



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

Authors: Hipfner, J. Mark, Morrison, Kyle W., and Darvill, Rachel

Source: Waterbirds, 34(1) : 82-88

Published By: The Waterbird Society

URL: <https://doi.org/10.1675/063.034.0110>

---

The BioOne Digital Library (<https://bioone.org/>) provides worldwide distribution for more than 580 journals and eBooks from BioOne's community of over 150 nonprofit societies, research institutions, and university presses in the biological, ecological, and environmental sciences. The BioOne Digital Library encompasses the flagship aggregation BioOne Complete (<https://bioone.org/subscribe>), the BioOne Complete Archive (<https://bioone.org/archive>), and the BioOne eBooks program offerings ESA eBook Collection (<https://bioone.org/esa-ebooks>) and CSIRO Publishing BioSelect Collection (<https://bioone.org/csiro-ebooks>).

Your use of this PDF, the BioOne Digital Library, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at [www.bioone.org/terms-of-use](http://www.bioone.org/terms-of-use).

Usage of BioOne Digital Library content is strictly limited to personal, educational, and non-commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

---

BioOne is an innovative nonprofit that sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

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

J. MARK HIPFNER<sup>1,\*</sup>, KYLE W. MORRISON<sup>2</sup> AND RACHEL DARVILL<sup>2</sup>

<sup>1</sup>Environment Canada, Pacific Wildlife Research Centre, R.R. #1, 5421 Robertson Road, Delta, British Columbia, V4K 3N2, Canada

<sup>2</sup>Centre for Wildlife Ecology, Simon Fraser University 8888 University Drive, Burnaby British Columbia, V5A 1S6, Canada

\*Corresponding author; E-mail: mark.hipfner@ec.gc.ca

**Abstract.**—The breeding success of Common Murres (*Uria aalge*) and Pelagic Cormorants (*Phalacrocorax pelagicus*) at Triangle Island, off British Columbia, Canada, was high from 2003 to 2006; four years in which a pair of Peregrine Falcons (*Falco peregrinus*) nested in the vicinity. However, in three years when the falcon eyrie was inactive (2007 to 2009), adult murres were depredated on the colony by Bald Eagles (*Haliaeetus leucocephalus*) and murre eggs were taken by Glaucous-winged Gulls (*Larus glaucescens*) after eagles flushed incubating murres. Consequently, breeding success in both species was low in 2007, then in 2008 and 2009 no murres bred successfully and no cormorants built nests. That a single pair of falcons protected thousands of seabirds is noteworthy for its local conservation implications. Bottom-up control of seabird breeding success has been well documented, but there appears need for a better understanding of the role of top-down mechanisms as a result of both the direct (consumptive) and indirect (non-consumptive) effects of top predators. Received 13 March 2010, accepted 26 August 2010.

**Key words.**—breeding success, facilitation, nesting association, raptors, seabirds.

Waterbirds 34(1): 82-88, 2011

Interspecific interactions within ecological communities can be broadly categorized as either negative (parasitism, predation and competition) or positive (facilitation and commensalism), depending on the fitness consequences for individuals of a focal species (Bruno *et al.* 2003). However, the positive interactions receive little attention (Bertness and Callaway 1994). Protective nesting associations—in which individuals of one species nest in close proximity to individuals of another species, the latter often either an insect or a raptorial bird that provides the focal species with refuge from predators—are a common form of facilitation in birds (Lima 2009; Quinn and Ueta 2008). Nesting associations can be vital to the success of population processes for the protected species, and they can have ecosystem-wide implications (Haemig 2001).

As a group, pelagic seabirds have evolved a variety of strategies to evade predators. These include breeding on mammal-free islands, using subterranean burrows as nest sites and visiting the nest site nocturnally (Lack 1968; McNeil *et al.* 1993). In addition, individuals often take routine steps to mini-

mize the day-to-day risks associated with visiting their nest sites (Addison *et al.* 2007; Harfenist and Ydenberg 1995). Many pelagic seabirds also nest colonially, but debate continues as to whether this putative anti-predator strategy tends to increase or decrease the predation rate (Clode 1993; Varela *et al.* 2007). Yet there are few accounts of pelagic seabirds nesting in association with protective heterospecifics (Quinn and Ueta 2008).

