

THE EFFECTS OF BOAT DISTURBANCE ON SEAIBRDS OFF SOUTHWESTERN
VANCOUVER ISLAND, BRITISH COLUMBIA

by

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Human disturbance can have direct and indirect impacts on birds. Many studies have investigated the effects of boat disturbance on waterbirds, but have focused on non-diving waterbirds or breeding colonies. This study focused on boat disturbance effects on diving waterbirds in marine waters off southwestern Vancouver Island, British Columbia, Canada. Observations of Marbled Murrelets (*Brachyramphus marmoratus*), Common Murres (*Uria aalge*), Rhinoceros Auklets (*Cerorhinca monocerata*) and Pelagic Cormorants (*Phalacrocorax pelagicus*) were collected in response to boat disturbances. Bird responses were categorized as No Reaction, Dive, or Flush. Variables of date, sea state, hour, group size, boat speed, approach distance, approach angle, average bird density, location, and average prey density were included in predictive models using multiple logistic regression. An information-theoretic approach (Akaike information criterion) was used in model selection. Three model-sets were developed for each species testing which variables best predicted if a bird would react (Dive or Flush), if a reacting bird would flush, and if a bird would remain within a site (No Reaction or Dive) or flush. General trends occurred among species, but models were species-specific. Marbled Murrelet, Common Murre, and Pelagic Cormorant appear to react based on a large number of parameters tested. Distance and speed best predicted reaction responses for Rhinoceros Auklets. Flushing response in birds that react (Dive or Flush) was best predicted by all parameters except average bird density in murrelets, by distance and speed in murres, by distance in auklets, and by time of day in cormorants. Bird density, sea state, and group size were all important predictors in determining if a murrelet would leave a site or remain. Prey density was the main parameter in predicting if murres abandoned sites, group size and prey density for auklets, and sea state, prey density, and group size for cormorants. Murrelets, murres and cormorants reacted at similar distances, with Common Murre being the most tolerant to boat approaches. Pelagic Cormorants reacted at greater distances than the other species. Increased sea state and decreased group size were the most significant parameters in determining reaction response. Observations and predictive logistic regression equations suggest that buffer zones of 150 m would eliminate most boat disturbance effects to Marbled Murrelets, Common Murres,

and Rhinoceros Auklets. Buffer zones of 200 m or more are required to reduce the effects of disturbance to Pelagic Cormorants. Restrictions on boat speed or time of day or year would not reduce disturbance effects. An exclusion zone parallel to shore out to 1 km would eliminate most boat disturbance effects to all these species, affording protection to foraging birds and some nesting colonies.

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1. Introduction

Human activity can have a broad range of impacts on birds (reviews in Gill *et al.* 1996, 2001, Hill *et al.* 1997, Carney and Sydeman 1999, Gill and Sutherland 2000, Nisbet 2000, Frid and Dill 2002). These impacts can have direct or indirect consequences ranging from reduced foraging rates (e.g. Galicia and Baldassarre 1997; Rees *et al.* 2005) and displacement from foraging areas (e.g. Pfister *et al.* 1992; Gill *et al.* 1996) to reduced nesting success (e.g. Anderson and Keith 1980; Schulz and Stock 1991) and even colony abandonment (Cairns *et al.* 1998; Skagen *et al.* 2001). Human-caused disturbance can also lead to direct mortality (e.g. stepped on, vehicle collisions) (see Ruhlen *et al.* 2003) and indirect mortality (i.e. greater predation rates) (Keller 1991; Mikola *et al.* 1994) of individuals. Some studies have even found disturbance effects to have an analogous, if potentially reversible, impact as habitat loss or degradation (Gill and Sutherland 2000; West *et al.* 2002).

From a strictly conservation point-of-view, human disturbance of wildlife only becomes an issue if it causes populations to decline (Gill *et al.* 1996, 2001), or abandon large regions of their range. As such, there have been efforts made to quantify the effects of human disturbance on wildlife populations (reviews by Hockin *et al.* 1992; Gill *et al.* 1996). Traditionally, studies focused on the degree of behavioural response as an indicator of a species susceptibility to disturbance events (review in Carney and Sydeman 1999). A common indicator of the threshold between staying and fleeing has been the flight distance (Ydenberg and Dill 1986), often termed the flight initiation distance. This flight initiation distance has been used in management recommendations to create buffer zones and set-back distances between human approaches and species (Erwin 1989; Rodgers and Smith 1995, 1997; Rodgers and Schwikert 2002; Carney and Sydeman 1999; Blumstein *et al.* 2002). Some studies have suggested that alert distance (the distance at which an individual alters its behaviour in response to the disturbance but does not flee) is a better proximate measure of disturbance (Rodgers and Smith 1995, 1997; Fernández-Juricic *et al.* 2001). Physiological changes (e.g. increased heart rate) may be triggered before behavioural responses are elicited (Nimon *et al.* 1995; Wilson and Culik 1995; Fowler 1999; Ackerman *et al.* 2004).

Frid and Dill (1996) defined the risk-disturbance hypothesis, which equates non-lethal human-caused disturbance with natural predation threat, to provide a predictive framework governing animal responses. This hypothesis is driven by the tradeoffs between the costs and

benefits of leaving an area when faced with a predation risk (Ydenberg and Dill 1986; Lima and Dill 1990; Lima 1998). Boat disturbance is not an exact analogy of predation, but threatening stimuli of any kind can induce anti-predator behaviour (Frid and Dill 2002). Birds that do not react to a boat still face a risk (that of collision), and in this sense boat disturbance and predation-risk can be considered analogous. Many factors may contribute to an individual's decision of staying or fleeing, for example: speed of approach (e.g. Burger 1998), angle of approach (e.g. Burger and Gochfeld 1990, 1991b; Bulova 1994), noise level (e.g. Burger 1983; Brown 1990; Delaney *et al.* 1999), amount of available suitable alternate habitat (e.g. Gill *et al.* 2001), distance of approach (e.g. Burger 1981; Belanger and Bedard 1989; Burger and Gochfeld 1991a, 1991b; Grubb and King 1991; Klein 1993; Roberts and Evans 1993; Fernández-Juricic and Telleria 2000).

