

Foraging space as a limited resource: inter- and intra-specific competition among sympatric pursuit-diving seabirds

R.A. Ronconi and A.E. Burger

Abstract: Competition is thought to play a fundamental role in structuring avian communities, yet this has been difficult to quantify and demonstrate in marine ecosystems. We tested for fine-scale competition over foraging space between sympatric pursuit-diving seabirds, Marbled Murrelet (*Brachyramphus marmoratus* (J.F. Gmelin, 1789)) and Common Murre (*Uria aalge* (Pontoppidan, 1763)). We simultaneously assessed the effects of inter- and intra-specific competition among these predators, predicting that the larger Common Murres would out-compete the smaller Marbled Murrelets for foraging space. A theodolite was used to map the fine-scale (± 2 m) distributions of birds on the water; distance from shore measurements and nearest-neighbour spatial statistics quantified the spatial overlap and segregation between species. Species distributions differed with respect to distance from shore, but overlapped extensively within 1200 m of the shoreline. Nearest-neighbour statistics, assessed with randomization tests, showed Marbled Murrelets foraging farther from Common Murres (mean distances 294 m) than from other Marbled Murrelets (95 m), but groups of Common Murres foraged with similar spacing among conspecifics (266 m) and competitors (186 m). These results suggest avoidance of Common Murres by Marbled Murrelets (interspecific competition) but intraspecific competition among Common Murres. Avoidance behaviour may minimize the impacts of aggression or competition, but by avoiding Common Murres, the Marbled Murrelets may also be reducing their foraging opportunities.

Résumé : On croit que la compétition joue un rôle fondamental dans la structuration des communautés d'oiseaux, bien qu'il soit difficile de le mesurer et le démontrer dans les écosystèmes marins. Nous avons vérifié à échelle fine l'existence de compétition pour l'espace de recherche de nourriture chez des oiseaux de mer sympatriques qui font de la plongée de poursuite, le guillemot marbré (*Brachyramphus marmoratus* (Gmelin, 1789)) et le guillemot marmette (*Uria aalge* (Pontoppidan, 1763)). Nous avons mesuré simultanément les effets de la compétition inter- et intra-spécifique entre ces prédateurs et avons prédit que l'espèce la plus grande, le guillemot marmette, gagnerait la compétition pour l'espace de recherche de nourriture contre le guillemot marbré plus petit. Nous avons cartographié à l'aide d'un théodolite les répartitions à échelle fine (± 2 m) des oiseaux sur l'eau; les distances de la rive et des méthodes statistiques basées sur le plus proche voisin ont permis de déterminer le chevauchement spatial et la ségrégation entre les espèces. Les répartitions des espèces varient en fonction de distance de la rive et se chevauchent considérablement sur les premiers 1200 m à partir de la ligne du rivage. Les statistiques basées sur le plus proche voisin, évaluées par des tests de randomisation, montrent les guillemots marbrés s'alimentant plus loin des guillemots marmettes (distance moyenne de 294 m) que des autres guillemots marbrés (95 m); cependant, les guillemots marmettes recherchent leur nourriture en maintenant un espacement semblable avec les autres guillemots marmettes (266 m) et avec leurs compétiteurs (186 m). Ces résultats indiquent que les guillemots marbrés évitent les guillemots marmettes (compétition interspécifique), mais qu'il existe une compétition intraspécifique entre les guillemots marmettes. Ce comportement d'évitement peut réduire les impacts de l'agression et de la compétition, mais, en évitant les guillemots marmettes, les guillemots marbrés réduisent peut-être aussi leurs occasions de se nourrir.

[Traduit par la Rédaction]

Introduction

Competition is thought to play a fundamental role in structuring avian communities (MacArthur 1958; Cody 1974; Schoener 1982; Lovette and Hochachka 2006). Nevertheless, mechanisms for competition remain unknown in many ecosystems, particularly in the marine environment where inter-

actions between birds and their prey are difficult to study. The principle of competitive exclusion suggests that competitors may not coexist without some differentiation of their resource use (Hardin 1960; Armstrong and McGehee 1980). Yet, inter- and intra-specific flocking behaviour is widespread among foraging seabirds preying on food patches.

Group foraging may increase foraging efficiency and allow

Received 9 June 2010. Accepted 25 January 2011. Published at www.nrcresearchpress.com/cjz on 12 April 2011.

R.A. Ronconi* and **A.E. Burger**. Department of Biology, University of Victoria, P.O. Box 3020, Station CSC, Victoria, BC V8W 3N5, Canada.

Corresponding author: R.A. Ronconi (e-mail: rronconi@dal.ca).

***Present address:** Department of Biology, Dalhousie University, 1355 Oxford Street, Halifax, NS B3H 4J1, Canada.

seabirds to effectively exploit spatially and temporally patchy prey in the marine environment (Davoren 2000; Grünbaum and Veit 2003; Speckman et al. 2003). By cueing in on other foraging seabirds, including conspecifics and other species, individuals can readily find and exploit schools of fish that may be near the sea surface for a brief period of time (Harrison et al. 1991; Haney et al. 1992; Camphuysen and Webb 1999; Silverman et al. 2004). Seabirds may also identify foraging areas from information transfer by seabirds near colonies or arriving at colonies from foraging areas (Wittenberger and Hunt 1985; Burger 1997; Barta and Giraldeau 2001). Thus, many seabirds appear to be adapted to group foraging behaviours to exploit prey in marine environments.

Group foraging is common among conspecific seabirds but is also frequently observed in mixed-species groups. Mixed-species flocking behaviour may occur in stages whereby certain species initiate flocks, others join in to benefit, and some species may even disperse flocks (Chilton and Sealy 1987; Harrison et al. 1991; Camphuysen and Webb 1999; Ostrand 1999; Silverman and Veit 2001). Presumably flocking seabirds are exploiting similar prey items. Thus, while prey are generally shared in mixed-species flocks, some species likely partition resources in such a way as to allow coexistence or they must compete and exclude others from the resources.

Competition for resources may take several forms including exploitation, interference, and pre-emptive competition (Gotelli 2001). Exploitation competition involves the direct depletion of a shared resource, though this has rarely been reported with seabirds because prey depletion is not easily measured (Birt et al. 1987). Interference competition, whereby groups of birds may reduce the exploitation efficiency of other birds, is much more common among seabirds where large flocks or large species may exclude or inhibit other seabirds from prey patches (Safina 1990; Shealer and Burger 1993; Ballance et al. 1997; Maniscalco et al. 2001; Henkel 2009). Alternatively, birds may compete for space as a limiting resource (pre-emptive competition; Gotelli 2001). Unlike exploitation and interference competition that directly inhibit the capture of food, in pre-emptive competition the resource (space) is renewable and becomes available again once the competitor leaves. Though seabirds regularly compete for nesting space at breeding colonies, competition for foraging space has not been demonstrated.

The coexistence and similar prey habits of many alcids (family Alcidae) present an interesting framework in which to test theories of interspecific competition or fine-scale niche partitioning among seabirds (Haney and Schauer 1994). Larger seabirds may exclude smaller birds when foraging for shared prey types (Piatt 1990; Maniscalco et al. 2001; Henkel 2009). Marbled Murrelets (*Brachyramphus marmoratus* (J.F. Gmelin, 1789); henceforth murrelets) and Common Murres (*Uria aalge* (Pontoppidan, 1763); henceforth murres) are two species of pursuit-diving alcids that often coexist in the coastal waters of western North America. The two alcids show considerable overlap in the diets, with both species favouring small schooling fish, as indicated by prey analysis (Carter 1984; Vermeer et al. 1987; Hay et al. 1992; Burkett 1995; Gaston and Jones 1998; Lance and Thompson 2005) and stable isotopes (Hobson 1990; Hobson et al. 1994). Within our study area, they show a high degree of overlap in meso-scale habitat use (Burger et al. 2008; Ron-

coni 2008). Mechanisms facilitating their coexistence remain unexplained. One recent study found no evidence of competition between these species at meso-scales (tens to hundreds of kilometres) in an area where both species had low mean densities (Henkel 2009). The potential for interspecific competition between murres and murrelets has never been tested at fine scales (<1 km), where effects of competition are most likely, or in areas where both species occur in high densities (mean densities of both species in our study area were 3–16 times higher than in Henkel's study (Burger et al. 2008; Ronconi and Burger 2009)). Such competition may have conservation implications for threatened murrelets in areas where murrelet and murre populations overlap (Burger et al. 2008).

We mapped the fine-scale (tens to hundreds of metres) distributions of groups of foraging murres and murrelets to test for inter- and intra-specific competition for foraging space within 4 km of shore, where their habitat preferences most strongly overlap. Distance from shore, as a proxy for water depth, was compared to examine fine-scale habitat partitioning. Nearest-neighbour analysis and randomization tests were used to test attraction or avoidance behaviour between these species. We hypothesized that (i) larger bodied murres, with deeper diving abilities, would more frequently occupy deeper waters, (ii) Marbled Murrelets, because of their smaller size, would exhibit interspecific competition demonstrated through avoidance of murres (Piatt 1990; Maniscalco et al. 2001), and (iii) the strength of competitive effects would increase seasonally as murre abundance increases towards the end of the summer (Burger et al. 2008). Common murres may also exhibit intraspecific competition (Falk et al. 2001; Davoren and Montevecchi 2003), which we tested by examining the relative spacing between murre groups vs. spacing between murre and murrelet groups—we predicted that the mean spacing between neighbouring murre groups would be consistent among seasons and larger than the spacing between murre and murrelet groups.