As a group, falcons often provide species nesting in their vicinity with refuge from predators because falcons aggressively defend the areas around their own nests from other raptors (Blanco and Tella 1997; Bogliani *et al.* 1999). Peregrine Falcons (*Falco peregrinus*), which average about 1.0 kg in body mass, coexist with the larger (~5.0 kg) Bald Eagles (*Haliaeetus leucocephalus*) on many seabird colonies along the Pacific coast of North America. Despite the difference in size, falcons are capable of killing eagles that encroach on their territories (White *et al.* 2002). Populations of both raptors are recovering following declines caused by environmental contaminants (Wiemayer *et al.* 1993), and as their numbers increase they are hav-

ing both direct (consumptive) and indirect (non-consumptive) effects on the population ecology of their prey (Butler *et al.* 2003; Ydenberg *et 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; Paine *et 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 (Stachowicz 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.

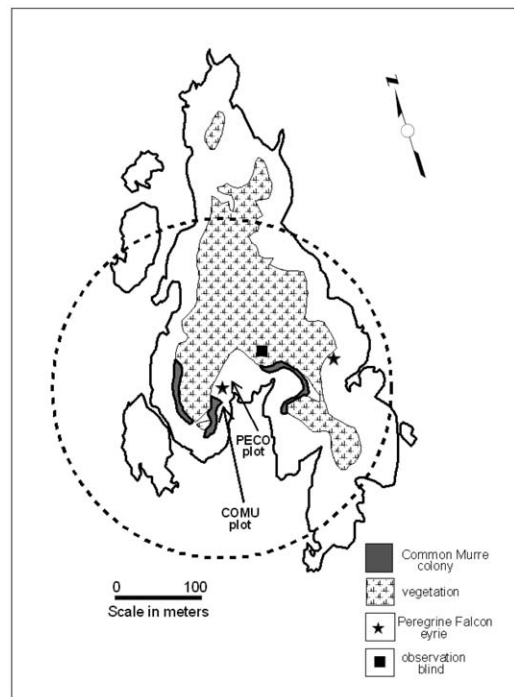
#### METHODS

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 fledging 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 airspace 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 fledged 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 one imma-

ture eagle took part in 2009. With predators active in this manner, the murres' breeding success was reduced in 2007 (54%), when a single falcon remained in the area of the colony through the season, and they suffered complete breeding failure (0%) in 2008 and 2009 when falcons were absent until late July (Fig. 2).

Breeding success in Pelagic Cormorants was highly variable in the four years when the falcon eyrie was active (0-75%), being low in 2003 (38%) and zero in 2005 (Fig. 3). Most losses in all years occurred after hatching, although we rarely knew the cause; we suspect that most mortality was a result of starvation and the eviction of young nestlings by their older and stronger siblings (Hipfner and Greenwood 2009). With the falcon eyrie inactive, the cormorants' breeding success was very low in 2007 (14%), and no nests were built on the monitoring plot in 2008 or 2009 (Fig. 3).

DISCUSSION

While nesting with aggressive heterospecifics is a common anti-predator strategy in birds (Quinn and Ueta 2008), the association we have described is noteworthy for several reasons. First, for the number of individuals involved: just one pair of Peregrine Falcons protected thousands of Common Murres and hundreds of Pelagic Cormorants nesting near the falcons' eyrie. Second, for the starkness of its consequences: compared to other colonies in the northeast Pacific,

**Table 1. Observation periods and a summary of our sightings of interactions between Common Murres, Bald Eagles and Glaucous-winged Gulls at Triangle Island in each year from 2003 to 2009.**

| Year | Observation period<br>(total d) | Number of sightings of                               |  |  |
|------|---------------------------------|--|--|--|
|      |                                 | Eagles flying<br>over the colony,<br>flushing murres | Eagles depredating<br>murres on the colony | Eagles facilitating<br>depredation of<br>murre eggs by gulls |
| 2003 | 11 May-28 August (70)           | 0  | 0  | 0  |
| 2004 | 29 April-26 August (85)         | 0  | 0  | 0  |
| 2005 | 26 April-1 August (72)          | 0  | 0  | 0  |
| 2006 | 8 May-9 August (70)             | 0  | 0  | 0  |
| 2007 | 27 May-30 August (78)           | 4  | 0  | 4  |
| 2008 | 22 May-12 August (57)           | 23   | 4  | 9  |
| 2009 | 18 May-22 July (41)             | 12   | 2  | 6  |