Some recent work refutes the flight initiation distance as an appropriate index of disturbance susceptibility (Gill *et al.* 2001; Beale and Monaghan 2004). In situations where alternate habitat is lacking, individuals that display a greater behavioural tolerance to disturbance may also experience the greatest fitness costs (Gill *et al.* 2001). Alternatively, individuals in superior physical condition may show greater responsiveness to human-induced disturbance (Beale and Monaghan 2004).

Diving waterbirds are unique in that three disturbance response options exist to them. An individual may choose to remain on the surface of a patch despite the predation threat, flush from the patch to reduce the risk of predation, or dive underneath the patch surface to reduce the cost of leaving the area while simultaneously reducing the predation threat. A diving waterbird may perceive predation risk from above-surface predators (e.g. raptors) differently than below-surface predators (e.g. sea lions). If this is the case, waterbirds should view the human-caused disturbance stimuli from boats as an above-surface predation threat, and react accordingly. Despite the diving option, no studies have measured diving as a response to disturbance. A dive initiation distance can be considered analogous to flight initiation distance in principle, but may represent a compromise between remaining alert to a predation threat and abandoning a site altogether.

Many studies have focused on waterbirds (see Carney and Sydeman 1999) and boat disturbance (Rogers and Smith 1995, 1997; Burger 1998; Rogers and Schwickert 2002; Ronconi and St. Clair 2002), but research has been biased towards non-diving waterbirds (e.g. Rodgers

and Smith 1997) and nesting colonies (Carney and Sydeman 1999). Few studies have investigated boat disturbance on waterbirds that forage on open-water environments, or that forage by diving for prey (e.g. Ronconi and St. Clair 2002).

Members of the families Alcidae and Phalacrocoracidae are widespread and often ubiquitous off the coast of western North America. In near-shore waters off southwestern Vancouver Island, British Columbia, Canada, Marbled Murrelets (*Brachyramphus marmoratus*), Common Murres (*Uria aalge*), Rhinoceros Auklets (*Cerorhinca monocerata*) (these three species collectively referred to as the alcids) and Pelagic Cormorants (*Phalacrocorax pelagicus*) are frequently observed. These species are all members of a fish-feeding diving-guild. The spatial range of these species places them at potential risk to disturbance from recreational and commercial boat activity. Few published studies have investigated boat disturbance on at-sea alcids or cormorants. Speckman *et al.* (2004) documented Marbled Murrelets, upon approach of a boat, swallowing prey that was being held for later delivery to nestlings. Human-caused disturbances can also affect the spatial distribution of seabirds at sea (Kuletz 1996).

In this study I investigated the responses of Marbled Murrelet, Common Murre, Rhinoceros Auklet, and Pelagic Cormorant to boat disturbances. Dive and flight initiation distances were recorded as measures of disturbance, and interpreted based on a variety of predictive variables.

2. Materials and Methods

2.1 Study Area

This study was conducted between 27 May and 5 August 2005 off southwest Vancouver Island. Observations were collected between Port San Juan, near the town of Port Renfrew, (48°33' N, 124°23' W) and Trevor Channel, near Bamfield (48°49' N, 125°08' W). This stretch of coastline follows the West Coast Trail (WCT) Unit of Pacific Rim National Park Reserve (PRNPR), and covers a linear distance of approximately 80 km (Fig. 1). The ocean depth within the study area was usually ≤ 40 m, within the diving depth potential for all focal species.

Most boat traffic in near-shore marine waters of the WCT was from sport fishermen in small (<9 m) motor vessels, and Parks Canada and Quu'as Trail Guardians staff in inflatable boats. Other marine traffic (e.g. charter passenger water-taxi, commercial fishing vessels) was infrequent. Boat activity was heaviest near areas of high salmon and crab harvesting potential,

such as Port San Juan, Camper Bay, Nitinat Narrows, and Barkley Sound. Boats generally operated at low speeds (< 15 km/hr) while trolling and faster (> 25 km/hr) while cruising. During the study period boat traffic was heaviest during the months of July and August, corresponding to peak runs of Chinook salmon (*Oncorhynchus tshawytscha*).

Two Canadian Coast Guard lightstations, a private residence, and a few Quu'as cabins were the only developments apparent from shore along the WCT coast. Marine activity originating from these sites was minimal.