Materials and methods

Study site

The study took place along the West Coast Trail (WCT) unit of Pacific Rim National Park Reserve on southwest Vancouver Island, British Columbia, Canada, between Cape Beale (48°47'N, 125°14'W) and Port San Juan (48°32'N, 124°29'W). Both murres and murrelets are common in summer in these nearshore waters (Burger et al. 2008; Ronconi and Burger 2009). The murrelets nest in adjacent old-growth forest on Vancouver Island. Murres nest at Tatoosh Island, Washington, within 25 km of the study area, but not within the study area; breeders do forage within the study area, but their numbers increase there after their breeding season ends in late July (Burger et al. 2008). Along this 70 km stretch of coast, observations were made at seven locations (Ronconi and Burger 2008). In 2004, sites were located at Pachena and Carmanah light stations. In 2005, we resurveyed from both light stations and added five additional survey sites accessed by hiking along the trail. At each of the five additional sites, surveys were conducted from two vantage points; however, these data were pooled for each site owing to limited sample sizes and proximity of sites (typically

<500 m apart). Surveys took place between 14 May and 9 August in each year.

Fine-scale mapping of seabird distributions

A digital theodolite (Nikon Total Station Model NPL-332 Pulse Laser) was used to map fine-scale distributions of seabirds on the water (Ronconi and St. Clair 2002; Wong et al. 2008). This technique measures angles that are used to calculate distances and plot locations with high precision—it has an accuracy within 1.7 m up to 2 km from shore (Denardo et al. 2001). We used the theodolite's scope (26× optical) to locate birds on the water, line up the bird in the cross hairs of the eyepiece, and measure angles to the birds. When positioned on a cliff top, the instrument measures vertical angles down (90° from the horizontal plane) and horizontal angles across (360° relative to north) to each object. Using these two angles and the height of the observer above sea level (a.s.l.), we calculated northings and eastings of the birds relative to the observer using basic trigonometric functions (Ronconi and St. Clair 2002). These relative northing and eastings were then converted to true geographical positions (UTM, zone 10, NAD83) based on the GPS position of the observer. To account for changing tide heights, observer height, measured by the theodolite, was recorded prior to each round of mapping or over a complete tidal sequence and used in conjunction with local tide tables to correct for tide height. At Carmanah and Pachena, the theodolite was used from the top of the lighthouse tower (~45 m a.s.l.), whereas the other sites were mapped from cliff tops (~20 to 25 m a.s.l.).

Seabird distributions were mapped systematically by searching for birds within the theodolite field of view in non-overlapping vertical sweeps (horizon to shoreline). Each scan consisted of a series of sweeps moving to the left or right, the direction of which was determined by the direction of drift by birds on the surface: scans were made against the current drift to avoid double-counting birds. During scans, one observer recorded the position of bird groups (individuals within ~3 m of each other) using the theodolite's built-in data storage and called out the species and group size to a second data recorder. Groups of birds were mapped rather than individual birds because of the slow speed of data recording by the instrument, and because individuals in groups were thought to be closer to each other than the potential instrument precision. Each complete scan of the entire study area was a replicate (Fig. 1) for analysis. Each replicate scan was completed in approximately 20 min to 1 h depending on the size of the study site and number of birds. Although birds may have moved during this time, this should make little difference in the analysis because we were primarily interested in nearest neighbours (below), which take only a few seconds to map. Samples were spread out seasonally as much as possible (see Table 1). All mapping was conducted under good visibility and low sea-state conditions (Beaufort sea-state typically ≤2, always ≤3). Shorelines were also mapped using the theodolite (Wong et al. 2008).

All birds were mapped up to as far as they could be detected (maximum ~4 km). However, the detectability of animals invariably declines with distance from the observer with any survey method (Buckland et al. 2001) and detectability may vary among species (Ronconi and Burger 2009). Ronconi (2008) used distance-sampling methodology for

point transects (Buckland et al. 2001) to model the detectability of seabirds as a function of distance from the theodolite. Modeling both off-shore and along-shore detectability provided boundaries for nearest-neighbour analyses, which require that both species be equally detectable. Based on detectability of Marbled Murrelets (the smaller species), boundaries were set at 1200 m from the theodolite station for surveys at Carmanah and Pachena, and at 1000 m for surveys at other sites (Ronconi 2008). Nearest-neighbour analysis was conducted on groups within these boundaries.

Calculations of spatial statistics

Seabird locations were mapped in a geographical information system (ArcGIS version 9.0; ESRI (Environmental Systems Research Institute, Inc.), Redlands, California, USA) and spatial analysis tools (Beyer 2004) were used to calculate spatial statistics. First, the distance of each group to the nearest shore was calculated for descriptive analyses of seabird locations relative to the coast. Second, we calculated nearest-neighbour distances (Perry et al. 2002; O'Sullivan and Unwin 2003) between the following contrast groups for each replicate scan: murrelet to murrelet (i.e., distance of each murrelet group to nearest murrelet group; MM–MM), murrelet to nearest murre (MM–CM), murre to nearest murre (CM–CM), and murre to nearest murrelet (CM–MM). Nearest-neighbour distances were averaged for each replicate scan, thus creating an index of spatial distribution and the unit of statistical analysis (below). The contrast groups may be interpreted so that MM–MM and CM–CM indices represent normal distances at which groups are distributed with respect to their own species, whereas MM–CM and CM–MM distances indicate how one species distributes itself with respect to the other species. We compared distances among the contrast groups to test for the null hypothesis of no interspecific avoidance behaviour (e.g., MM–MM = MM–CM) or the alternate hypothesis of avoidance (MM–MM < MM–CM if murrelets were avoiding murre). Note that nearest-neighbour statistics may be subject to edge effects owing to data truncation (i.e., the 1200 and 1000 m boundaries imposed on the study area) when the nearest neighbour of a group of birds is farther away than the edge of the study area. However, we felt that this bias was less important than a bias introduced by missed birds owing to poor detectability outside of the truncation boundary. Moreover, because most birds occurred within 1200 m of shore (Fig. 2), mean nearest-neighbour values calculated from within the study area would mask the bias of edge effects. The edge effect may be more important for scans with few birds present, but measures were taken to control for this (see Statistical analysis).

Statistical analysis

We used weighted least-squares ANOVA (SPSS version 15.0; SPSS Inc., Chicago, Illinois, USA) to tests for differences among nearest-neighbour contrast groups (MM–MM, CM–CM, MM–CM, CM–MM) and to test for effects of spatial (site) and temporal (year and month) factors influencing nearest-neighbour distances for each of the four nearest-neighbour contrast groups separately. Tukey's honestly significant difference (HSD) post hoc analysis was used to test for differences among groups for factors with >2 variables (i.e., month and site). Cases were weighted because

Fig. 1. Distributions of Marbled Murrelets (*Brachyramphus marmoratus*) and Common Murres (*Uria aalge*) mapped by theodolite at Carnah Bay, southwest Vancouver Island, in 2004. Each map shows an example of a single scan (birds mapped in a single series of sweeps) representative of seabird distributions in each of three time periods. The shoreline was also mapped at high tide using the theodolite. The 1200 m radius is the limit of reliable detection for both species and the cut-off distance for nearest-neighbour analysis (for details see the Materials and methods).

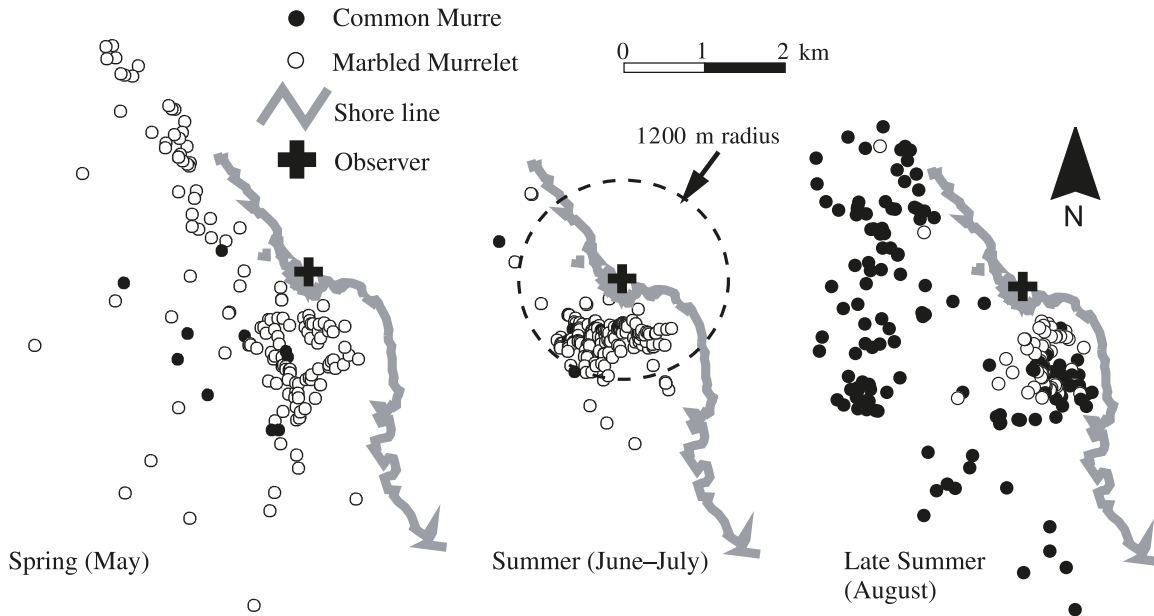


Table 1. Summary statistics of the numbers of Marbled Murrelets (MM; *Brachyramphus marmoratus*) and Common Murres (CM; *Uria aalge*) recorded by theodolite mapping along the West Coast Trail, Southwest Vancouver Island.

