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Author(s) :J. Mark Hipfner, Kyle W. Morrison and Rachel Darvill

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Peregrine Falcons Enable Two Species of Colonial Seabirds to Breed Successfully by Excluding Other Aerial Predators

J. MARK HIPFNER^{1,*}, KYLE W. MORRISON² AND RACHEL DARVILL²

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ing both direct (consumptive) and indirect (non-consumptive) effects on the population ecology of their prey (Butler et al.2003; Ydenberget al.2004). For example, Bald Eagles frequently depredate Common Murres (*Uria aalge*) on seabird colonies in the north-east Pacific, and while hunting them often cause the murres to "flush en masse" from their open-topped breeding sites. Peregrine Falcons, which usually take small seabirds up to about 0.5 kg in mass (Beebe 1960; Painet al 1990), pose little threat to seabirds as large as the northern murres (*U. a. inornata*) that breed in British Columbia and Alaska (Ainley et al. 2002; Hipfner and Greenwood 2008). By "flushing murres, eagles enable large gulls (*Larus* spp.) and corvids to take unattended eggs and chicks (Parrish 1995). Over time, the aerial predators can drive local murre colonies into decline (Parrish et al. 2001). An increasing population of Bald Eagles is also thought to underlie declines in Pelagic Cormorant (*Phalacrocorax pelagicus*) populations across western North America (Carter et al.2009; Chatwin et al.2002; Harris et al.2005).

Here, we report on the changes that took place with the development and termination of a protective nesting association involving thousands of Common Murres and hundreds of Pelagic Cormorants, but just a single pair of Peregrine Falcons. Ecological facilitation in its various forms can have dramatic effects on community structure (Stachowitz 2001), and events during our seven-year study (2003-2009) also enabled us to assess retrospectively the potential landscape-level effects of raptor dynamics on the seabird community of the region.

METHODS

Puffin Rock on Triangle Island (50°52N, 129°05W) supports the largest Common Murre (~3000 pairs) and Pelagic Cormorant (~400 pairs) colonies in British Columbia, Canada. Triangle Island also supports large Peregrine Falcon, Bald Eagle and Glaucous-winged Gull (*Larus glaucescens*) populations (Rodway et al. 1990).

We used standard protocols (Birkhead and Nettleship 1980) to monitor the timing and success of breeding in Common Murres and Pelagic Cormorants in 2003 to 2009. Detailed descriptions are available elsewhere (Hipfner and Greenwood 2008, 2009). Briefly, as

weather allowed, we observed murres (50-60 pairs) and cormorants (14-25 pairs) breeding within the borders of small cliff-face breeding plots for 2-3 h daily. Observations were made through a 20-60x spotting scope from a blind situated ~50 m from the cormorant plot, and ~70 m from the murre plot (Fig. 1). From the blind, we had an unobstructed view of breeding sites (for murres, which do not build nests) and nests (for cormorants, which do). We recorded dates of egg-laying, hatching and "edging" for all pairs that bred within the plot boundaries, and made notes of the activities of Peregrine Falcons, Bald Eagles and Glaucous-winged Gulls if they had obvious effects. The falcons' breeding season, including the period of territorial (nest) defense, overlapped the entire murre breeding season and all but the tail end of the cormorant breeding season.

Common Murres lay a single-egg clutch, and we considered an individual pair to have bred successfully if their single egg hatched and their nestling then survived at least 15 d before disappearing. Pelagic Cormorants usually lay clutches of three to six eggs, and we considered an individual pair to have bred successfully if one or more of their eggs hatched and one or more of their nestlings then survived at least 35 d before disappearing.