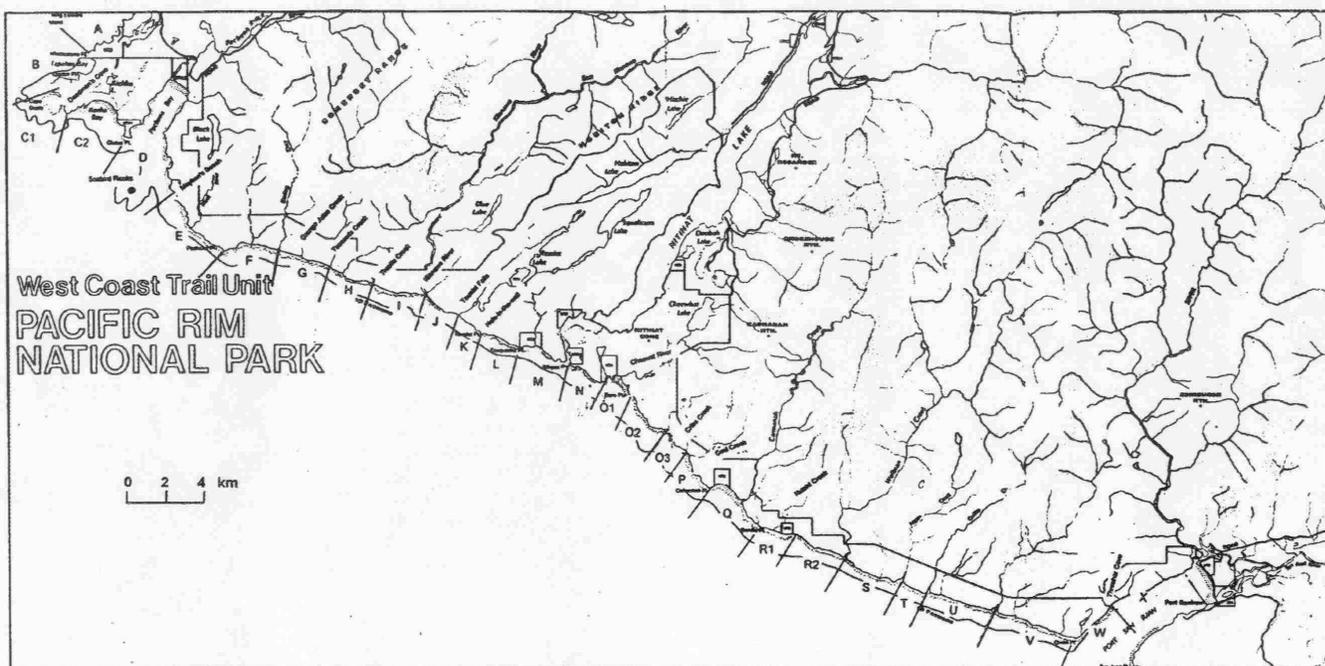


Fig. 1: Study area. Map of the West Coast Trail Unit of Pacific Rim National Park Reserve, Vancouver Island. Letter codes along coastline are location sector codes.

2.2 Data Collection

2.2.1 At-sea Surveys

Observations were collected from a grey-coloured 5 m long rigid-hull inflatable boat with a 50 hp. four-stroke Yamaha outboard motor. Data were collected between 0600 hrs and 2000 hrs. The observers' eye-level was approximately 1.5 m above the sea surface. Birds could easily be observed up to 200 m; beyond this distance detection of surface birds was reduced. Visibility was greatly reduced in rougher seas and in foggy conditions, and no observations that occurred during sea states greater than 3 on the Beaufort Scale (large wavelets, crests begin to break, scattered whitecaps) or during fog were included in analyses. Typically

two observers and one boat operator were present on the boat. Each observer recorded all bird detections from dead ahead to directly off the port or starboard beam (from 0° to 90°). With two observers, a 180° visual hemisphere in front and to each side of the boat was monitored. Observers were in constant communication to prevent double-counting of birds directly in front of the boat (0°). Observers alternated between sides of the boat at non-fixed intervals, as well as alternated between observing and driving the boat, so that any potential observer bias was spread evenly across observations.

Survey transects followed one of three types. Fine-scale transects occurred at 8 sites between Carmanah Bay and Pachena Point, and each followed 3-4 transect lines, running perpendicular to shore from the 5 m depth-contour out to the 30 m depth-contour (approximately 1.5 km offshore) with 500 m spacing between transect-lines. Fine-scale transects were characterized by a constant speed of about 10 km/hr, set to allow the echosounder to function.

Coarse-scale transects were also limited to a 10 km/hr speed to accommodate the echosounder. These transects followed a zig-zag pattern along the coast between Port San Juan and Trevor Channel between the 5 m and 30 m depth-contours.

High-speed transects occurred at all locations between Port San Juan and Trevor Channel, especially while travelling between fine-scale sites. These transects alternated speeds of around 25 km/hr and 35 km/hr between subsequent fine-scale sites, or after approximately 10 minutes of travel. High-speed transects ran parallel to the shore following the 10-m depth-contour. The depth-contour occurred far enough from shore (about 500-1000 m) to avoid frequent obstacles (e.g. rocks and kelp beds), but within a range of broad spatial overlap among species.

Observations, covering all birds of the four focal species, were recorded into hand-held micro-cassette recorders and later transcribed onto data sheets. The data recorded for each individual observation were: species, group size (if associating with one or more hetero- or conspecific individuals), distance from the boat at the time of reaction or closest distance (m), angle from the boat at time of reaction or closest distance, response (categorized as No Reaction, Dive, or Flush), date, time, location (from GPS), boat speed (km/hr), and environmental conditions of Beaufort sea state, swell (m), wind speed (km/h), wind direction, cloud cover (%), precipitation (presence/absence), and visibility (km). A bird was considered to have reacted at the moment of diving or flushing.

Group size was defined by the number of conspecific or heterospecific individuals associating spatially or behaviourally, and with spacing between individuals of not more than 2 m. Individuals within a group were considered behaviourally dependent of each other, and treated as a single data point within the data set. Individuals that were in groups, but which displayed mixed reactions (e.g. one bird dove, another flushed) were not considered as separate independent observations, and were excluded from analyses ($n = 74$).

Distance from the boat to individual bird(s) was estimated in metres. Observers were trained in distance estimation at the start of the season using floating weights attached to rope and dragged behind the boat at pre-calibrated distances of 25 m, 50 m, and 100 m. Distance was noted at the instant of reaction (dive or flush), or at the point of closest contact for individuals with no reaction. Angle was also recorded from the boat to the individual bird(s) at the point of reaction. Angles were estimated at 22.5° increments, such that observations were assigned as 0° (dead ahead), 22°, 45°, 67° or 90° (off the port or starboard beam). All non-reacting individuals were assigned to a default angle of 90°.