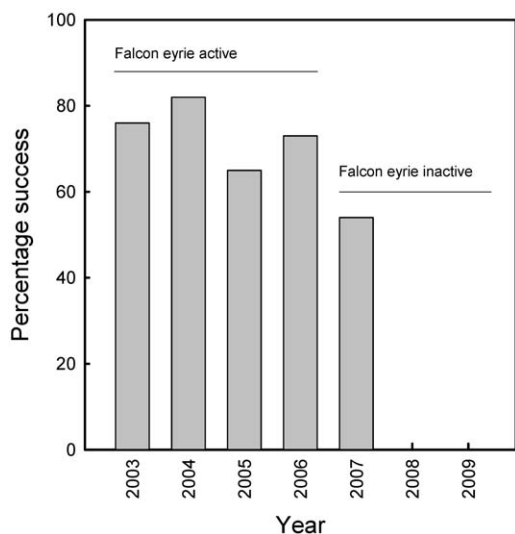


Figure 2. Percentage of monitored Common Murre pairs ( $n = 50\text{--}60$  per year) that raised chicks to fledging age (15+ d) in each year from 2003 to 2009 at Triangle Island. Success was higher in years in which the Peregrine Falcon eyrie was active. Note that the eyrie was inactive in 2007 but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

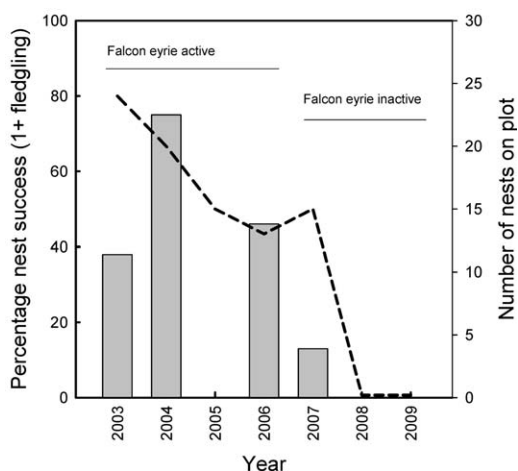


Figure 3. Percentage of monitored Pelagic Cormorant pairs that raised at least one chick to fledging age in each year from 2003 to 2009 at Triangle Island (vertical bars, left axis). Sample size is indicated by the number of nests built on the monitoring plot (dashed line, right axis). No nests were 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 (*Cerorhinca monocerata*) 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 murres 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 away were abandoned as the entire regional population aggregated to breed on Puffin Rock (Hipfner 2005). Before this shift, Common Murres suffered repeated breeding failures on and around Triangle Island: in 1978 (Vermeer *et al.* 1979), 1982, 1984 and 1989 (Rodway *et al.* 1990), and 1995 (J. Parrish unpublished data). Both Rodway and Parrish cited the taking of large numbers of eggs by gulls as an important cause of failure. Concurrently, the number of Peregrine Falcon eyries at Triangle Island increased from three in 1989 (Rodway *et al.* 1990) to five in 2001 (TIRS, unpublished data). One of the new eyries, which probably became active between 1996 and 2001, was the one located in the midst of the Common Murre colony on Puffin Rock. There is close correspondence, then, between the initial appearance of the falcon eyrie and the aggregation by murres in its immediate vicinity. Likewise, Common Murre and Pelagic Cormorant populations increased through the 1980s at Tatoosh Island, Washington State, in step with Peregrine Falcons (Paine *et al.* 1990). We suggest that these large, cliff-nesting seabirds may be drawn to nest in association with Peregrine Falcons, potentially driving medium-scale patterns in their distribution and (apparent) abundance. Like other species (Boulinier and Danchin 1997), the seabirds may settle to breed among reproductively successful conspecifics, and success may be higher in the vicinity of nesting falcons.

In 2009, several groups of murres split from the aggregation. The largest of these groups (~200 pairs) settled in atypical habitat—on a steep, grass-covered slope in the midst of an active Tufted Puffin colony—just above a Peregrine Falcon eyrie on the east

side of Puffin Rock (Fig. 1). The murres displaced many puffins in the process. Debate continues as to why colonial seabirds form satellite colonies (Jackson *et al.* 2005). For Common Murres at Tatoosh Island, it appeared to be a response to environmental factors that affect food availability (Zador *et al.* 2009). But at Triangle Island, it appeared to be aimed at reducing predation risk, as Kildaw *et al.* (2008) suggested for Black-legged Kittiwakes (*Rissa tridactyla*) in Alaska.