	<i>n</i>	All data			Observations within 1200 m from shore		
		MM	CM	MM:CM ratio	MM	CM	MM:CM ratio
May	23	4559	462	9.9	4211	334	12.6
June	35	4518	368	12.3	4344	259	16.8
July	29	2653	2808	0.9	2493	1309	1.9
August	8	524	1048	0.5	496	706	0.7
2004 (all months)	45	9362	4189	2.2	8783	2268	3.9
2005 (all months)	50	2892	497	5.8	2761	340	8.1

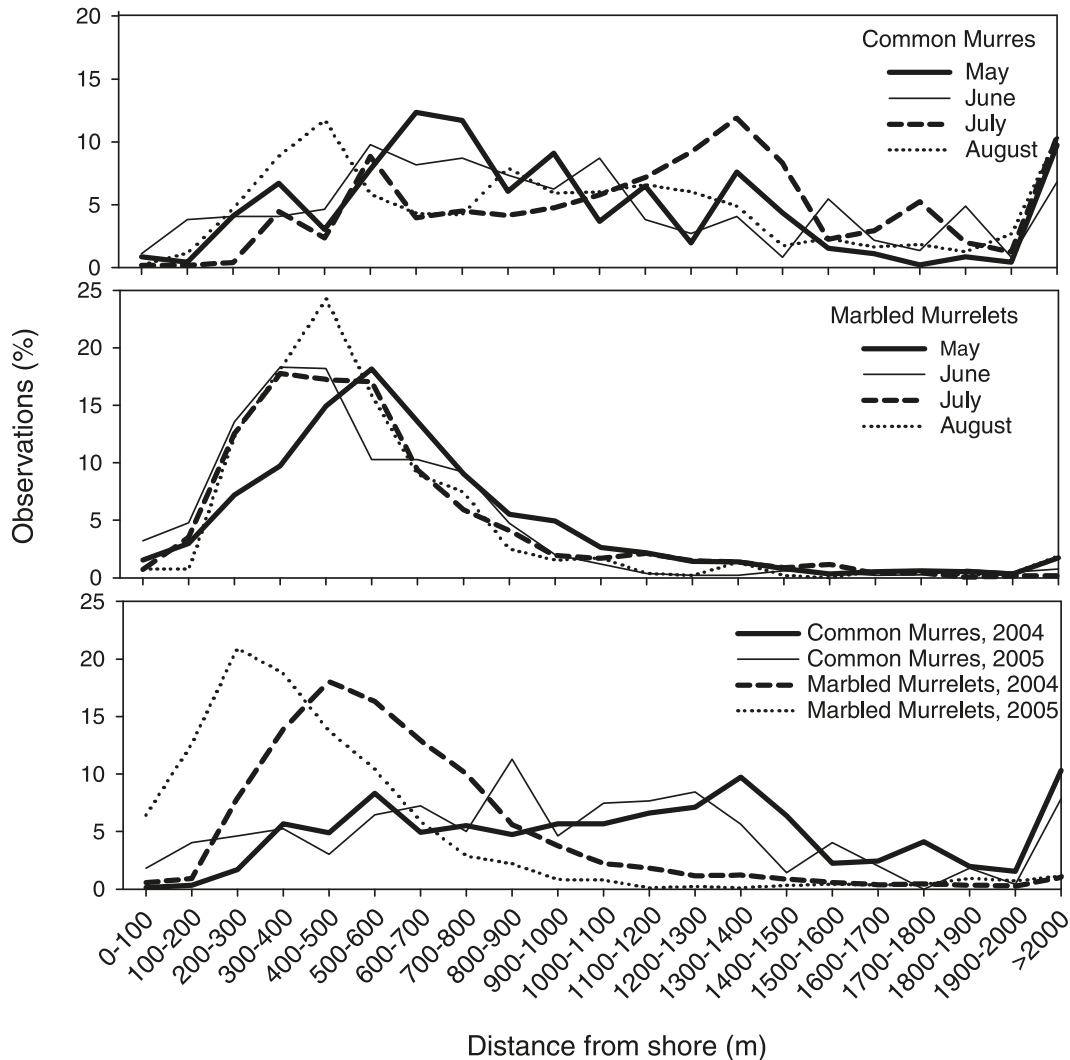
Note: All data includes observations up to 4 km from shore (regarding limitations of detectability beyond 1.2 km from the observer see the Materials and methods). *n* is the number of scans conducted by theodolite.

mean nearest-neighbour measures may be sensitive to numbers of birds present in the study area. For example, if only two or three individuals are mapped, and these individuals by chance are situated far from each other, then the mean nearest-neighbour statistics will be very large and thus provide outliers in the data set. Boxplots were used to identify extreme values (values >1.5 times the interquartile range; Benjamini 1988): 28 nearest-neighbour statistics were identified as outliers (12 MM–MM, 3 CM–CM, 6 MM–CM, and 7 CM–MM), most of which had fewer than five points mapped for one of the two species. Rather than discarding outliers (which accounted for ~10% of the data set and would have removed a large part of the natural variance in the data), we retained trials with small numbers of birds by assigning them less weight than other trials. Trials with 2, 3, 4, and 5 individuals of one species were weighted at 0.2, 0.4, 0.6, and 0.8, respectively, and all other trials received a full weight of 1 (note

nearest-neighbour statistics cannot be calculated when only one individual was mapped).

It is important to note that the spatial patterns observed with nearest-neighbour statistics may simply be a function of bird abundance in the study area rather than a true pattern; e.g., when more birds are present they are likely to be closer together. We assessed the effects of murrelet and murre abundance (no. of groups mapped) in two ways. First, we used linear regressions to test the correlation and direction (positive or negative) of associations between bird abundance and nearest-neighbour statistics. Second, randomization tests were used as an alternative method to test the statistical significance of spatial data (Fortin and Jacquez 2000). Because CM–MM and MM–CM nearest-neighbour statistics are sensitive to unequal proportions of each species in the study area, randomization tests were conducted to test whether these statistics represent a distinct spatial

Fig. 2. Annual and seasonal variation in distribution of Marbled Murrelets (*Brachyramphus marmoratus*) and Common Murres (*Uria aalge*) relative to shore along the West Coast Trail, southwest Vancouver Island. Note that because of decreased detectability with distance from shore, mapping and distributional data is less reliable beyond 1.2 km from shore.



pattern or simply an artifact of bird numbers. Permutation tests were conducted using a code generated in MATLAB (MathWorks, Natick, Massachusetts, USA) that randomly swapped the identity of murrelet (MM) and murre (CM) locations within each replicate scan while maintaining the same locations and numbers of MM and CM in each scan. By randomizing only species identities, we were able to control for the natural, observed variability in spatial structure (locations) and species composition (ratios of CM:MM) that existed in the data set. Nearest-neighbour statistics were recalculated for each permutation. For each scan, 1000 permutations were conducted and the statistical significance (random vs. nonrandom distribution) was determined by comparing the observed nearest-neighbour statistic with respect to the 1000 randomized nearest-neighbour statistics. With 1000 permutations, a distribution was considered non-random if the value of the observed statistic was less than the values of the lowest 50 randomized statistics ($\alpha = 0.05$). Randomization tests were conducted for all scans with more than one individual of each species. Throughout the paper, all statistics are reported as means \pm SE.

Results

Seabird distributions were mapped at seven sites over 2 years. The number of scans for each year were 45 in 2004 (Carmanah Bay, 20; Pachena Point, 25) and 50 in 2005 (Carmanah Bay, 23; Pachena Point, 4; Dare Point, 5; Skagit Bluffs, 6; Valencia Bluffs, 4; Tsusiat Bluffs, 6; Tsuquadra Point, 3; for site locations see Ronconi and Burger 2008). Coverage was most extensive seasonally and annually at Carmanah Bay. Examples of seasonal variation in bird distributions at Carmanah are shown in three replicate scans from 2004 (Fig. 1).