Observers' watches and the echosounder were synchronized with the Global Positioning System (GPS). The paper-trace of the echosounder was marked at 2-min intervals during the surveys. The synchronization of sounder time-lines with GPS and watch-time, allowed average prey densities to be calculated and matched to individual bird observations. The vertical depth output of the sounder was manually changed from 20 m to 40 m as depths dropped below 20 m, or from 40 m to 20 m as the depth became shallower.

2.2.2 *On-shore scans*

A Nikon NPL-332 digital theodolite with 26x magnification was used from shore at the Carmanah lightstation to track individual birds reacting to a boat disturbance event. The theodolite was mounted onto a surveyor's tripod, levelled, and calibrated to a visible landmark of known horizontal angle, at the start of each tracking session. Both the research crew's boat and occasional Parks Canada inflatable boats were monitored as they drove in or near Carmanah Bay. Theodolite scanning tracked just in front of the boat's path to locate the origin point of any individuals that flushed. Upon flushing an individual was followed in the theodolite's field-of-view, with points digitally entered along the flight path. The landing point, or last known location of the bird was the last point recorded. Each point entered was automatically designated

a unique number code. The codes and corresponding function (e.g. point 4 = flight path) were written down immediately after tracking of an individual was terminated.

2.3 Data Analysis

2.3.1 Echosounder Interpretation

Sounder output was automatically recorded onto a paper-trace. Transparencies, marked with 5 m depth intervals, were placed over top of the paper output. For each 1 min interval and for every 5 m of depth (up to 40 m) the average prey density was visually scored on a scale of 0 (no prey) to 9 (near saturation) based on the amount and intensity of output (Piatt 1990; Burger *et al.* 2004). Output due to surface slicks, debris, and kelp was identifiable, based on the signal pattern and surface observations, and excluded from the density scores. Salmon and other large (i.e. non-prey) fish were identifiable as single distinct traces on the output and excluded. Remaining traces were assumed to be small schooling fish or euphausiids as found by Burger *et al.* (2004) in the same region. Actual prey density does not increase linearly with the intensity of the sounder output. Prey scores were squared to account for this discrepancy (Forbes and Nakken 1972). I calculated the mean of the squared prey density at all depths within each 1 min interval, and these means were then averaged within transects. As seabird-prey associations within this region may best be mapped at a 1 to 10 km scale (Burger *et al.* 2004), the transect-sized scale (~ 1.5 km) seemed appropriate for analysis.

2.3.2 Location Designation

Location was automatically updated via GPS track as UTM (NAD83) coordinates. Locations were matched to observations by synchronized time stamps, and later converted into 21 sectors (coded A to X) as designated by Parks Canada seabird surveys along the West Coast Trail (Fig. 1). For inclusion in analyses sector codes were re-assigned a numeric value, with code X (southernmost sector) re-assigned a value of 1, and code A (northernmost sector) as 21.

2.3.3 Theodolite Points

Theodolite points were automatically recorded as a series of horizontal and vertical angles. The elevation of the theodolite above sea level (adjusted for tide height) was determined. Basic trigonometric functions were used to determine a pseudo-Northing and Easting based on an origin of (0,0) for each recorded point. These false Northings and Eastings were added to the actual UTM location of the digital theodolite to determine the precise UTM location for every

observation (Ronconi and St. Clair 2002). UTM locations could then be directly compared to determine the distance that the flushed birds travelled.

2.3.4 Statistical Analyses

2.3.4a Parameters and Model Building

Variables of group size, distance, angle, response, time, location, boat speed (km/hr), Beaufort Sea State, swell (m), wind speed (km/h), wind direction, cloud cover (%), precipitation (presence/absence), and visibility (km) were recorded. Swell, wind speed, wind direction, cloud cover, precipitation and visibility were subsequently dropped from analyses due to a large number of missing entries. Date was converted into Julian Date (e.g. 01 Jan = 001, 07 June = 157) and Time to hour of observation. Because the angle of all No Reaction responses was set at 90°, the resulting lack of variation in this value eliminated angle as a variable in any tests comparing No Reaction response to Dive or Flush responses.

Average prey density was included as an independent variable. These data could only be recorded at speeds of 10 km/hr due to echosounder constraints. The average bird density (birds/km²) for Marbled Murrelet, Common Murre, and Rhinoceros Auklet was calculated using data from the Parks Canada seabird database from the years 1994-2004 for Marbled Murrelet and 1993-1996 for Common Murre and Rhinoceros Auklet. High bird density should reflect areas of high value to birds (i.e. good foraging areas). Bird density data for Common Murre and Rhinoceros Auklet did not include sectors A, B, W and X, consequently observations of these species were excluded for those sections.

Location was retained as a variable to test for spatial effects independent of bird density. This was especially relevant to Common Murre and Rhinoceros Auklet, as areas of high bird density may have shifted since the 1993-1996 period. No bird density was available for Pelagic Cormorant.

As not all variables (e.g. angle, prey density, speed) could be included in one model, three separate model sets were developed for each species. These model sets tested which variables or combination of variables best predicted: (1) which parameters elicited any reaction (Dive or Flush) (the Reaction-No Reaction model); (2) which parameters triggered a *reacting* bird to flush rather than dive (the Dive-Flush model); and (3) which parameters triggered a bird to leave (flush from) an area rather than dive or not react (the Flush-Stay model).

All models were run using logistic regression in SPSS 12.0. I defined three sets of *a priori* candidate models including univariate models and a global model containing all parameters and biologically meaningful interactions. All models included parameters of date, sea state, hour, group size, distance, bird density, location, and interaction of group size by distance. Boat speed and interactions of distance by speed, and speed by group size were included in the Reaction-No Reaction and Dive-Flush models. The Dive-Flush model also included angle, and the Flush-Stay model included prey density and interaction of prey density by distance. Bird density was not a variable in any of these models involving Pelagic Cormorants.