Our study provides further evidence of the powerful nonconsumptive effects that top predators can have on ecosystem functions (Peckarsky *et al.* 2008). On other seabird islands, introduced cats (*Felis domesticus*) are known to keep seabirds safe from rats (*Rattus* spp.), which are smaller but ultimately more dangerous predators (Courchamp *et al.* 1999). In contrast, we have described a natural system in which a smaller predator (Peregrine Falcon) kept seabirds safe from a larger and more dangerous predator (Bald Eagle). Our study also contributes to the debate about what factors limit seabird breeding success, a debate that has focused heavily on bottom-up (Kitaysky *et al.* 2007) rather than top-down (Oro and Furness 2002) mechanisms.

From a conservation perspective, we note that Common Murres currently breed at only two sites in British Columbia, and the colony at Triangle Island is an order of magnitude larger than the one at the Kerouard Islands in Haida Gwaii (Hipfner 2005). A handful of Thick-billed Murres (*Uria lomvia*), the only breeding aggregation in Canada's Pacific, also breeds at Triangle Island (Vallée and Cannings 1983). Murres are the most frequent victims of bycatch in net fisheries operating along the British Columbia coast (Smith and Morgan 2005), and the decline in the murre population in the Scott Islands has raised concerns about fisheries impacts (Hipfner 2005; Hamel *et al.* 2009). However, managers need to be mindful that local declines and the redistribution of colonies on the landscape may be a result of behaviors that prey employ to minimize predation risk (Kenyon *et al.* 2007). Nonetheless, maintaining locally healthy breeding popu-

lations of both murre species over the long term will probably depend on the consistent production of offspring from Triangle Island, and this may be possible only in the presence of Peregrine Falcons.

## ACKNOWLEDGMENTS

We thank the many field workers helped us collect these data; the Canadian Coast Guard and West Coast Helicopters for transporting our field crews to and from Triangle Island; M. Court, J. Higham and C. Smith for logistical support; and M. Lemon for preparing Fig. 1. Financial support was provided mainly by Environment Canada and Simon Fraser University. The research was carried out under annual Migratory Bird permits from Environment Canada (permit number 59-03-0362 in 2003), and a permit from BC Parks to work on the Anne Vallee Ecological Reserve (ST9910186). Finally, we thank J. Parrish for allowing us to cite her unpublished report, R. Butler and A. Gaston for reviews of the draft manuscript, and D. Duffy plus an anonymous reviewer for feedback during the review process.