Distance from shore and numbers of birds

Patterns in seabird distributions relative to the shoreline indicate that murrelets and murres generally occupied distinctive areas with the greatest overlap occurring between waters 400 and 1000 m from shore (Fig. 2). This distributional pattern appeared to be consistent among years though murrelet groups foraged closer to shore in 2005 (454 ± 10 m) than 2004 (626 ± 6 ; $t_{[5800]} = 15.85$, $p < 0.001$). Groups of

Common Murres also foraged closer to shore in 2005 (859 ± 16 m) than in 2004 (1088 ± 17 ; $t_{[1545]} = 5.83$, $p < 0.001$). The area of overlap between species was also consistent among seasons with some intraseasonal variation (Fig. 2). Murrelets foraged farther from shore in May (distance from shore: 648 ± 9 m) than in other summer months (June: 521 ± 8 m; July: 549 ± 10 m; August: 572 ± 23 m; ANOVA, $F_{[3,5798]} = 39.91$, $p < 0.001$). Conversely, Common Murres foraged significantly closer to shore in May (884 ± 40 m) and June (874 ± 38 m) than in July (1163 ± 23 m) or August (1051 ± 29 m) ($F_{[3,1543]} = 20.72$, $p < 0.001$).

Overall, murrelets were more abundant than murres in both years and most months (Table 1). More than 90% of all Marbled Murrelets and 50% of all Common Murres observed were within 1200 m from shore, suggesting a high degree of spatial overlap within this nearshore environment. In both years, murrelets were numerically dominant over murres, with ratios ranging from 5 to 13 Marbled Murrelets for every Common Murre. Seasonally, however, murre numbers increased towards the end of the summer as murrelet numbers decreased so that the ratio approached 1:1 in August (Table 1).

Groups of birds were mapped, thus some assessment of group size is important to the interpretation of results and towards understanding potential for within group competition. Both species typically foraged singly or in small groups: group size was 2.1 ± 0.03 ($n = 5802$) and 3.0 ± 0.2 ($n = 1549$) for murrelets and murres, respectively. Group sizes were larger in 2004 than in 2005 for both murrelets (2.3 ± 0.04 vs. 1.7 ± 0.03 , respectively; $t_{[5800]} = 11.53$, $P < 0.001$) and murres (3.3 ± 0.3 vs. 1.8 ± 0.1 , respectively; $t_{[1547]} = 2.77$, $P = 0.006$). Group size varied significantly among months during each year (ANOVA, $P < 0.001$), except for murrelets in 2005 ($F_{[3,1759]} = 1.907$, $P = 0.126$). In general, murrelet group sizes decreased seasonally towards August as murre group sizes increased, matching the changes in their respective densities.

Nearest-neighbour distributions

Nearest-neighbour distances were significantly different among contrast groups (weighted ANOVA, $F_{[3,270]} = 27.63$, $P < 0.001$). On average, murrelet groups foraged within 95 ± 14 m of other murrelet groups (Fig. 3). Marbled Murrelets, however, were significantly ($P < 0.001$) farther from Common Murres (MM–CM contrast; 294 ± 21 m) than they were to other murrelets suggesting avoidance of murres. Groups of Common Murre (CM–CM) were significantly more dispersed than those of murrelets ($P < 0.001$) with nearest neighbours at 267 ± 20 m. The distance at which Common Murres were located from nearest Marbled Murrelets (CM–MM contrast) was 186 ± 21 m, which was significantly closer than murre groups to other murre groups (CM–CM; $P < 0.036$), suggesting that murres may be attracted to murrelet aggregations, but this attraction hypothesis is later contradicted by the results of the randomization tests below.

To investigate the year, month, and site influences on nearest-neighbour relationships, we conducted weighted least-squares ANOVA for each contrast group separately (Table 2). MM–MM nearest neighbours were influenced by month ($P = 0.027$) and site ($P = 0.006$), but post hoc tests showed only marginally significant differences between

June and July ($P = 0.085$) and greater distances between neighbours at Pachena compared with other sites ($P = 0.039$) and Carmanah ($P = 0.110$). CM–CM nearest-neighbour statistics showed no significant differences (model $P > 0.208$) among years, sites, or months. With MM–CM contrasts, murrelets foraged closer to murres in 2004 than in 2005 ($P = 0.005$), but month and site effects were not significant, suggesting that murrelets maintained a minimum distance from murres at all sites and during all seasons. CM–MM contrasts were most strongly affected by month (murres were farther from murrelets in July–August than in May–June; $P < 0.007$) and year (2005 > 2004; $P < 0.001$). Together these results suggest that spatial distribution and associations between these species were influenced by annual variability (MM–CM, CM–MM) and seasons (MM–MM, CM–MM), but less so by sites (MM–MM).

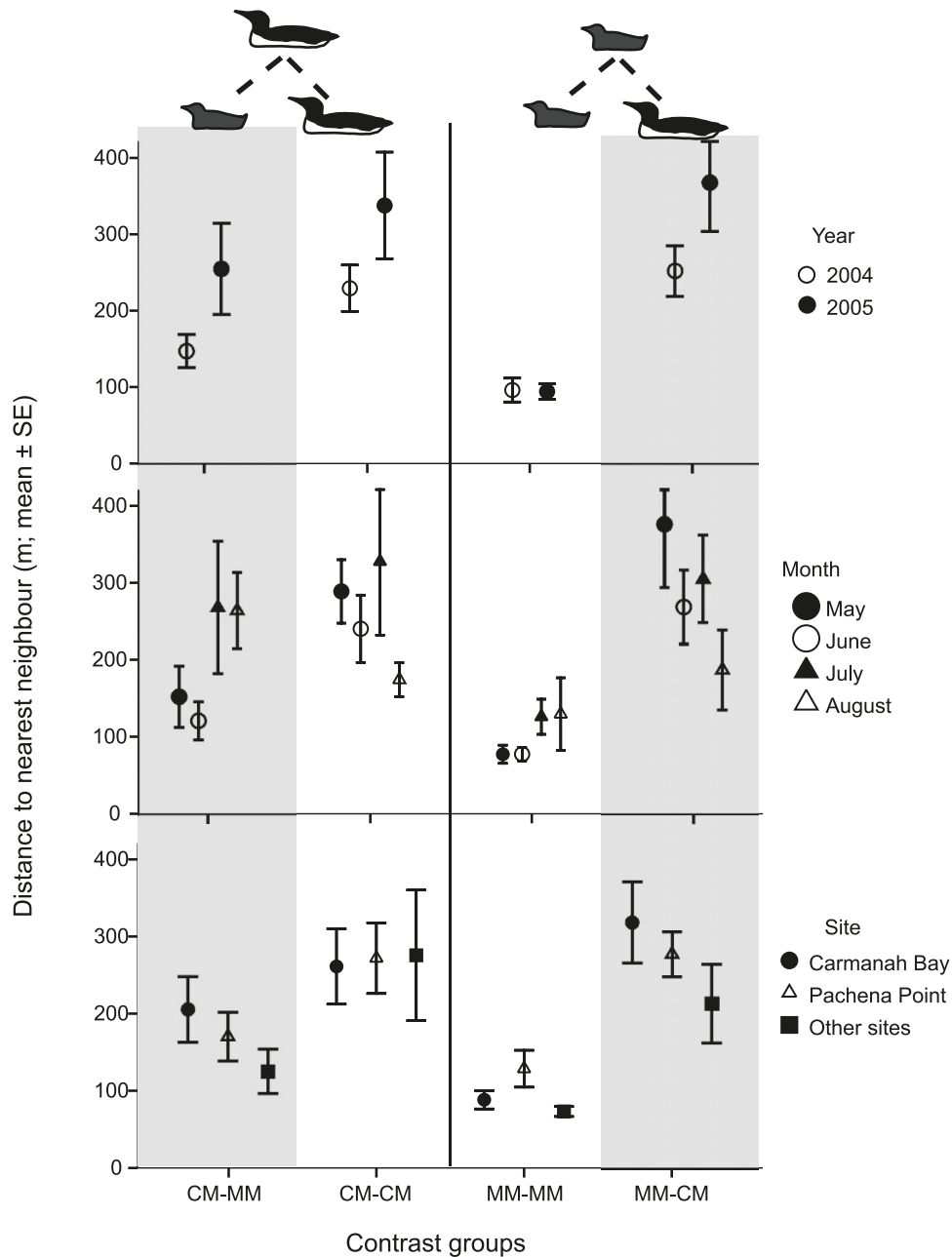
Linear regression was used to examine the direction and strength of correlations between nearest-neighbour statistics and bird abundance (Table 3). Not surprisingly, these analyses suggested intra- and inter-specific crowding as bird abundance increased: when more birds were in the study area, they were closer together. One unexpected result was a positive correlation between abundance of Common Murres and MM–MM nearest-neighbour distances, suggesting that murrelet groups dispersed as Common Murres crowded the study area. However, this correlation may be confounded by decreasing murrelet densities in the later part of the summer when the abundance of Common Murres increased.

Randomization tests

Randomization tests assessed the significance of MM–CM and CM–MM statistics, which are sensitive to the proportions of each species mapped in each scan. From 60 scans with >1 individual of each species, MM–CM and CM–MM nearest-neighbour statistics were nonrandom during 33% and 40% of the replicates, respectively. This suggests that during most of the trials, the spatial patterns between murres (CM) and murrelets (MM) were random; however, in at least one-third of the trials, the spatial patterns were nonrandom. The 20 nonrandom trials of MM–CM statistics show that interspecific MM–CM distances are much greater than conspecific MM–MM distances (Fig. 4). Therefore, this provides additional support for the murrelet avoidance hypothesis whereby murrelets forage farther from murres than they do from other murrelets and this is not due solely to random distributions of murrelets and murres. In contrast, the 24 nonrandom trials for CM–MM statistics show that interspecific CM–MM distances are equal to conspecific CM–CM distances (Fig. 4). Thus, murres are evenly distributed among murrelets and other murres, refuting the attraction hypothesis.