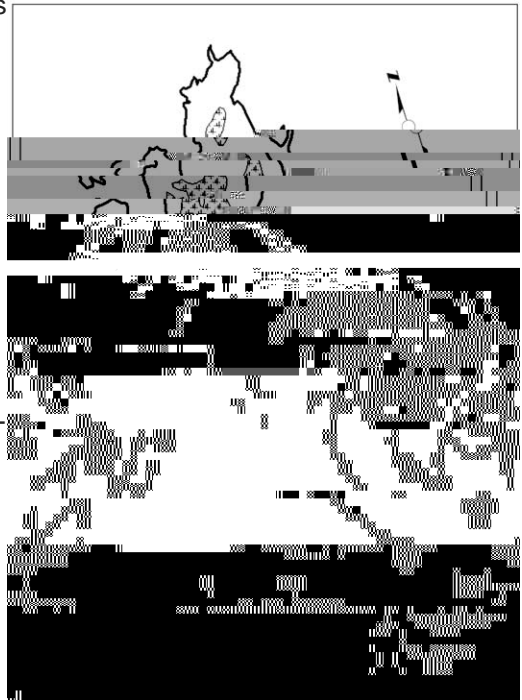


Figure 1. Map of the study site (Puffin Rock at Triangle Island) showing the extent of the Common Murre colonies, as well as the locations of the two Peregrine Falcon eyries (stars), the observation blind (square), and the Common Murre and Pelagic Cormorant plots. The dotted line indicates the approximate area that the Peregrine Falcons protect, i.e. 200 m radius around the eyrie (Cade 1960 in White et al. 2002).

RESULTS

A single pair of Peregrine Falcons bred in association with the Common Murres and Pelagic Cormorants on our monitoring plots in 2003-2006 (Fig. 1). Assuming that the falcons attack any raptor that intrudes within 200 m of their nest (Cade 1960 in White et al 2002), then the entire murre colony and much of the cormorant colony fell under air-space that the falcons protected (Fig. 1). In 2007, a single falcon remained in the vicinity of the colony through most of the summer but there was no activity at the eyrie. In 2008 and 2009, the eyrie was inactive and only in late July and early August did we see one or two falcons in the area of the colony.

When the falcon eyrie was active, we never saw Bald Eagles fly over the murre colony, depredate murres on the colony, or enable Glaucous-winged Gulls to take eggs by flushing incubating murres (Table 1). Protected from eagles, Common Murres bred successfully: between 65% and 82% of pairs reared their single chicks in these four years. Note that success was lowest in 2005 (Fig. 2).

In contrast, during the three years when the falcon eyrie was inactive, eagles did on occasion fly over the colony and depredate adult murres (Table 1). Incubating murres were forced to flush when this happened and gulls immediately flew in to take murre eggs; we saw as many as 18 eggs taken during a single episode. Only one or more immature eagle(s) were involved in these activities in 2008, but at least one adult and on single epinephelus was lowj T1.9 Ir0phe t2,4.t200yo5939P0.030phev de Muullkea sil0phe(0%Twinvo3338n Murres and te inhighy ovarible 1n the aour years.when cMst olloseucMural uears.wccauulld aftr tat c-

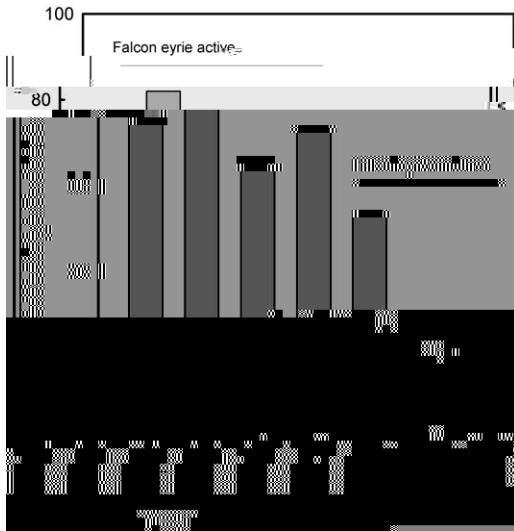


Figure 2. Percentage of monitored Common Murre pairs (n = 50-60 per year) that raised chicks to fledging age (15+ d) in each year from 2003 to 2009 at Triangle Island. Success was higher in years in which the Peregrine Falcon eyrie was active. Note that the eyrie was inactive in 2007 but a single falcon remained in the vicinity of the colony through most of the summer.