2.3.4b Model Selection

An information-theoretic approach facilitated model selection (Burnham and Anderson 2002). Akaike's Information Criterion (AIC) was used to assess the relative strength of support for each model. The second-order Akaike Information Criterion (AIC_c) was computed for each model as AIC_c scores better reflect the strength of each model where $n / K < \sim 40$ (where K was the number of parameters). At high sample sizes the AIC_c values approximate the AIC scores, and the same result was derived (Burnham and Anderson 2002). AIC_c was defined as:

$$AIC_c = -2(\log\text{-likelihood}) + 2K + \frac{2K(K + 1)}{(n - K - 1)}$$

Before AIC analysis, any observations with missing cases were excluded to ensure all parameters had an equal sample size. Delta AIC (Δ_i) and Akaike weights (w_i) were calculated as measures of model strength based on the candidate set of models. Delta AIC values within two score points of the highest ranked model were considered to have very strong support (Burnham and Anderson 2002). The Akaike weight provides a probability of a given model being the best among the candidate set. Evidence ratios were calculated in some cases to compare models. The evidence ratio is the ratio of the Akaike weight of the model of interest (w_j) to the top model (w_i).

Parameter estimates are also presented. Parameter estimates include the estimated coefficient \pm standard error ($\beta \pm SE$) and odds ratio with 95% confidence interval.

2.3.5. Means and Predictive Equations

Mean values are presented \pm standard error (SE) unless otherwise stated.

Logistic regression equations were used to graph the reaction probability based on distance, group size, and sea state. The logistic regression equation follows the formula

$$\text{logit}(P) = b_0 + b_1x_1 + \dots + b_nx_n$$

Solving for the probability (P), the formula is re-arranged as

$$P_{(x)} = \frac{1}{1 + (e^{-(b_0 + (b_1 \cdot x_1))})}$$

where b is the estimated log-odds ratio (slope), and x is a given value (e.g. 10 m for the distance equation, 3 individuals for the group size equation).

3. Results

3.1 Disturbance Results

I collected 4819 behavioural observations during 26 sampling days between 28 May and 04 August. Of the individuals sampled 2852 birds (59.2%) showed no reaction in response to the approach of the boat, 1158 (24.0%) dove, and 809 (16.8%) flushed. Alcids all had No Reaction responses most frequently, and Flush responses the least, while Pelagic Cormorants most often flushed (Fig. 2).

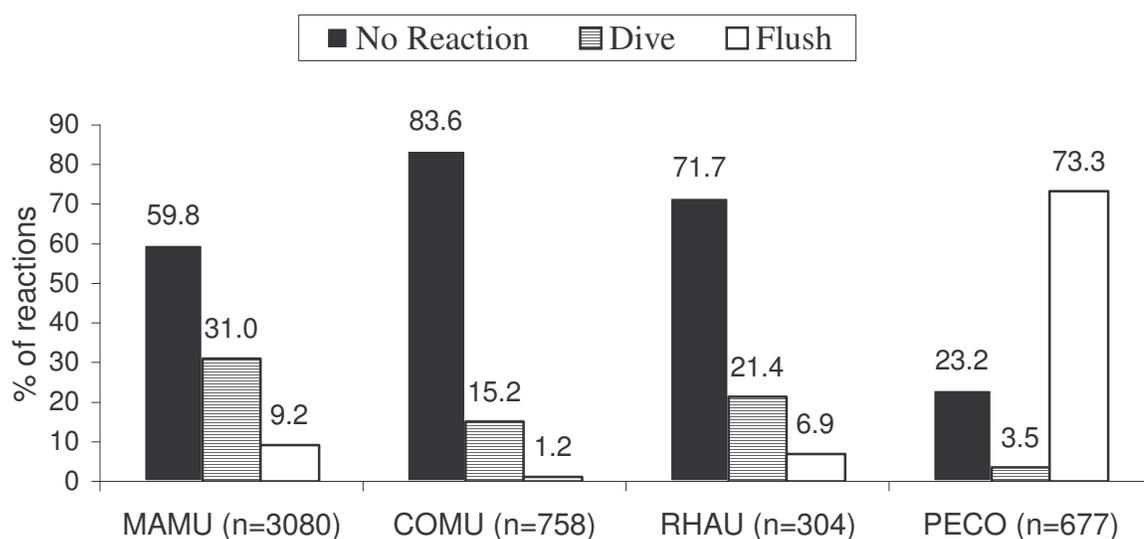


Fig. 2: Total percentage of responses (No Reaction, Dive, and Flush) for each species studied, Marbled Murrelet (MAMU), Common Murre (COMU), Rhinoceros Auklet (RHAU), and Pelagic Cormorant (PECO). Sample sizes were numbers of observations. Alcids all show similar trends, Pelagic Cormorants had a much higher percentage of flushing birds than alcids.

Alcids also all had decreasing reactions up to about a 100 m distance from the boat, while cormorants continued to react strongly at distances greater than 100 m (Fig. 3). Each species was best considered discretely, both for management purposes and as disturbance predictors may be unique to the species (and even individual).