Comparison of trials between random and nonrandom MM–CM distributions may reveal conditions that support avoidance behaviour. Student's *t* tests showed significantly more murrelet groups (63.3 ± 11.4) in the nonrandom trials than in the random trials (34.3 ± 4.5) ($t_{[58]} = 2.83$, $P < 0.001$). Number of groups of Common Murres did not differ between random and nonrandom trials (random: 6.6 ± 0.9 ; nonrandom: 6.8 ± 1.4 ; $t_{[58]} = 0.12$, $P = 0.733$). This suggests that murrelets more effectively avoid murres when murrelets are more abundant. Moreover, there was a seasonal decline in the number of trials showing avoidance behaviour by

Fig. 3. Nearest-neighbour distances (mean \pm SE) measuring spatial distributions of Marbled Murrelets (MM; *Brachyramphus marmoratus*) and Common Murres (CM; *Uria aalge*) at seven sites along the West Coast Trail, southwest Vancouver Island, in 2004 and 2005. Contrast groups compare the mean distances between each pair (e.g., CM-MM = mean distance between murres and the nearest murrelet). These results show that murre groups forage closer to murrelets than to other murres, but that murrelet groups forage farther from murres than to other murrelets, i.e., avoidance of other species by murrelets.



murrelets (nonrandom trials): May = 40% of trials ($n = 15$), June = 38% ($n = 21$), July = 35% ($n = 17$), and August = 0% ($n = 7$). However, it is uncertain if this decline in avoidance behaviour was due to reduced numbers of murrelets or increased presence of murres. In contrast, there was no clear seasonal trend in nonrandom trials of CM-MM distances (indicating even spacing of murres to murrelets): May = 47% of trials, June = 24%, July = 41%, and August = 71%.

Discussion

This study provides a unique approach towards the investigation of intra- and inter-specific competition measured at fine spatial scales. The theodolite method allowed the measurement of spatial distribution of potential competitors without any disturbance and by simultaneously considering a large number of both species. Repeated sampling through

Table 2. Results of weighted least-squares ANOVA testing for spatial and temporal factors influencing nearest-neighbour distances between Marbled Murrelet (MM; *Brachyramphus marmoratus*) and Common Murre (CM; *Uria aalge*).

Model	Model fit			Variable significance			
	<i>F</i>	df	<i>p</i>	Variable	<i>F</i>	df	<i>p</i>
MM–MM	3.21	6, 86	0.007	Year	3.21	1	0.077
				Month	3.21	3	0.027
				Site	5.37	2	0.006
CM–CM	1.47	6, 54	0.208	Year	4.08	1	0.048
				Month	1.01	3	0.394
				Site	0.30	2	0.740
MM–CM	3.02	6, 53	0.013	Year	8.40	1	0.005
				Month	1.49	3	0.227
				Site	3.11	2	0.053
CM–MM	5.28	6, 53	<0.001	Year	16.06	1	<0.001
				Month	4.43	3	0.007
				Site	3.09	2	0.054

Note: Models were constructed for each of four nearest-neighbour contrast groups (MM to nearest MM, CM to CM, MM to CM, and CM to MM). Spatial and temporal factor included year (2004 and 2005), site (Carmanah, Pachena, other), and month (May, June, July, August). For details on case weighting see Materials and methods.

Table 3. Effects of bird abundance on spatial distributions of Marbled Murrelets (MM; *Brachyramphus marmoratus*) and Common Murres (CM; *Uria aalge*).

NN statistic	Effect	<i>r</i> ²	df	<i>F</i>	<i>P</i>	Interpretation
Effects of Marbled Murrelet abundance on nearest-neighbour statistics						
MM–MM	↑ abundance = ↓ NN	0.128	92	13.37	<0.001	Intraspecific crowding: murrelet groups are forced close together
CM–CM	No effect	0.027	60	1.65	0.204	
MM–CM	No effect	0.007	59	0.42	0.520	
CM–MM	↑ abundance = ↓ NN	0.131	59	8.75	0.004	Interspecific crowding: murre groups are forced close murrelets
Effects of Common Murre abundance on nearest-neighbour statistics						
MM–MM	↑ abundance = ↑ NN	0.041	92	3.93	0.051	Dispersal: increased murre abundance causes murrelets to disperse
CM–CM	↑ abundance = ↓ NN	0.081	60	5.22	0.026	Intraspecific crowding: murre groups are forced close together
MM–CM	↑ abundance = ↓ NN	0.055	59	3.35	0.072	Interspecific crowding: murrelet groups are forced close to murrelets
CM–MM	No effect	0.001	59	0.07	0.796	

Note: Linear regression was used to examine correlations between bird abundance and changes in nearest-neighbour (NN) statistics.

the season allows examination of temporal variables including seasonal changes in density of the two potential competitors. The results of distance from shore measurements, nearest-neighbour metrics, and randomization tests show clear evidence that murrelets tend to avoid murre, but this is not affected by the seasonal increase in murre densities or the corresponding seasonal decline in murrelet numbers. Conversely, murre were neither attracted to or avoiding murrelet groups, but instead displayed regular spacing suggesting interspecific competition among murre groups. We discuss the roles that segregation and competition play in supporting the co-existence of these conspecific predators.

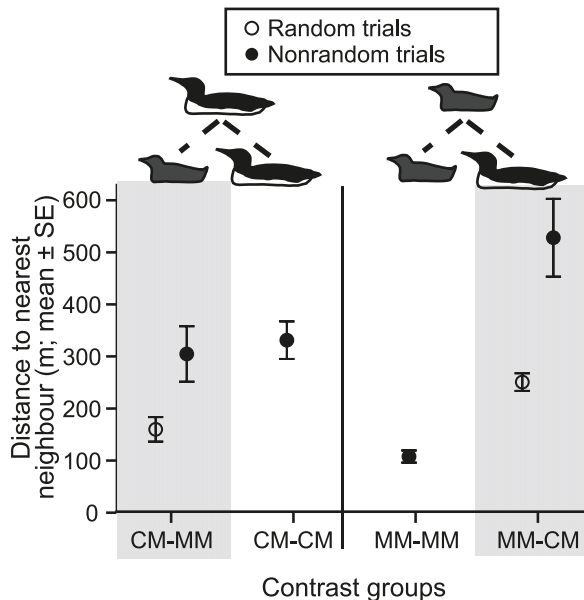
Spatial segregation

Our data show evidence of spatial segregation (i.e., habitat partitioning and avoidance of murre by murrelets), consistent with other studies of sympatric alcids (Piatt 1990; Burger

et al. 2008; Henkel 2009) whereby smaller alcids tend to avoid larger species either in space or time. These results are often scale-dependent. At scales of several kilometres, Burger et al. (2008) found Marbled murrelets to be segregated from Common Murres in the nearshore zone (~200 m from shore) but usually showed aggregation in areas approximately 600 m from the shoreline. At the smallest scales (~280 m) analysed by Burger et al. (2008), murrelets rarely encountered larger alcids—a distance nearly identical to that observed in this study (mean distance of 294 m between murrelets and nearest murre groups). Our results are also consistent with studies which show that murrelets seldom participate in mixed-species feeding flocks especially where they encounter other larger diving birds (Hoffman et al. 1981; Porter and Sealy 1981; Chilton and Sealy 1987).

We observed general differences in spatial distributions between Marbled Murrelets and Common Murres. Murrelets

Fig. 4. Randomization tests and the nearest-neighbour distances (mean \pm SE) measuring spatial distributions of Marbled Murrelets (MM; *Brachyramphus marmoratus*) and Common Murres (CM; *Uria aalge*). Contrast groups compare the mean distances between each pair (e.g., CM–MM = mean distance between murres and the nearest murrelet). Randomization tests were used to test the significance of the spatial patterns between CM–MM and MM–CM. Random trials are those where CM and MM locations are interchangeable, whereas the nonrandom trials are those where the spatial distributions between CM and MM do not occur by chance.



preferred nearshore waters and murres were more evenly distributed over distances up to 1500 m from shore (Burger et al. 2008; this study). These distributions may, in part, be related to water depths that increase monotonically with distance from shore in this region (Burger et al. 2008). Although murrelets seldom ventured into deeper water, murres frequently foraged in shallow nearshore waters (<1 km of shore) and in August they often outnumbered murrelets in this favoured range of the murrelets (Burger et al. 2008; this study). The murrelet's horizontal niche space was therefore completely overlapped by that of the murre. Partitioning of habitat by diving depth was unlikely in these nearshore waters, because depths were generally <30 m (Burger et al. 2008) and within the diving range of both species (Burger 1991; Mathews and Burger 1998).

Effects of changing densities

The effects of competition may be density-dependent whereby competition is stronger when an animal's neighbours (competitors) are at higher densities (Gurevitch et al. 1992). Because both murre and murrelet densities changed seasonally in our study area, this allowed for investigation of density-dependent effects on spatial segregation between species. We might expect competitive interactions to be strongest in July and August rather than in May or June, because as the season progressed, the proportions of murres to murrelets increased and murres used nearshore waters in higher numbers.