## LITERATURE CITED

- Addison, B., R. C. Ydenberg and B. D. Smith. 2007. Tufted Puffins (*Fratercula cirrhata*) respond to predation danger during colony approach flights. *Auk* 124: 63-70.
- Ainley, D. G., D. N. Nettleship, H. R. Carter and A. E. Storey. 2002. Common Murre (*Uria aalge*). In *The birds of North America*, No. 666 (A. Poole and F. Gill, Eds.). The Academy of Natural Sciences, Philadelphia, and The American Ornithologists' Union, Washington, D.C.
- Beebe, F. L. 1960. The marine Peregrine Falcons of the northwest Pacific coast. *Condor* 62: 145-189.
- Bertness, M. D. and R. Callaway. 1994. Positive interactions in communities. *Trends in Ecology and Evolution* 9: 191-193.
- Birkhead, T. R. and D. N. Nettleship. 1980. Census methods for murre, *Uria* species: A unified approach. *Canadian Wildlife Service Occasional Paper* 43.
- Blanco, G. and J. L. Tella. 1997. Protective association and breeding advantages of choughs nesting in lesser kestrel colonies. *Animal Behaviour* 54: 335-342.
- Bogliani, G., F. Sergio and G. Tavecchia. 1999. Woodpeckers nesting in association with hobby falcons: advantages and choice rules. *Animal Behaviour* 57: 125-131.
- Boulinier, T. and E. Danchin. 1997. The use of conspecific reproductive success for breeding patch selection in territorial migratory species. *Evolutionary Ecology* 11: 505-517.
- Bruno, J. F., J. J. Stachowicz and M. D. Bertness. 2003. Inclusion of facilitation into ecological theory. *Trends in Ecology and Evolution* 18: 119-125.
- Butler, R. W., R. C. Ydenberg and D. B. Lank. 2003. Waders on a changing predator landscape. *Wader Study Group Bulletin* 100: 130-133.
- Carter, H. R., P. N. Hebert and P. V. Clarkson. 2009. Decline of Pelagic Cormorants in Barkley Sound, British Columbia. *Wildlife Afield* 4: 3-32.
- Chatwin, T. A., M. H. Mather and T. D. Giesbrecht. 2002. Changes in Pelagic and Double crested cormorant nesting populations in the Strait of Georgia, British Columbia. *Northwestern Naturalist* 83: 109-117.
- Clode, D. 1993. Colonially breeding seabirds - predators or prey? *Trends in Ecology and Evolution* 8: 336-338.
- Courchamp, F., M. Langlais and G. Sugihara. 1999. Cats protecting birds: Modelling the mesopredator release effect. *Journal of Animal Ecology* 68: 282-292.
- Haemig, P. D. 2001. Symbiotic nesting of birds with formidable animals: A review with applications to biodiversity conservation. *Biodiversity and Conservation* 10: 527-540.
- Hamel, N. J., A. E. Burger, K. Charleton, P. Davidson, S. Lee, D. F. Bertram and J. K. Parrish. 2009. Bycatch and beached birds: Assessing mortality impacts in coastal net fisheries using marine bird strandings. *Marine Ornithology* 37: 41-60.
- Harfenist, A. and R. C. Ydenberg. 1995. Parental provisioning and predation risk in Rhinoceros Auklets (*Cerorhinca monocerata*)—effects on nestling growth and fledging. *Behavioral Ecology* 6: 82-86.
- Harris, M. L., L. K. Wilson and J. E. Elliott. 2005. An assessment of PCBs and OC pesticides in eggs of Doublecrested (*Phalacrocorax auritus*) and Pelagic (*Phalacrocorax pelagicus*) Cormorants from the west coast of Canada, 1970-2002. *Ecotoxicology* 14: 607-625.
- Hipfner, J. M. 2005. Population status of the Common Murre *Uria aalge* in British Columbia, Canada. *Marine Ornithology* 33: 67-69.
- Hipfner, J. M. 2009. Euphausiids in the diet of a North Pacific seabird: Annual and seasonal variation and the role of ocean climate. *Marine Ecology Progress Series* 390: 277-289.
- Hipfner, J. M., M. R. Charette and G. S. Blackburn. 2007. Subcolony variation in breeding success in the Tufted Puffin (*Fratercula cirrhata*): Association with foraging ecology and implications. *Auk* 124: 1149-1157.
- Hipfner, J. M. and J. L. Greenwood. 2008. Breeding biology of the Common Murre at Triangle Island, British Columbia, 2002-2007. *Northwestern Naturalist* 89: 76-84.
- Hipfner, J. M. and J. L. Greenwood. 2009. Timing and success of breeding in Pelagic Cormorants at Triangle Island, British Columbia, 2003-2008. *Northwestern Naturalist* 90: 238-243.
- Hipfner, J. M., L. A. McFarlane-Tranquilla and B. Addison. 2008. Do marine birds use environmental cues to optimize egg production? An experimental test based on relaying propensity. *Journal of Avian Biology* 39: 611-618.
- Jackson, A. L., S. Bearhop and D. R. Thompson. 2005. Shape can influence the rate of colony fragmentation in ground nesting seabirds. *Oikos* 111: 473-478.
- Kenyon, J. K., B. D. Smith and R. W. Butler. 2007. Can redistribution of breeding colonies on a landscape mitigate changing predation danger? *Journal of Avian Biology* 38: 541-551.
- Kildaw, D., D. B. Irons and C. L. Buck. 2008. Habitat quality and metapopulation dynamics of Black-Legged Kittiwakes *Rissa tridactyla*. *Marine Ornithology* 36: 35-45.
- Kitaysky, A. S., J. F. Piatt and J. C. Wingfield. 2007. Stress hormones link food availability and population pro-