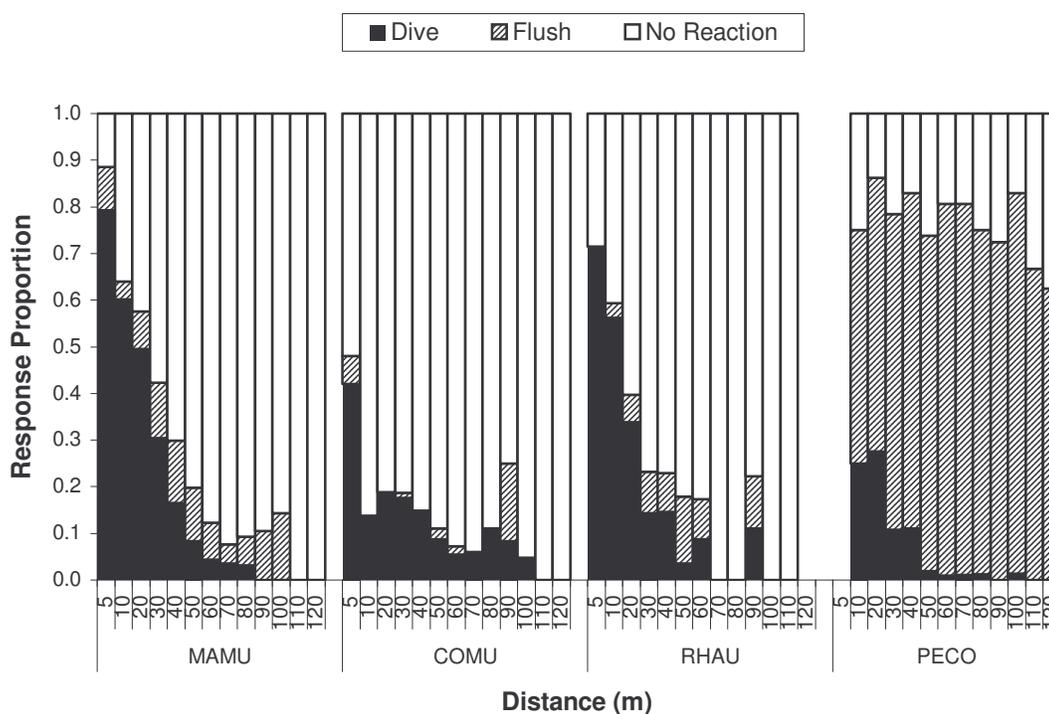


Fig. 3: Proportions of responses (No Reaction, Dive, and Flush) for each species studied, Marbled Murrelet (MAMU), Common Murre (COMU), Rhinoceros Auklet (RHAU), and Pelagic Cormorant (PECO) at approach distances from 5 to 120 metres. Alcids show similar trends, Pelagic Cormorants had a much higher percentage of flushing birds than alcids.

Distances of reaction were similar for all alcids, and the No Reaction and Flush (flight initiation distance) distances were nearly equal within each bird species studied. The dive initiation distance for all species was about half that of the flush initiation distance. The angle of reaction was lower for flushing birds than diving birds (except for Rhinoceros Auklet where it was equal). Group size was also lower for reacting birds than non-reacting birds. The mean values for approach distances, group size and approach angles are shown in Table 1.

Table 1: Mean distances, group sizes, and angles, \pm standard error (SE) for Marbled Murrelet, Common Murre, Rhinoceros Auklet and Pelagic Cormorant for each response type (No Reaction, Dive, and Flush).

	<i>Non-reacting Birds</i>	<i>Diving Birds</i>	<i>Flushing Birds</i>
A) Marbled Murrelet			
Distance to Boat (\pm SE) (m)	42.1 \pm 0.5	20.9 \pm 0.4	36.3 \pm 1.1
Distance to Boat Range (m)	5 - 140	0 - 80	5 - 100
Group Size (\pm SE)	1.8 \pm 0.03	1.5 \pm 0.03	1.4 \pm 0.04
Angle to Boat (\pm SE)	90°	44.3 \pm 1.0°	40.0 \pm 1.8°
B) Common Murre			
Distance to Boat (\pm SE) (m)	37.4 \pm 1.0	26.0 \pm 1.9	41.9 \pm 11.7
Distance to Boat Range (m)	2 - 150	1 - 100	2 - 90
Group Size (\pm SE)	1.5 \pm 0.09	1.0 \pm 0.03	1.2 \pm 0.15
Angle to Boat (\pm SE)	90°	49.5 \pm 3.1°	34.8 \pm 11.3°
C) Rhinoceros Auklet			
Distance to Boat (\pm SE) (m)	43.0 \pm 1.7	21.8 \pm 1.9	38.6 \pm 4.0
Distance to Boat Range (m)	5 - 140	2 - 90	10 - 90
Group Size (\pm SE)	1.7 \pm 0.11	1.4 \pm 0.15	1.4 \pm 0.13
Angle to Boat (\pm SE)	90°	44.1 \pm 3.9°	43.7 \pm 5.5°
D) Pelagic Cormorant			
Distance to Boat (\pm SE) (m)	73.9 \pm 2.8	37.9 \pm 4.5	72.7 \pm 1.4
Distance to Boat Range (m)	10 - 200	10 - 100	10 - 200
Group Size (\pm SE)	1.2 \pm 0.04	1.0 \pm 0.00	1.1 \pm 0.02
Angle to Boat (\pm SE)	90°	45.8 \pm 7.0°	32.5 \pm 1.0°

Results for each focal species are presented below.

3.1.1 Marbled Murrelet

A total of 3080 observations of Marbled Murrelets were recorded. Of these, 59.8% showed no behavioural responses to boat approaches, 31% dove, and 9.2% flushed (Fig. 2). The mean approach distance is greatest for non-reacting birds, and least for diving birds (Table 1). Group size and approach angle are highest for non-reacting birds, intermediate for diving birds, and lowest for flushing birds (Table 1). Increased sea state (Appendix A, Fig. 4) and decreased group size (Appendix A, Fig. 5) increased Dive and/or Flush responses in all cases. Murrelets seemed to stop diving at approach distances of 90 m or greater, and stopped flushing at 100 m (Fig. 3). The modelled reaction equation for distance (Appendix A, Fig. 6) showed that while 50% of birds react at 25 m, this probability dropped to 10% at 70 m, and 0% at 120 m.