Our nearest-neighbour results did not support these predictions but showed that murre distances from murrelets instead increased in July and August (Fig. 3). This is likely due to generally low densities of murrelets rather than avoidance behaviour by murres.

The lack of evidence for density-dependent competition and avoidance effects may simply be a function of the mathematical properties of nearest-neighbour calculations, which were accounted for by randomization tests (Fortin and Jacques 2000). One third of spatial patterns between MM–CM were nonrandom, suggesting avoidance of murres by murrelets, and the frequency of nonrandom distributions declined seasonally. Thus, as murrelet densities decrease and murre densities increase, avoidance behaviour becomes more difficult for murrelets later in the summer. Indeed, increasing numbers of murres might be responsible for the emigration of murrelets from the West Coast Trail area in late summer when prey taken by these alcids is still apparently available (Burger et al. 2008).

Alternatively, seasonal or annual changes in resource use (Mills 2007) or availability (DuBowy 1988) may also be contributing to observed changes in bird numbers, distribution patterns, and strength of competitive interactions. Prey concentrations were slightly higher in 2004 than in 2005 (Ronconi and Burger 2008), perhaps alleviating some of the competitive pressure in that year when murrelets foraged closer to murres (MM–CM distances were greater in 2005 than 2004). Relationships between prey availability and strength of competitive interactions deserve more investigation in future studies.

Inter- and intra-specific competition

There is evidence that carnivores generally experience effects from both interspecific and intraspecific competition (Gurevitch et al. 1992). Murrelets and murres are both piscivores that exhibit considerable dietary overlap in both the species and size classes of prey taken (Carter 1984; Vermeer et al. 1987; Hay et al. 1992; Hobson et al. 1994; Burkett 1995; Gaston and Jones 1998; Lance and Thompson 2005). This suggests that they may compete for food resources and be susceptible to both inter- and intra-specific competition. Although many studies have investigated either inter- or intra-specific competition, this study provides a unique perspective on the interaction between both forms of competition.

Although murres may readily cue in on conspecifics as indicators of foraging opportunities (Davoren et al. 2003b), the large distances between neighbouring murre groups (~300 m) suggest that murres may experience intraspecific competition, an observation made in other studies of murres (Falk et al. 2001; Davoren and Montevecchi 2003). Prey densities can play an important role in the strength of intraspecific competition (Triplet et al. 1999). In areas of low prey density, murres are also found at lower densities, suggesting that intraspecific interference competition may play a role in prey capture (Davoren et al. 2003a). However, low prey densities in 2005 (Ronconi and Burger 2008) did not result in greater spacing between murres even when bird abundance decreased. The closer proximity of murre groups to murrelets than to other murres suggests that intraspecific competition may be greater than interspecific competition for murres, as

neighbouring murrelet groups pose little threat of competition. Nevertheless, murrelets still forage in groups so they are not avoiding conspecifics altogether, and there are likely complex social behaviours involved.

Marbled Murrelet groups, on the other hand, foraged in much closer proximity to each other (<100 m) and avoided foraging near murrelets (typically >250 m). Thus, murrelets appeared to segregate themselves from murrelets suggesting stronger interspecific than intraspecific competition. Group foraging, typically in pairs, is thought to be beneficial for murrelets (Strachan et al. 1995) but has disadvantages when groups become large (Kuletz 2005). The effects of interspecific competition among seabirds are more strongly felt between species of different sizes (Piatt 1990; Rome and Ellis 2004) and within foraging guilds (Henkel 2009). Thus, mixed-species flocking may not be beneficial for all individuals or species. As a result, murrelets avoid foraging in close proximity with several larger species of seabirds, though the reverse is true for the larger Common Murres (Henkel 2009; this study).

We suggest that competition is occurring; however, we have not identified the proximate mechanism supporting this interaction. Although direct competitive interactions do occur between feeding seabirds (Hoffman et al. 1981; Piatt 1987), we did not observe any aggressive interactions between murrelets and murrelets. Instead, murrelets may be responding to passive interference competition, such as the disruption of prey schools making them less available to competitors (Lewis et al. 2001; Dill et al. 2003). Alternatively, higher vertebrates may simply avoid risk even when the frequency of predation or competitive events is rare (Nilsson et al. 2000; Heithaus and Dill 2006). The perception of risk (Preisser et al. 2005) might be sufficient to cause murrelets to avoid close encounters with murrelets. Murrelets might therefore minimize the impacts of aggression or competition, but by avoiding murrelets, the murrelets are also reducing their foraging opportunities and this might still have negative consequences.

Coexistence

This study provides evidence of spacing behaviour and fine-scale segregation, which promotes coexistence by reducing competition within foraging areas. Our study focused on the spatial component of these species foraging, yet there may be additional ways in which murrelets avoid competition with the murrelets. These might include changes to their prey selections or diurnal foraging patterns (some preferred prey species such as Pacific sand lance (*Ammodytes hexapterus* Pallas, 1814) show strong diurnal patterns in availability; e.g., Robards and Piatt 1999). We do not know what differences there might be in the vertical distributions of these alcid species or the methods used to attack prey. Foraging on lower prey densities may allow Atlantic Puffins (*Fratercula arctica* (L., 1758)) to coexist with Common Murres that require higher daily caloric intake of food because of their larger body size (Piatt 1990). Murrelets may also be better adapted to exploit small, scattered schools of fish than other piscivorous seabirds (Ostrand et al. 1998; Kuletz 2005).

Coexistence of similar-sized and potentially competitive species of Alcidae may be facilitated by the complexity of

marine habitats that create broad niches for species to exploit (Haney and Schauer 1994). In parts of Alaska, Marbled Murrelets show considerable ecological overlap with the closely related Kittlitz's Murrelet (*Brachyramphus brevirostris* (Vigors, 1829)), suggesting potential for interspecific competition (Day and Nigro 2000), but subtle differences in habitat preferences facilitate the ecological partitioning between these coexisting species (Day et al. 2003). We found some evidence of spatial partitioning with respect to distance from shore for murrelets and murrelets, and meso-scale habitat selection may provide an additional mechanism of spatial segregation (Burger et al. 2008; Ronconi 2008). For other apparently competitive seabird species, fine-scale niche partitioning, rather than interspecific competition, can facilitate coexistence (Garthe et al. 1999).

Conclusions

The effects of competition, whether intraspecific or interspecific, among sympatric seabirds are difficult to demonstrate (Birt et al. 1987; Nilsson et al. 2000; Lewis et al. 2001) but are likely important in shaping seabird communities in many ecosystems. Other studies provide indirect evidence for intraspecific competition (Falk et al. 2001; Davoren and Montevecchi 2003) and interspecific competition (Piatt 1990; Garthe et al. 1999; Rome and Ellis 2004; Henkel 2009) among seabirds. Our study is the first to demonstrate fine-scale avoidance behaviour by one species relative to a larger species in the same guild within a context where competition for shared prey is expected. We also provide evidence of intraspecific competition whereby the larger species maintain minimum distance among foraging groups, regardless of overall bird densities.

Given that Marbled Murrelets share most of their range with murrelets and other larger piscivores (Gaston and Jones 1998), consideration should be given to the possible effects of competition at sea on the persistence and recovery of this threatened species. In California, for example, where murrelets are greatly reduced and endangered, efforts are underway to restore and increase the populations of murrelets following devastating oil spills and fisheries bycatch (Parker et al. 2007). In parts of Alaska where murrelet numbers have declined in relation to populations of gulls that kleptoparasitize murrelets, some have speculated that increasing gull numbers could be detrimental to the recovery of murrelet populations (Hunt 1995; Kuletz 2005). A better understanding of competitive interactions among sympatric species can help managers to better monitor the dynamics of changing and recovering avian communities.

Acknowledgements

Many thanks go to Sarah Wong, Nathan Hentze, and Heather Milligan for field assistance. We thank Parks Canada staff and Canadian Coast Guard lighthouse keepers, especially Jerry and Janet Etkorn and Scott Bell, for accommodation and logistical help. Hal Whitehead, Dalhousie University, generously developed the randomization procedures for this study. This study was funded by the British Columbia Forest Science Program, Environment Canada Science Horizons Youth Internship, Parks Canada, Natural Sciences and Engineering Research Council of Canada (NSERC operating grant to A.E.B. and CGS-D scholarship to R.A.R.),

Endangered Species Recovery Fund (World Wildlife Fund and Canadian Wildlife Service), and the Society of Canadian Ornithologists. R.A.R. was supported by the Killam Trust, Dalhousie University, during the final preparation of the manuscript.