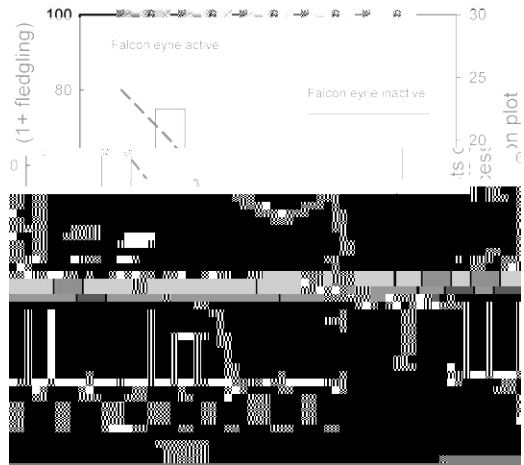


Figure 3. Percentage of monitored Pelagic Cormorant pairs that raised at least one chick to fledging age in each year from 2003 to 2009 at Triangle Island (vertical bars, left axis). Sample size is indicated by the number of nests built on the monitoring plot (dashed line, right axis). No nests were built, thus no offspring were produced - in the last two years when the Peregrine Falcon eyrie was inactive. Note that the eyrie was inactive in 2007 but a single falcon remained in the vicinity of the colony throughout most of the summer.

breeding success at Triangle Island was above average for murres (Hipfner and Greenwood 2008) and close to average for cormorants (Hipfner and Greenwood 2009) while the eyrie was active. But murres and cormorants both failed completely in two of the three years when the eyrie was inactive, and only in these years did we see Bald Eagles kill adult murres and facilitate the taking of murre eggs by Glaucous-winged Gulls after incubating murres flushed. That the breeding success of murres and cormorants was intermediate in the year when a single falcon remained in the vicinity of the inactive eyrie further suggests that falcon presence and successful breeding by seabirds were causally linked. While other studies report year-to-year variation in the benefits of nesting associations (Smith et al. 2007), rarely are the population-level effects so dramatic (Haemig 2001). Finally, the nesting association is noteworthy for its local conservation implications, in that it involved virtually the entire breeding population of Common Murres in British Columbia (Hipfner 2005).

The breeding success of three burrow-nesting seabirds, Cassin's Auklet (*Ptychoramphus aleuticus*), Rhinoceros Auklet (*Cerorhincomonocerata*) and Tufted Puffin (*Fratercula cirrhata*), was below normal values at Triangle Island in 2003 and 2005 (Hipfner et al. 2007; Hipfner et al. 2008; Wolf et al. 2009). These were years of low success for Pelagic Cormorants (2003 and 2005) and Common Murres (2005) as well, compared to the other years when the falcon eyrie was active (2004, 2006). The mean mass of offspring at nest departure also was markedly lower in murres in 2005 ($168 \text{ g} \pm 18$ (95% CI)) than in any other year (range from $210 \text{ g} \pm 11$ in 2002 to $228 \text{ g} \pm 13$ in 2004; Hipfner and Greenwood 2008).

Both the 2003 El Niño event and especially the 2005 atmospheric blocking event reduced the availability of prey to marine top predators, including seabirds (Mackas et al. 2007; Sydeman et al. 2006). However, the burrow-nesting species bred successfully in the cold-water year of 2008 (Hipfner 2009), and their success was close to long-term averages in 2009 (Triangle Island Research Station, unpublished data). Yet the murres and

cormorants failed completely in 2008 and 2009. The discrepancy suggests that the termination of the nesting association with falcons triggered a switch from bottom-up to top-down control of the breeding success of murre and cormorants.

In the period from 1989 to 2003, Common Murre breeding populations in the Scott Islands archipelago declined by about 25%, and several subcolonies comprised of up to 1,000 individuals and located up to 15 km

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