Reaction-No Reaction Model

According to AIC_c ranking, the global model and a model excluding location, were the only ones found to be highly predictive of reaction (Appendix B, Table 2). The Akaike weight indicated that the global model had a 70.8% chance of being the best among all candidate models tested. Parameter estimates indicate that the probability of reaction (Dive or Flush) increases

with sea state, hour, bird density and location. Increases in date, group size, distance, and (surprisingly) speed decrease probability of reaction. Of those variables, sea state and group size had the most significant effect on reaction. For every one incremental increase in sea state, an individual was 27.4% (odds-ratio = 1.274) more likely to react, and was 23.2% (odds-ratio = 0.768) less likely to react with every increase in group size (Appendix C, Table 3).

Dive-Flush Model

The best approximating model for predicting whether a reacting bird would flush included the variables date, sea state, hour, group size, distance, speed, location and interactions of distance by speed, group by distance and speed by group (Appendix B, Table 4). It had an Akaike weight of 0.73, and included neither bird density nor angle of reaction. There was a positive relationship between flush response and sea state and distance, and a negative relationship between the variables date, group size, speed and location (Appendix C, Table 5). In this model the odds-ratio predicting flushing was 1.434 for sea state and 0.824 for group size.

Flush-Stay Model

There was substantial evidence for four models within this set ($\Delta AIC_c < 2$) (Appendix B, Table 6). All four models included bird density, sea state, and group size as important predictive parameters. One model included only these parameters, another included hour, the third added only fish density, and the fourth included an interaction term between group and distance. The top-ranked model had an Akaike weight of 0.32, and was the simplest model of that reduced set ($K = 3$). The second-ranked model had 12% lower probability of being the best model, according to the evidence ratio. As the top model also had the highest Akaike weight, included the fewest parameters, and contained the core parameters present in all models with substantial evidence, it was assumed to be the best choice. Bird density, sea state and group size were the best predictors in determining if a murrelet will flush from an area. Marbled Murrelets have a 63.2% greater chance of leaving an area with increases in sea state, and 32.8% lower chance of leaving an area with increases in group size (Appendix C, Table 7).

3.1.2 Common Murre

A total of 758 observations of Common Murre were recorded from at-sea surveys. Of these, 83.6% showed no behavioural responses to boat approaches, 15.2% dove, and 1.2% flushed (Fig. 2). Mean approach distance was lowest for diving birds (Table 1). Mean approach angle was

lowest for flushing birds, and group size lower for reacting birds than non-reacting birds. As very few Common Murres flushed, variance among parameters concerning flushing was quite large, and caution was needed in interpreting these results. Sea state increases did not greatly increase the probability of reaction in murres (Appendix A, Fig. 4). Reaction responses generally stopped at approach distances greater than 100 m, and the probability equation showed that while only 30% of birds reacted at immediate distances, this was further reduced to 10% at 70 m (same as for murrelets) (Appendix A, Fig. 6).

Reaction-No Reaction Model

According to AIC_c ranking, three models were worth consideration as the best model. The highest-ranked model included sea state, group size, distance, speed, hour, date, and bird density (Appendix B, Table 2). It had a model weight of 0.40 and was 2.3 times more likely than the second best model. The second-best model was identical but included location as a variable. The third highest-ranked model had variables sea state, distance, group size, speed, date, hour, location, and interactions of distance by speed, group by distance, and speed by group. Given that the highest-ranked model has a greater weighted value, and included the fewest parameters, it can be assumed that it was the best model out of the candidate set. Group size was the most predictive univariate parameter as probability of reaction decreased with increased group size by 70.2% (odds ratio = 0.298) (Appendix C, Table 3).

Dive-Flush Model

There was a general lack of concordance between models in the dive-flush set for Common Murre. There was evidence ($\Delta\text{AIC}_c < 2$) supporting eight of the candidate models. These eight models had a likelihood of best model ranging from 3.9% to 9.8% (Appendix B, Table 4). The highest-ranked model used variables distance and group. The next two highest-ranked models were tied in AIC_c score and included parameters of distance, group and speed for one model, and speed, group and distance by group for the other. The highest-ranked model was only 1.15 times and 1.68 times more likely respectively than the simpler models of distance and angle, and distance alone. Confidence intervals for all odds-ratio estimates showed that only distance did not include the value 1 within the interval (95% C.I. = 1.003, 1.062) (Appendix C, Table 5). The univariate model 'distance', though weak, was considered the best approximating

model for predicting whether a reacting bird would flush, despite the lower AIC_c scores of some models.

Flush-Stay Model

There was substantial evidence for five models within this set ($\Delta AIC_c < 2$). All five models included fish density as an important predictive parameter. The highest-ranked model was univariate. The next four models were bivariate and in order of rank included sea state, distance, location, and group size (Appendix B, Table 6). The top model was 2.45 times more likely than the second best model. All confidence intervals for the odds-ratio bound one, but average prey density appears to be the most significant parameter (Appendix C, Table 7) predicting if a bird will flush from an area. Increased prey density reduced the likelihood of a bird fleeing the site.

3.1.3 Rhinoceros Auklet

A total of 304 observations of Rhinoceros Auklet were recorded from at-sea surveys. Of these, 71.7% showed no behavioural responses to boat approaches, 21.4% dove, and 6.9% flushed (Fig. 2). Rhinoceros Auklets followed the same trends as Marbled Murrelet and Common Murre, with mean distance being lowest for diving birds, group size being highest for non-reacting birds, and approach angle being lowest for flushing birds (Table 1). As with the other alcids, Rhinoceros Auklets had a 10% probability of reaction at 70 m from boats (Appendix A, Fig 6), and approached 0% reaction probability at 120 m. Similarly, all reaction responses seemed to cease at distances of more than 100 m based on the raw data (Fig. 3). Increased reaction probability occurred with smaller group sizes (Appendix A, Fig. 5) and more severe sea states (Appendix A, Fig. 4).

