   | 0.007426       | -0.007171      | 6514 | 1 | 6514 | 870698 | 68 | 12804 | 0.50872 | 0.478135 |
| Calcium (mg/dl)          | 0.124599   | 0.015525       | 0.0001047      | 4   | 1  | 4   | 276 | 68 | 4   | 1.07234 | 0.304086 |
| Butyrate (μmol/l)        | 0.005104   | 0.000026       | -0.014679      | 2739 | 1 | 2739 | 105135628 | 68 | 1546112 | 0.00177 | 0.966551 |
| ALP (U/l)                | 0.056854   | 0.003232       | -0.011426      | 8341 | 1 | 8341 | 2572087 | 68 | 37825 | 0.22051 | 0.640151 |

**Note:** Urea was included as log urea.

**Table 2. Summary of characteristics of the seven studied Rockhopper Penguin colonies at Saunders Island, Falkland Islands.**

| Colony name | Penguin chicks | Nests of Cormorants | Predators (15 min) | Distance to the sea (m) | Elevation (m) | PE = mgh (joules) | Chick:adult ratio |
|-------------|----------------|---------------------|--------------------|------------------------|--------------|-------------------|------------------|
| Rookery 1   | 237            | 52                  | 9.80               | 143.14                 | 67           | 1969.8            | 2.443            |
| Rookery 2   | 132            | 36                  | 9.40               | 193.57                 | 69           | 2018.6            | 2.576            |
| Rookery 3   | 189            | 93                  | 6.66               | 229.11                 | 72           | 2116.8            | 3.023            |
| Neck 1      | 535            | 13                  | 9.57               | 100.2                  | 46           | 1352.4            | 2.004            |
| Neck 2      | 198            | 0                   | 11.85              | 70.87                  | 37           | 1087.8            | 1.532            |
| Neck 3      | 251            | 0                   | 12.85              | 37.74                  | 26           | 764.4             | 1.576            |
| Neck 4      | 334            | 285                 | 4.57               | 234.23                 | 81           | 2381.4            | 3.766            |
Differences in productivity among colonies

Productivity differed significantly among colonies (Wald = 792.08, P < 0.0001). Colonies with a higher proportion of breeding cormorants exhibited higher Rockhopper Penguin productivity (mean ± SD with cormorants = 2.82 ± 0.66 chicks/adult; without = 1.50 ± 0.28 chicks/adult; Wald = 47.76, R² = 0.524, P < 0.0001).

Variation in colony productivity was best explained by the interaction between predation pressure and the proportion of breeding cormorants at the colony. The most competitive model (AICc weight = 67.7%; Table 3) included the interaction of these two explanatory variables (proportion of cormorants, β = 1.56, SE = 0.36, 95% CI = 0.85 to 2.28; predatory pressure, β = −1.79, SE = 0.81, 95% CI = −3.37 to −0.21; predatory pressure × proportion of cormorants β = −2.97, SE = 4.04, 95% CI = −10.88 to 4.94; Fig. 3). The main effects, proportion of cormorants and predatory pressure, are well supported and working in opposite directions: Productivity increases when the proportion of cormorants increases and decreases when the proportion of predators increases. Additionally, this model shows a weak interaction between those two covariates, showing that in our study, the predatory pressure affects productivity at colonies with the lowest proportion of breeding cormorants (Fig. 3).

**DISCUSSION**

The penguin colonies that we studied differed in elevation, their distance from the sea and the proportion of breeding cormorants present (from 0% to 46% of the total nests in the colony), but these factors are in fact highly correlated. Elevation in particular was a critical determinant of the proportion of breeding cormorants in mixed colonies as cormorants tended to nest in upper colonies further from
the sea (Fig. 1). These nesting patterns confused our ability to clearly differentiate between colony positions vs. the effect of the proportion of breeding cormorants on penguin productivity at these colonies. We observed an increase in penguin productivity when the proportion of breeding cormorants increased, especially in colonies at higher elevation, and those having lower proportions of cormorants per penguin chicks (Fig. 3). We found this relationship despite the increased energy spent by an adult Rockhopper Penguin breeding at higher elevations (>3 times higher) compared to birds breeding at lower-elevation colonies. In addition, Rockhopper Penguin chicks at higher-elevation sites were younger, and in poorer nutritional condition than chicks at lower-elevation sites. The latter were closer to the coast, potentially increasing food delivery through proximity to food resources, or by reducing the energetic demand on adults feeding chicks.