- cesses in seabirds. *Marine Ecology Progress Series* 352: 245-258.
- Lack, D. 1968. *Ecological adaptations for breeding in birds*. Methuen, London, UK.
- Lima, S. L. 2009. Predators and the breeding bird: behavioral and reproductive flexibility under the risk of predation. *Biological Reviews* 84: 485-513.
- McNeil, R., P. Drapeau and R. Pierotti. 1993. Nocturnality in colonial waterbirds: occurrence, special adaptations and suspected benefits. Pages 187-246 in *Current Ornithology* (D. M. Power, Ed.). Plenum Press, New York, New York.
- Mackas, D. L., S. Batten and M. Trudel. 2007. Effects on zooplankton of a warmer ocean: Recent evidence from the Northeast Pacific. *Progress in Oceanography* 75: 223-252.
- Oro, D. and R. W. Furness. 2002. Influences of food availability and predation on survival of kittiwakes. *Ecology* 83: 2516-2528.
- Paine, R. T., J. T. Wootton and P. D. Boersma. 1990. Direct and indirect effects of Peregrine Falcon predation on seabird abundance. *Auk* 107: 1-9.
- Parrish, J. K. 1995. Influence of group size and habitat type on reproductive success in Common Murres (*Uria aalge*). *Auk* 112: 390-401.
- Parrish, J. K., M. Marvier and R. T. Paine. 2001. Direct and indirect effects: Interactions between Bald Eagles and Common Murres. *Ecological Applications* 11: 1858-1869.
- Peckarsky, B. L., P. A. Abrams, D. I. Bolnick, L. M. Dill, J. H. Grabowski, B. Luttbeg, J. L. Orrock, S. D. Peacor, E. L. Preisser, O. J. Schmitz and G. C. Trussell. 2008. Revisiting the classics: Considering nonconsumptive effects in textbook examples of predator-prey interactions. *Ecology* 89: 2416-2425.
- Quinn, J. L. and M. Ueta. 2008. Protective nesting associations in birds. *Ibis* 150 (Suppl. 1): 146-167.
- Rodway, M. S., M. J. F. Lemon and K. R. Summers. 1990. *British Columbia Seabird Colony Inventory: Scott Islands*. Canadian Wildlife Service Technical Report Series 40. Environment Canada, Delta, British Columbia.
- Smith, P. A., H. G. Gilchrist, J. N. M. Smith and E. Nol. 2007. Annual variation in the benefits of a nesting association between Red Phalaropes (*Phalaropus fulicarius*) and Sabine's Gulls (*Xema sabini*). *Auk* 124: 276-290.
- Smith, J. L. and K. H. Morgan. 2005. An assessment of seabird bycatch in longline and net fisheries in British Columbia. Canadian Wildlife Service Technical Report Series 401. Environment Canada, Delta, British Columbia.
- Stachowicz, J. J. 2001. Mutualism, facilitation, and the structure of ecological communities. *BioScience* 51: 235-246.
- Sydeman, W. J., R. W. Bradley, P. Warzybok, C. L. Abraham, J. Jahncke, K. D. Hyrenbach, V. Kousky, J. M. Hipfner and M. D. Ohman. 2006. Planktivorous auklet *Ptychoramphus aleuticus* responses to ocean climate, 2005: Unusual atmospheric blocking? *Geophysical Research Letters* 33.
- Vallée, A. J. and R. J. Cannings. 1983. Nesting of the Thick-billed Murre *Uria lomvia*, in British Columbia, Canada. *Canadian Field-Naturalist* 97: 450-451.
- Varela, S. A. M., E. Danchin and R. H. Wagner. 2007. Does predation select for or against avian coloniality? A comparative analysis. *Journal of Evolutionary Biology* 20: 1490-1503.
- Vermeer, K., L. Cullen and M. Porter. 1979. A provisional explanation of the reproductive failure of Tufted Puffins *Lunda cirrhata* on Triangle Island, British Columbia. *Ibis* 121: 348-354.
- White, C. M., N. J. Clum, T. J. Cade and W. G. Hunt. 2002. Peregrine Falcon (*Falco peregrinus*). In *The birds of North America*, No. 660 (A. Poole and F. Gill, Eds.). The Academy of Natural Sciences, Philadelphia, and The American Ornithologists' Union, Washington, D.C.
- Wiemayer, S. N., C. M. Burick and C. J. Stafford. 1993. Environmental contaminants in Bald Eagle eggs (1980-1984) and further interpretations of relationships to productivity and shell thickness. *Archives of Environmental Contaminants and Toxicology* 13: 529-549.
- Wolf, S. G., W. J. Sydeman, J. M. Hipfner, C. L. Abraham, B. R. Tershy and D. A. Croll. 2009. Range-wide reproductive consequences of ocean climate variability for the seabird Cassin's Auklet. *Ecology* 90: 742-753.
- Ydenberg, R. C., R. W. Butler, D. B. Lank, B. D. Smith and J. Ireland. 2004. Western sandpipers have altered migration tactics as peregrine falcon populations have recovered. *Proceedings of the Royal Society of London Series B-Biological Sciences* 271: 1263-1269.
- Zador, S. G., J. K. Parrish and A. E. Punt. 2009. Factors influencing subcolony colonization and persistence in a colonial seabird, the Common Murre *Uria aalge*. *Marine Ecology Progress Series* 376: 283-293.