References

- Armstrong, R.A., and McGehee, R. 1980. Competitive exclusion. *Am. Nat.* **115**(2): 151–170. doi:10.1086/283553.
- Ballance, L.T., Pitman, R.L., and Reilly, S.B. 1997. Seabird community structure along a productivity gradient: Importance of competition and energetic constraint. *Ecology*, **78**(5): 1502–1518. doi:10.1890/0012-9658(1997)078[1502:SCSAAP]2.0.CO;2.
- Barta, Z., and Giraldeau, L.A. 2001. Breeding colonies as information centers: a reappraisal of information-based hypotheses using the producer–scrounger game. *Behav. Ecol.* **12**(2): 121–127. doi:10.1093/beheco/12.2.121.
- Benjamini, Y. 1988. Opening the box of a boxplot. *Am. Stat.* **42**(4): 257–262. doi:10.2307/2685133.
- Beyer, H.L. 2004. Hawth's analysis tools for ArcGIS. Available from <http://www.spatialecology.com/htools/> [accessed 15 January 2006].
- Birt, V.L., Birt, T.P., Goulet, D., Cairns, D.K., and Montevecchi, W. A. 1987. Ashmole's halo: direct evidence for prey depletion by a seabird. *Mar. Ecol. Prog. Ser.* **40**(3): 205–208. doi:10.3354/meps040205.
- Buckland, S.T., Anderson, D.R., Burnham, K.P., Laake, J.L., Borchers, D.L., and Thomas, L. 2001. Introduction to distance sampling: estimating abundance of biological populations. Oxford University Press, Oxford.
- Burger, A.E. 1991. Maximum diving depths and underwater foraging in alcids and penguins. *Can. Wildl. Serv. Occas. Pap. No. 68*. pp. 9–15.
- Burger, A.E. 1997. Arrival and departure behavior of Common Murres at colonies: evidence for an information halo? *Colon. Waterbirds*, **20**(1): 55–65. doi:10.2307/1521764.
- Burger, A.E., Hitchcock, C.L., Stewart, E.A., and Davoren, G.K. 2008. Coexistence and spatial distributions of Marbled Murrelets (*Brachyramphus marmoratus*) and other alcids off southwest Vancouver Island, British Columbia. *Auk*, **125**(1): 192–204. doi:10.1525/auk.2008.125.1.192.
- Burkett, E. 1995. Marbled murrelet food habits and prey ecology. *In* Ecology and conservation of the Marbled Murrelet. Edited by C.J. Ralph, G.L. Hunt, M.G. Raphael, and J.F. Piatt. U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station, Albany, Calif. Gen. Tech. Rep. PSW-GTR-152. pp. 223–246.
- Camphuysen, K., and Webb, A. 1999. Multi-species feeding associations in North Sea seabirds: jointly exploiting a patchy environment. *Ardea*, **87**(2): 177–198.
- Carter, H.R. 1984. At-sea biology of the Marbled Murrelet (*Brachyramphus marmoratus*) in Barkley Sound, British Columbia. M.Sc. thesis, University of Manitoba, Winnipeg.
- Chilton, G., and Sealy, S.G. 1987. Species roles in mixed-species feeding flocks of seabirds. *J. Field Ornithol.* **58**(4): 456–463.
- Cody, M.L. 1974. Competition and the structure of bird communities. Princeton University Press, Princeton, N.J.
- Davoren, G.K. 2000. Variability in foraging in response to changing prey distributions in rhinoceros auklets. *Mar. Ecol. Prog. Ser.* **198**: 283–291. doi:10.3354/meps198283.
- Davoren, G.K., and Montevecchi, W.A. 2003. Consequences of foraging trip duration on provisioning behaviour and fledging condition of common murres *Uria aalge*. *J. Avian Biol.* **34**(1): 44–53. doi:10.1034/j.1600-048X.2003.03008.x.
- Davoren, G.K., Montevecchi, W.A., and Anderson, J.T. 2003a. Distributional patterns of a marine bird and its prey: habitat selection based on prey and conspecific behaviour. *Mar. Ecol. Prog. Ser.* **256**: 229–242. doi:10.3354/meps256229.
- Davoren, G.K., Montevecchi, W.A., and Anderson, J.T. 2003b. Search strategies of a pursuit-diving marine bird and the persistence of prey patches. *Ecol. Monogr.* **73**(3): 463–481. doi:10.1890/02-0208.
- Day, R.H., and Nigro, D.A. 2000. Feeding ecology of Kittlitz's and Marbled murrelets in Prince William Sound, Alaska. *Waterbirds*, **23**(1): 1–14.
- Day, R.H., Prichard, A.K., and Nigro, D.A. 2003. Ecological specialization and overlap of *Brachyramphus* murrelets in Prince William Sound, Alaska. *Auk*, **120**(3): 680–699. doi:10.1642/0004-8038(2003)120[0680:ESA00B]2.0.CO;2.
- Denardo, C., Dougherty, M., Hastie, G., Leaper, R., Wilson, B., and Thompson, P.M. 2001. A new technique to measure spatial relationships within groups of free-ranging coastal cetaceans. *J. Appl. Ecol.* **38**(4): 888–895. doi:10.1046/j.1365-2664.2001.00639.x.
- Dill, L.M., Heithaus, M.R., and Walters, C.J. 2003. Behaviorally mediated indirect interactions in marine communities and their conservation implications. *Ecology*, **84**(5): 1151–1157. doi:10.1890/0012-9658(2003)084[1151:BMIIIM]2.0.CO;2.
- DuBowy, P.J. 1988. Waterfowl communities and seasonal environments: temporal variability in interspecific competition. *Ecology*, **69**(5): 1439–1453. doi:10.2307/1941641.
- Falk, K., Dall'Antonia, L., and Benvenuti, S. 2001. Mapping pre- and post-fledging foraging locations of thick-billed murres in the North Water polynya. *Ecography*, **24**(6): 625–632. doi:10.1034/j.1600-0587.2001.240601.x.
- Fortin, M.-J., and Jacquez, G.M. 2000. Randomization tests and spatially autocorrelated data. *Bull. Ecol. Soc. Am.* **81**(3): 201–205.
- Garthe, S., Freyer, T., Huppert, O., and Wolke, D. 1999. Breeding Lesser Black-Backed Gulls *Larus graellsii* and Herring Gulls *Larus argentatus*: coexistence or competition? *Ardea*, **87**(2): 227–236.
- Gaston, A.J., and Jones, I.L. 1998. The Auks: Alcidae. Bird families of the World. Vol. 5. Oxford University Press, Oxford.
- Gotelli, N.J. 2001. A primer of ecology. 3rd ed. Sinauer Associates, Inc., Sunderland, Mass.
- Grünbaum, D., and Veit, R.R. 2003. Black-browed albatrosses foraging on Antarctic krill: density-dependence through local enhancement? *Ecology*, **84**(12): 3265–3275. doi:10.1890/01-4098.
- Gurevitch, J., Morrow, L.L., Wallace, A., and Walsh, J.S. 1992. A meta-analysis of competition in field experiments. *Am. Nat.* **140**(4): 539–572. doi:10.1086/285428.
- Haney, J.C., and Schauer, A.E.S. 1994. Environmental variability facilitates coexistence within an alcid community at sea. *Mar. Ecol. Prog. Ser.* **103**(3): 221–237.
- Haney, J.C., Frstrup, K.M., and Lee, D.S. 1992. Geometry of visual recruitment by seabirds to ephemeral foraging flocks. *Ornis Scand.* **23**(1): 49–62. doi:10.2307/3676427.
- Hardin, G. 1960. The competitive exclusion principle. *Science* (Washington, D.C.), **131**(3409): 1292–1297. doi:10.1126/science.131.3409.1292. PMID:14399717.
- Harrison, N.M., Whitehouse, M.J., Heinemann, D., Prince, P.A., Hunt, G.L., and Veit, R.R. 1991. Observations of multispecies seabird flocks around South Georgia. *Auk*, **108**(4): 801–810.
- Hay, D.E., Healey, M.C., Ware, D.M., and Wilimovsky, N.J. 1992. Distribution, abundance, and habitat of prey fish on the west coast of Vancouver Island. *In* The ecology, status, and conservation of marine and shoreline birds of the west coast of Vancouver Island. Edited by K. Vermeer, R.W. Butler, and K.H. Morgan. Can. Wildl. Serv. Occas. Pap. No. 75. pp. 22–29.
- Heithaus, M.R., and Dill, L.M. 2006. Does tiger shark predation risk