Thus, while the positive relationship between the proportion of cormorants and penguin productivity might reflect a possible mechanism resulting in higher productivity at higher-elevation sites, it is more difficult to hypothesize a mechanism whereby site location itself (i.e., elevation) is positively associated with productivity. This is especially true given the energetic constraints faced by penguins nesting farther from the sea. On other hand, differences in the proportion of predators could be explained by differences in colony elevation rather than the presence of cormorants. However, given that the Striated Caracara is the primary predator on our sites and they can fly between colonies, site location and distance between colonies (~200 m maximum distance) is unlikely to affect their densities.
Fig. 3. The predicted values of productivity (chick/adult ratio) and 95% CI (shaded area), for the interaction between predation pressure (predators/Rockhopper chick) and the proportion of cormorants (cormorants/rockhopper chick).
The real conundrum in this system is that, while Rockhopper Penguin productivity increased with the proportion of breeding cormorants in the colonies and, concurrently with elevation, chick condition was reduced at these higher-elevation colonies. Higher-elevation colonies appear to be lower in quality, at least in terms of raising penguin chicks in good physical condition, but more chicks are produced per breeding adult at these higher-elevation colonies compared to colonies closer to the sea. How might this contradiction be explained?

The availability of better breeding territories (Sergio and Newton 2003) is one factor behind the tendency for some individuals in bird populations to choose to breed early relative to other individuals (Moreno 1998). This usually leads to increased productivity (Penteriani et al. 2003a) and better nutritional condition for offspring fledged earlier (Ferrer 1994). The younger age of chicks found at higher-elevation colonies in our study indicates a delay in the initiation of breeding. First-arriving adult Rockhopper Penguins select colonies closer to the coast and start to breed earlier, while adults arriving later find little remaining optimal habitat and are forced to occupy colonies at higher elevations and more distant from the sea, which in turn requires increased effort to access the nest site. The increased index to relative energy expenditure for adult penguins to commute between the sea and higher-elevation colonies can be as much as 3.11 times greater compared with our index to relative energy expenditure in lower-elevation colonies (see Table 2).

Three different mechanisms, not mutually exclusive, have been suggested to explain the crèche behavior of penguin chicks: (1) protection from predation (Pettingill 1960, Jouventin 1971), (2) reduction in the rate of heat loss (Yeates 1975, Le Maho 1977), and (3) a response to the aggressive behavior of adults toward the chicks of other parents (Seddon and van Heezik 1993, Penteriani et al. 2003b). According to the “dilution effect” (Delm 1990), larger crèche sizes should result in decreased risk of predation for each individual chick, likely because the proportion of chicks at the crèche periphery decreases quickly as the crèche gets larger. Larger crèches thus offer more protection for a greater number of chicks (Hamilton 1971). That is especially evident when predators prey on chicks from the ground, as does the Striated Caracara, probably a strategy to compensate for the high wind speeds that predominate at the Falkland Islands (V. Morandini and M. Ferrer, personal observation).

Our results suggest that crèche sizes and adult aggressiveness largely determined Rockhopper Penguin chick movements during the crèche phase. In fact, the number of steps taken by chicks increased as crèche size decreased and when adult aggressive interactions became more frequent. This indicates that Rockhopper Penguin chicks move more when they are in smaller crèches and in response to attacks from adults, with similar findings reported for Chinstrap Penguins (Pygoscelis antarctica; Penteriani et al. 2003b). Additionally, Rockhopper Penguin chicks moved significantly shorter distances when cormorants were breeding at the colony. Our results show that predatory pressure, mainly by Striated Caracaras, together with the presence of breeding cormorants can explain aggregation size of Rockhopper Penguin chicks, indicated by the smaller size of crèches when cormorants are present and when predatory pressure is lower. Our data are consistent with previous studies that indicate that the size of penguin crèches serves as protection against predation (Pettingill 1960, Jouventin 1971, Young 1994). In addition, in mixed colonies crèche sizes are smaller and penguin chicks move less than in colonies without cormorants. Indeed, Rockhopper Penguin productivity is 1.8 times higher when cormorants are present, indicating a protector role for this species. The aggressive behavior of breeding cormorants toward predators would explain why Rockhopper chicks benefit from the presence of breeding cormorants in the colonies. As cormorants start the breeding cycle slightly later
than Rockhoppers, adult cormorants are still brooding nestlings on their nests while Rockhopper chicks are already in crèches (V. Morandini and M. Ferrer, personal observation), with most of the adults foraging outside the colonies during most of the day. While brooding their nestlings, cormorants are extremely aggressive toward predators around their own nests (V. Morandini and M. Ferrer, personal observation). At higher proportions of breeding cormorants, the chance that a predator is attacked by an adult cormorant increases, especially for predators that prey from the ground, like caracaras.

The number of nesting cormorants was higher in colonies located at higher elevations as was penguin productivity (i.e., penguin chick/adult ratio). Even if penguin chicks in higher-elevation colonies were younger and in poorer body condition, the number of young per adult was higher in these colonies at the end of the crèche phase. This higher productivity in higher-elevation colonies regardless of lower chick nutritional condition appears to reflect the higher average survival rate of chicks due to the protection of breeding cormorants.

Our results support the protector species hypothesis, with higher Rockhopper Penguin productivity occurring when nesting among Imperial Cormorants (the protector species). The proportion of the colony consisting of the protector species and the abundance of predators at the colony affected overall colony productivity. Differences in age, nutritional condition, and body measurements of penguin chicks between colonies with and without the protector species clearly indicated that chicks under the protection of cormorants are in general younger and with decreased nutritional condition compared to chicks in monospecific. Despite these differences, however, a higher number of penguin chicks per adults were found in colonies "protected" by cormorants.

Mixed-species colonies are widespread among avian species, particularly seabirds (Quinn and Ueta 2008). Previous studies have shown cost/benefit trade-offs between protective and protected species (Pius 1998). In our case, an evident benefit for the cormorant would be the "dilution effect" (Delm 1990, Ainley et al. 2005); the aggressive behavior of the protective species toward predators, although increasing the number of potential prey, decreases risk to cormorant chicks through the presence of penguin chicks. Alternatively, we would expect that protected species would pay a cost when nesting near a protective host (Burger 1984, Quinn and Ueta 2008). The most common cost is predation by the protective species itself, or forced desertions and predation on eggs or offspring. In our studied colonies, however, we never observed aggression by cormorants toward penguin chicks or adults. Some authors have proposed that because of the benefits, protected species actively choose to nest near a protective species (Haemig 1999, Quinn and Ueta 2008). In most cases, protected species start breeding after the protective species (Quinn and Ueta 2008), a pattern interpreted by some authors as being support for the active choice hypothesis (Haemig 1999). In our system, cormorants start to breed a little later than Rockhopper Penguins, and consequently, there are no selection options for the breeding penguins (Pole-Evans, personal communication). More likely, our results indicate that later-breeding penguins are forced to breed in higher-elevation colonies, because early breeders occupy all the lower colonies and cormorants occupy those higher-elevation areas.

Protective nesting associations are recognized as being potentially important for conservation, particularly for preserving avian biodiversity (Haemig 2001). At the Falkland Islands, upon educational and conservation actions to protect raptors being implemented, the population of Striated Caracara increased, being now almost three times the population present during the 1960s (Reeves and Bildstein 2018). The increase is also partially explained by a greater availability of human waste and sheep carcasses that caracaras eat during winter, probably increasing their survival rate (Rexer-Huber and Bildstein 2013). Coincidentally, Imperial Cormorant populations at the Falkland Islands seem to be decreasing, owing to unrelated factors (http://www.falkland.s.net/falklands/birds/ks.htm). On the basis of our results and in the context of the decreasing population of Rockhopper Penguin at the Falkland Islands during recent years (Bingham 2002), we predict that increased abundance of predators (mainly caracaras), and decreased abundance of the protective species (cormorants), may well
contribute to further population decrease among Rockhopper Penguins at Saunders Island, Falkland Islands.

Our study revealed a paradox: High-quality adult penguins, those arriving early and occupying the lower colonies closer to the coast, produced better-nourished chicks earlier in the season. Yet they fledged half the number of chicks than did later breeders. Later breeders are forced by unavailability of optimal habitat to nest in higher-elevation colonies, and therefore expend, at least three times more energy each time they return to the colony to feed their chicks. However, later breeders find themselves nesting among cormorants who provide predator protection. In contrast, high-quality adults occupying colonies closer to sea level, with lower provisioning energetic costs, are fledging fewer offspring than low-quality ones. Return rates of juvenile penguins to breeding colonies may differ by up to 25% for lighter penguin chicks that crèche at lighter weights compared to those that crèche at heavier weights (Ainley et al. 2018). Thus, differences in return rates between early fledging and well-nourished chicks versus late fledging, poor-nourished ones are expected for Rockhopper Penguins in our study (Chapman et al. 2011, Ainley et al. 2018). These potential differences will ultimately affect recruitment of young birds into the breeding population. Based on our study, in order to compensate for the benefits accrued to late breeders in mixed colonies against breeding earlier in monospecific colonies, the offspring produced by early breeders would have to double their juvenile survival rates to recruit the same number of offspring into the breeding population. We suggest that recruitment into the breeding populations as a result of both strategies should be considered in future studies in order to fully understand the consequences of breeding cormorants for Rockhopper Penguin colonies. Regardless, we predict that with a decrease in predation pressure from caracaras, the productivity of Rockhopper Penguins will increase in monospecific colonies, consequently decreasing the benefit of breeding in mixed colonies.