- influence foraging habitat use by bottlenose dolphins at multiple spatial scales? *Oikos*, **114**(2): 257–264. doi:10.1111/j.2006.0030-1299.14443.x.
- Henkel, L.A. 2009. Co-occurrence and aggregation of marine birds and mammals in Monterey Bay, California, USA. *Mar. Ecol. Prog. Ser.* **387**: 295–303. doi:10.3354/meps08082.
- Hobson, K.A. 1990. Stable isotope analysis of Marbled Murrelets: evidence for freshwater feeding and determination of trophic level. *Condor*, **92**(4): 897–903. doi:10.2307/1368725.
- Hobson, K.A., Piatt, J.F., and Pitocchelli, J. 1994. Using stable isotopes to determine seabird trophic relationships. *J. Anim. Ecol.* **63**(4): 786–798. doi:10.2307/5256.
- Hoffman, W., Heinemann, D., and Wiens, J.A. 1981. The ecology of seabird feeding flocks in Alaska. *Auk*, **98**(3): 437–456.
- Hunt, G.L. 1995. Monospecific and mixed species foraging associations of Marbled Murrelets. In *Ecology and conservation of the Marbled Murrelet*. Edited by C.J. Ralph, G.L. Hunt, M.G. Raphael, and J.F. Piatt. U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station, Albany, Calif. Gen. Tech. Rep. No. PSW-GTR-152. pp. 255–256.
- Kuletz, K.J. 2005. Foraging behavior and productivity of a non-colonial seabird, the Marbled Murrelet (*Brachyramphus marmoratus*), relative to prey and habitat. Ph.D. thesis, Department of Biology, University of Victoria, Victoria, B.C.
- Lance, M.M., and Thompson, C.W. 2005. Overlap in diets and foraging of Common Murres (*Uria aalge*) and Rhinoceros Auklets (*Cerorhinca monocerata*) after the breeding season. *Auk*, **122**(3): 887–901. doi:10.1642/0004-8038(2005)122[0887:OIDAFO]2.0.CO;2.
- Lewis, S., Sherratt, T.N., Hamer, K.C., and Wanless, S. 2001. Evidence of intra-specific competition for food in a pelagic seabird. *Nature (London)*, **412**(6849): 816–819. doi:10.1038/35090566. PMID:11518965.
- Lovette, I.J., and Hochachka, W.M. 2006. Simultaneous effects of phylogenetic niche conservatism and competition on avian community structure. *Ecology*, **87**(Suppl. 7): S14–S28. doi:10.1890/0012-9658(2006)87[14:SEOPNC]2.0.CO;2. PMID:16922299.
- MacArthur, R.H. 1958. Population ecology of some warblers of northeastern coniferous forests. *Ecology*, **39**(4): 599–619. doi:10.2307/1931600.
- Maniscalco, J.M., Ostrand, W.D., Suryan, R.M., and Irons, D.B. 2001. Passive interference competition by Glaucous-winged Gulls on Black-legged Kittiwakes: a cost of feeding in flocks. *Condor*, **103**(3): 616–619. doi:10.1650/0010-5422(2001)103[0616:PICBGW]2.0.CO;2.
- Mathews, N.J.C., and Burger, A.E. 1998. Diving depth of a Marbled Murrelet. *Northwest. Nat.*, **79**(2): 70–71. doi:10.2307/3536705.
- Mills, A.M. 2007. Foraging segregation in a breeding bird guild declines following nesting. *Can. J. Zool.* **85**(1): 141–150. doi:10.1139/Z06-194.
- Nilsson, P.A., Nilsson, K., and Nystrom, P. 2000. Does risk of intraspecific interactions induce shifts in prey-size preference in aquatic predators? *Behav. Ecol. Sociobiol.* **48**(4): 268–275. doi:10.1007/s002650000235.
- O'Sullivan, D., and Unwin, D.J. 2003. Geographical information analysis. John Wiley and Sons, Inc., Hoboken, N.J.
- Ostrand, W.D. 1999. Marbled Murrelets as initiators of feeding flocks in Prince William Sound, Alaska. *Waterbirds*, **22**(2): 314–318.
- Ostrand, W.D., Coyle, K.O., Drew, G.S., Maniscalco, J.M., and Irons, D.B. 1998. Selection of forage-fish schools by Murrelets and Tufted Puffins in Prince William Sound, Alaska. *Condor*, **100**(2): 286–297. doi:10.2307/1370269.
- Parker, M.W., Kress, S.W., Golightly, R.T., Carter, H.R., Parsons, E. B., Schubel, S.E., Boyce, J.A., McChesney, G.J., and Wisely, S.M. 2007. Assessment of social attraction techniques used to restore a Common Murre colony in central California. *Waterbirds*, **30**(1): 17–28. doi:10.1675/1524-4695(2007)030[0017:AOSATU]2.0.CO;2.
- Perry, J.N., Liebholt, A.M., Rosenberg, M.S., Dungan, J., Miriti, M., Jakomulska, A., and Citron-Pousty, S. 2002. Illustrations and guidelines for selecting statistical methods for quantifying spatial pattern in ecological data. *Ecography*, **25**(5): 578–600. doi:10.1034/j.1600-0587.2002.250507.x.
- Piatt, J.F. 1987. Behavioural ecology of Common Murre and Atlantic Puffin predation on capelin: implications for population biology. Ph.D. thesis, Memorial University of Newfoundland, St. John's, N.L.
- Piatt, J.F. 1990. The aggregative response of common murres and Atlantic puffins to schools of capelin. *Stud. Avian Biol.* **14**: 36–51.
- Porter, J.M., and Sealy, S.G. 1981. Dynamics of seabird multispecies feeding flocks: chronology of flocking in Barkley Sound, British Columbia, in 1979. *Colon. Waterbirds*, **4**: 104–113. doi:10.2307/1521122.
- Preisser, E.L., Bolnick, D.I., and Benard, M.F. 2005. Scared to death? The effects of intimidation and consumption in predator–prey interactions. *Ecology*, **86**(2): 501–509. doi:10.1890/04-0719.
- Robards, M.D., and Piatt, J.F. 1999. Biology of the genus *Ammodytes*, the sand lances. In *Sand lance: a review of biology and predator relations and annotated bibliography*. Edited by M.D. Robards, M.F. Willson, R.H. Armstrong, and J.F. Piatt. U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station, Portland, Ore. Res. Pap. No. PNW-RP-521. pp. 1–16.
- Rome, M.S., and Ellis, J.C. 2004. Foraging ecology and interactions between Herring Gulls and Great Black-backed Gulls in New England. *Waterbirds*, **27**(2): 200–210. doi:10.1675/1524-4695(2004)027[0200:FEAIBH]2.0.CO;2.
- Ronconi, R.A. 2008. Patterns and processes of marine habitat selection: foraging ecology, competition and coexistence among coastal seabirds. Ph.D. thesis, Department of Biology, University of Victoria, Victoria, B.C.
- Ronconi, R.A., and Burger, A.E. 2008. Limited foraging flexibility: increased foraging effort by a marine predator does not buffer against scarce prey. *Mar. Ecol. Prog. Ser.* **366**: 245–258. doi:10.3354/meps07529.
- Ronconi, R.A., and Burger, A.E. 2009. Estimating seabird densities from vessel transects: distance sampling and implications for strip transects. *Aquat. Biol.* **4**(3): 297–309. doi:10.3354/ab00112.
- Ronconi, R.A., and St. Clair, C.C. 2002. Management options to reduce boat disturbance on foraging black guillemots (*Cepphus grylle*) in the Bay of Fundy. *Biol. Conserv.* **108**(3): 265–271. doi:10.1016/S0006-3207(02)00126-X.
- Safina, C. 1990. Bluefish mediation of foraging competition between Roseate and Common Terns. *Ecology*, **71**(5): 1804–1809. doi:10.2307/1937588.
- Schoener, T.W. 1982. The controversy over interspecific competition. *Am. Sci.* **70**: 586–595.
- Shealer, D.A., and Burger, J. 1993. Effects of interference competition on the foraging activity of tropical Roseate Terns. *Condor*, **95**(2): 322–329. doi:10.2307/1369355.
- Silverman, E.D., and Veit, R.R. 2001. Associations among Antarctic seabirds in mixed species feeding flocks. *Ibis*, **143**(1): 51–62. doi:10.1111/j.1474-919X.2001.tb04169.x.
- Silverman, E.D., Veit, R.R., and Nevitt, G.A. 2004. Nearest neighbors as foraging cues: information transfer in a patchy environment. *Mar. Ecol. Prog. Ser.* **277**: 25–35. doi:10.3354/meps277025.
- Speckman, S.G., Piatt, J.F., and Springer, A.M. 2003. Deciphering the social structure of Marbled Murrelets from behavioral observations at sea. *Waterbirds*, **26**(3): 266–274. doi:10.1675/1524-4695(2003)026[0266:DTSSOM]2.0.CO;2.

- Strachan, G., McAllister, M., and Ralph, C.J. 1995. Marbled Murrelet at-sea and foraging behavior. *In* Ecology and conservation of the Marbled Murrelet. *Edited by* C.J. Ralph, G.L. Hunt, M.G. Raphael, and J.F. Piatt. U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station, Albany, Calif. Gen. Tech. Rep. PSW-GTR-152. pp. 247–253.
- Triplet, P., Stillman, R.A., and Goss-Custard, J.D. 1999. Prey abundance and the strength of interference in a foraging shorebird. *J. Anim. Ecol.* **68**(2): 254–265. doi:10.1046/j.1365-2656.1999.00280.x.
- Vermeer, K., Sealy, S.G., and Sanger, G.A. 1987. Feeding ecology of Alcidae in the eastern North Pacific Ocean. *In* Seabirds: feeding biology and role in marine ecosystems. *Edited by* J.P. Croxall. Cambridge University Press, Cambridge, UK. pp. 187–227.
- Wittenberger, J.F., and Hunt, G.L. 1985. The adaptive significance of coloniality in birds. *In* Avian biology. Vol. 8. *Edited by* D.S. Farner, J.R. King, and K.C. Parkes. Academic Press, Toronto. pp. 1–77.
- Wong, S.N.P., Ronconi, R.A., Burger, A.E., and Hansen, B. 2008. Marine distribution and behavior of juvenile and adult Marbled Murrelets off southwest Vancouver Island, British Columbia: applications for monitoring. *Condor*, **110**(2): 306–315. doi:10.1525/cond.2008.8377.