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LITERATURE CITED

Aguilera, E., J. Moreno, and M. Ferrer. 1993. Blood chemistry values in three Pygoscelis penguins. Comparative Biochemistry and Physiology Part A: Physiology 105:471–473.

Ainley, D. G., et al. 2018. Post-fledging survival of Adélie penguins at multiple colonies: chicks raised on fish do well. Marine Ecology Progress Series 601:239–251.

Ainley, D. G., G. Ballard, B. J. Karl, and K. M. Dugger. 2005. Leopard seal predation rates at penguin colonies of different size. Antarctic Science 17:335–340.

Ainley, D. G., and R. J. Boekelheide. 1990. Seabirds of the Farallon Islands: ecology, structure and dynamics of an upwelling system community. Stanford University Press, Palo Alto, California, USA.

Alonso-Alvarez, C., M. Ferrer, J. Vinuela, and J. A. Amat. 2003. Plasma chemistry of chinstrap penguin Pygoscelis antarctica during fasting periods: a case of poor adaptation to food deprivation? Polar Biology 26:14–19.

Bates, D., M. Mächler, B. Bolker, and S. Walker. 2015. Fitting linear mixed-effects models using lme4. Journal of Statistical Software 67:1–48.

Baylis, A. M. M., A. C. Wolfaardt, S. Crofts, P. A. Pistorius, and N. Ratcliffe. 2013. Increasing trend in the number of southern rockhopper penguins (Eudyptes chrysocephalus) breeding at the Falkland Islands. Polar Biology 36:1007–1018.

Belopolski, L. O. 1957. Ecology of colonial seabirds of the Barents Sea. Academy of Science of the USSR, Moscow, Russia.

Bingham, M. 2002. The decline of Falkland Islands penguins in the presence of a commercial fishing industry. Revista Chilena De Historia Natural 75:805–818.

Brodie, J. F., C. E. Aslan, H. S. Rogers, K. H. Redford, J. L. Maron, J. L. Bronstein, and C. R. Groves. 2014. Secondary extinctions of biodiversity. Trends in Ecology and Evolution 29:664–672.
Brown, R. G. B. 1967. Breeding success and population growth in a colony of Herring and Lesser Black-backed Gulls Larus argentatus and L. fuscus. Ibis 109:502–515.

Burger, J. 1984. Grebes nesting in gull colonies: protective associations and early warning. American Naturalist 123:327–337.

Burnham, K. P., and D. R. Anderson. 2002. Multimodel inference: understanding AIC and BIC in model selection. Sociological Methods and Research 33:261–304.

Catry, P., M. Lecoq, and I. J. Strange. 2008. Population growth and density, diet and breeding success of striated caracaras Phalacrocorax australis on New Island, Falkland Islands. Polar Biology 31:1167–1174.

Chapman, E. W., E. E. Hofmann, D. L. Patterson, C. A. Ribic, and W. R. Fraser. 2011. Marine and terrestrial factors affecting Adélie penguin Pygoscelis adeliae chick growth and recruitment off the western Antarctic Peninsula. Marine Ecology Progress Series 436:273–289.

Cherel, Y., F. Freby, J. Gilles, and J. P. Robin. 1993. Comparative fuel metabolism in gentoo and king penguins: adaptation to brief versus prolonged fasting. Polar Biology 13:263–269.

Cherel, Y., J. P. Robin, and Y. L. Maho. 1988. Physiology and biochemistry of long-term fasting in birds. Canadian Journal of Zoology 66:159–166.

Cullen, J. M. 1960. Some adaptations in the nesting behaviour of terns. Pages 153–157 in G. Bergmann, K. O. Donner, and L. von Haartman, editors. Proceedings of the XII International Ornithological Congress. Tilgmannin Kirjapaino, Helsinki, Finland.

Delm, M. M. 1990. Vigilance for predators: detection and dilution effects. Behavioral Ecology and Sociobiology 26:337–342.

Dewasmes, G., Y. Le Maho, A. Cornet, and R. Groscolas. 1980. Resting metabolic rate and cost of locomotion in long-term fasting emperor penguins. Journal of Applied Physiology 49:888–896.

Dobado-Berrios, P. M., and M. Ferrer. 1997. Age-related changes of plasma alkaline phosphatase and inorganic phosphorus, and late ossification of the cranial roof in the Spanish imperial eagle Aquila adalberti CL. Brehm, 1861). Physiological Zoology 70:421–427.

Dyracz, A., J. Witkowski, and J. Okulewicz. 1981. Nesting of ‘timid’ waders in the vicinity of ‘bold’ ones as an antipredator adaptation. Ibis 123:542–545.

Erwin, R. M. 1979. Species interactions in a mixed colony of Common Terns Sterna hirundo and Black Skimmers Rynchops niger. Animal Behaviour 27:1054–1062.

Ferrer, M. 1990. Hematological studies in birds. Condor 92:1085–1086.

Ferrer, M. 1994. Nutritional condition of Spanish imperial eagle nestlings Aquila adalberti. Bird Study 41:120–123.

Ferrer, M., V. Morandini, L. Perry, and M. Bechard. 2017. Factors affecting plasma chemistry values of the black-browed albatross Thalassarche melanophris. Polar Biology 40:1537–1544.

Fuchs, E. 1977. Predation and anti-predator behaviour in a mixed colony of terns Sterna sp. and black-headed gulls Larus ridibundus with special reference to the sandwich tern Sterna sandvicensis. Ornis Scandinavica 8:17–32.

Gaglio, D., R. B. Sherley, T. R. Cook, P. G. Ryan, and T. Flower. 2018. The costs of kleptoparasitism: a study of mixed-species seabird breeding colonies. Behavioral Ecology 29:939–947.

Garcia-Rodriguez, T., M. Ferrer, F. Recio, and J. Castroviejo. 1987. Circadian rhythms of determined blood chemistry values in buzzards and eagle owls. Comparative Biochemistry and Physiology 88:663–669.

Götmark, F., and M. Andersson. 1980. Breeding association between common gull Larus canus and Arctic skua Stercorarius parasiticus. Ornis Scandinavica 11: 121–124.

Griffin, T. M., and R. Kram. 2000. Biomechanics: Penguin waddling is not wasteful. Nature 408:929.

Griffiths, R., M. C. Double, K. Orr, and R. J. Dawson. 1998. A DNA test to sex most birds. Molecular Ecology 7:1071–1075.

Haemig, P. D. 1999. Predation risk alters interactions among species: competition and facilitation between ants and nesting birds in a boreal forest. Ecology Letters 2:178–184.

Haemig, P. D. 2001. Symbiotic nesting of birds with formidable animals: a review with applications to biodiversity conservation. Biodiversity and Conservation 10:527–540.

Hamilton, W. D. 1971. Geometry for the selfish herd. Journal of Theoretical Biology 31:295–311.

Hoogland, J. L., and P. W. Sherman. 1976. Advantages and disadvantages of bank swallow Riparia riparia coloniality. Ecological Monographs 46:33–58.

Hylander, K., and J. Ehrlein. 2013. The mechanisms causing extinction debts. Trends in Ecology and Evolution 28:341–346.

Jouventin, P. 1971. Comportement et structure sociale chez le manchot empeureur. La Terre Et La Vie 25:510–586.

Krebs, J. R. 1974. Colonial nesting and social feeding as strategies for exploiting food resources in the Great Blue Heron Ardea herodias. Behaviour 51: 99–134.

Kuussaari, M., et al. 2009. Extinction debt: a challenge for biodiversity conservation. Trends in Ecology and Evolution 24:564–571.

Lack, D. 1968. Bird migration and natural selection. Oikos 19:1–9.
Le Maho, Y. 1977. The emperor penguin: a strategy to live and breed in the cold: Morphology, physiology, ecology, and behavior distinguish the polar emperor penguin from other penguin species, particularly from its close relative, the king penguin. American Scientist 65:680–693.

Levene, H. 1960. Robust tests for equality of variances. Pages 278–292 in I. Olkin, S. G. Ghurye, W. Hoeffding, W. G. Madow, and H. B. Mann, editors. Contributions to probability and statistics. Stanford University Press, Stanford, California, USA.

Morandini, V., and M. Ferrer. 2019. Nutritional condition determines behavioral response of nesting Black-browed albatrosses to a shy-bold continuum test. Ethology Ecology & Evolution 31:266–276.

Morandini, V., M. Ferrer, L. Perry, and M. Bechard. 2018. Blood chemistry values in nestlings of Rockhopper Penguins (Eudyptes chrysocome): the effect of sex and body condition. Polar Biology 41:2533–2541.

Moreno, J. 1998. The determination of seasonal declines in breeding success in seabirds. Etologia 6:17–31.

Murphy, R. C. 1925. The bird islands of Peru. G.P. Putnam’s Sons, New York, New York, USA.

Nelson, B. 2005. Pelicans, cormorants, and their relatives. Oxford University Press, Oxford, UK.

Nuechterlein, G. L. 1981. ‘Information parasitism’ in mixed colonies of western grebes and Forster’s terns. Animal Behaviour 29:985–989.

Penteriani, V., J. Balbontin, and M. Ferrer. 2003a. Simultaneous effects of age and territory quality on fecundity in Bonelli’s Eagle Hieraaetus fasciatus. Ibis 145:77–82.

Penteriani, V., J. Vinuela, J. Beillure, J. Bustamante, and M. Ferrer. 2003b. Causal and functional correlates of brood amalgamation in the chinstrap penguin Pygoscelis antarctica: parental decision and adult aggressiveness. Polar Biology 26:538–544.

Pettingill, J. O. S. 1960. Creche behavior and individual recognition in a colony of Rockhopper Penguins. Wilson Bulletin 72:209–221.

Pinshow, B., M. A. Fedak, and K. Schmidt-Nielsen. 1977. Terrestrial locomotion in penguins: It costs more to waddle. Science 195:592–594.

Pius, S., and P. Leberg. 1998. The protector species hypothesis: Do black skimmers find refuge from predators in gull-billed tern colonies? Ethology 104:273–284.

Poibleau, M., L. Demongin, H. J. van Noordwijk, I. J. Strange, and P. Quillfeldt. 2010. Sexual dimorphism and use of morphological measurements to sex adults, immatures and chicks of rockhopper penguins. Ardea 98:217–225.

Pöysä, H., E. Lammli, S. Pöysä, and V. M. Väänänen. 2019. Collapse of a protector species drives secondary endangerment in waterbird communities. Biological Conservation 230:75–81.

Quinn, J. L., and M. Ueta. 2008. Protective nesting associations in birds. Ibis 150:146–167.

R Core Team. 2013. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org/

Reeves, M., and K. L. Bildstein. 2018. Distribution and abundance of breeding Striated Caracaras in the Falkland Islands (Malvinas). Journal of Raptor Research 52:309–316.

Reeves, M., S. Crofts, and K. L. Bildstein. 2018. Distribution and abundance of breeding striated caracaras in the Falkland Islands (Malvinas). The Journal of Raptor Research 52:309–315.

Rexer-Huber, K., and K. L. Bildstein. 2013. Winter diet of Striated Caracara Phalcoboenus australis (Aves, Polyborinae) at a farm settlement on the Falkland Islands. Polar Biology 36:437–443.

Seddon, P. J., and Y. van Heezik. 1993. Chick creching and intraspecific aggression in the jackass penguin (Conglomerado de pichones y agresión intraspecífica en Spheniscus demersus). Journal of Field Ornithology 64:90–95.

Sergio, F., and I. Newton. 2003. Occupancy as a measure of territory quality. Journal of Animal Ecology 72:857–865.

Smith, A. J. 1975. Studies of breeding sandwich terns. British Birds 68:142–156.

Viñuela, J. 1991. Ecologia reproductiva del Milano negro (Milvus migrans) en el Parque Nacional de Doñana. Dissertation. Universidad Complutense de Madrid, Madrid, Spain.

Williams, T. D. 1995. The Penguins: Spheniscidae. Pages 143–152 in J. N. Davies, editor. Bird families of the world. Volume 2. Oxford University Press, Oxford, UK.

Woods, R. W., and A. Woods. 1997. Atlas of breeding birds of the Falkland Islands. Anthony Nelson, Oswestry, UK.

Yeates, G. W. 1975. Microclimate, climate and breeding success in Antarctic penguins. Pages 397–409 in B. Stonehouse, editor. The biology of penguins. University Park Press, London, UK.

Young, E. 1994. Skua and penguin: predator and prey. Cambridge University Press, Cambridge, UK.