Reaction-No Reaction Model

One model within this set was within two AIC_c scores of the highest-ranked model, but another was close enough ($AIC_c = 2.08$) to warrant further investigation (Appendix B, Table 2). The highest-ranked model included sea state, distance, group size, speed and date. The second highest model included only distance and speed, while the third highest included group size. The weights of the two highest ranked models were similar ($w_i = 0.276$ and 0.269) and higher than the third model ($w_i = 0.098$). Distance was included in all three candidate-models. The odds-ratio confidence interval for distance did not contain 1 (95% confidence interval = 0.947, 0.975).

All other parameters bound 1 in their confidence intervals (Appendix C, Table 3). An evidence ratio between the top and second-best models was only 1.03. ‘Distance and speed’ was considered the most parsimonious model. Birds were less likely to react with increased distance and increased speed.

Dive-Flush Model

The dive-flush model candidate set contained nine models supported by AIC_c score. Distance and speed was the highest-ranked with a 14.2% chance of being the correct model out of the candidate set. The model ‘speed + group + distance by group + group by speed + distance by speed’ was the second highest-ranked model, followed by a univariate distance model. With little additional variation being explained by the inclusion of more parameters, either the distance or ‘distance + speed’ models were considered best. Distance was the only parameter with a confidence interval that did not bound 1 (95% C.I. = 1.017, 1.085). The evidence ratio between the top-model and the distance model was low (1.17). Distance was chosen as the best model for predicting if reacting birds would flush.

Flush-Stay Model

There was substantial evidence for four models within this set (Appendix B, Table 6). The highest model included variables sea state, distance, group, prey density, date, and a group by distance interaction. The second highest model contained only the parameters group size and prey density. All supported models included prey density and group size. The top model had an Akaike weight of 0.16 versus 0.11 for the second best model. The odds-ratio confidence interval for hour did not bound 1 (Appendix C, Table 7), but this parameter was not selected in any models. Prey density and group size were likely the greatest individual predictors, but the model ‘distance + group size + prey density + date + group by distance’ was chosen as the prime model in the Flush-Stay model set.

3.1.4 Pelagic Cormorant

A total of 677 observations of Pelagic Cormorant were recorded from at-sea surveys. Of these, 23.2% showed no behavioural responses to boat approaches, 3.5% dove, and 73.3% flushed (Fig. 2). Pelagic Cormorants followed the same pattern in mean distances, group sizes, and approach angles as the alcids, but cormorants reacted at greater distances, and over a greater range of distance (Table 1). Diving rates for Pelagic Cormorants were lower at approach

distances greater than 50 m, but flushing remained greater than 70% even at distances more than 100 m (Fig. 3). Increased sea state increased probability of reaction (Appendix A, Fig. 4), and increased group size reduced reaction probability (Appendix A, Fig. 5). The group size affect was stronger for Pelagic Cormorants than for the alcids.

Reaction-No Reaction Model

The global model was the highest-ranked model predicting reaction. It included the variables sea state, distance, group size, speed, date, hour, location, and the interactions distance by speed, group by distance, and speed by group. Akaike weight for this model was 0.32. There was a positive relationship between reaction and sea state ($\beta = 0.27$), and a negative relationship between reaction and hour, group size, and location ($\beta = -0.079$ to -0.763) (Appendix C, Table 3). There was no relationship between date and reaction ($\beta = 0.01$). Changes in group size affected reaction probability greatest, with individuals being 54.4% less likely to react per unit increase in group size.

Dive-Flush Model

The dive-flush model candidate set contained three models with high AIC_c support (Appendix B, Table 4). The top model had a model weight of 0.210. It included hour, location, and distance by group. The third top model differed by including distance. The evidence ratio between the top and third-highest models was 2.24. The second top model did not include hour which was a good predictor based on the parameter estimates ($\exp\beta = 0.850$) (Appendix C, Table 5). The model 'hour + location + distance by group' was the best model out of this candidate set.

Flush-Stay Model

The two competing models within this set differed by a single parameter. The second highest-ranking model included distance, group size, prey density, date and group by distance interaction. The top model also included sea state. The weight of the top model was 0.31 (Appendix B, Table 6). There was substantial evidence to accept the top-model in this case. Parameter estimates indicate that group size may be the most significant single variable in predicting cormorants' decisions to leave an area ($\exp\beta = 0.59$) (Appendix C, Table 7). Pelagic Cormorants were 41.4% less likely to leave an area with increases in group size.

3.2 Theodolite Surveys

Theodolite observation of disturbance events occurred on 12 days between 27 May and 05 August. Flights in response to an approaching boat were tracked from origin to termination for six Marbled Murrelets and 31 Pelagic Cormorants. For murrelets, the mean flight distance was 115.84 ± 21.6 m (range 51.0 – 203.7 m) with an average flight time of 40.2 ± 19.7 s (range 8 – 130 s). The time to resume foraging after landing was 65.2 ± 35.4 s ($n = 4$, range 23.7 – 171.0 s) (Figs. 7 & 8). For cormorants, the mean flight distance was 667.0 ± 120.4 m (range 39.5 – 2922.3 m) with an average flight time of 88.1 ± 15.7 s ($n = 28$, range 5 – 362 s). Time to resume foraging after landing was 279.9 ± 79.8 s ($n = 7$, range 79.0 – 720.0 s) (Figs. 7 & 8). On eight occasions (25.8%) Pelagic Cormorants terminated their flights by landing on rocks.

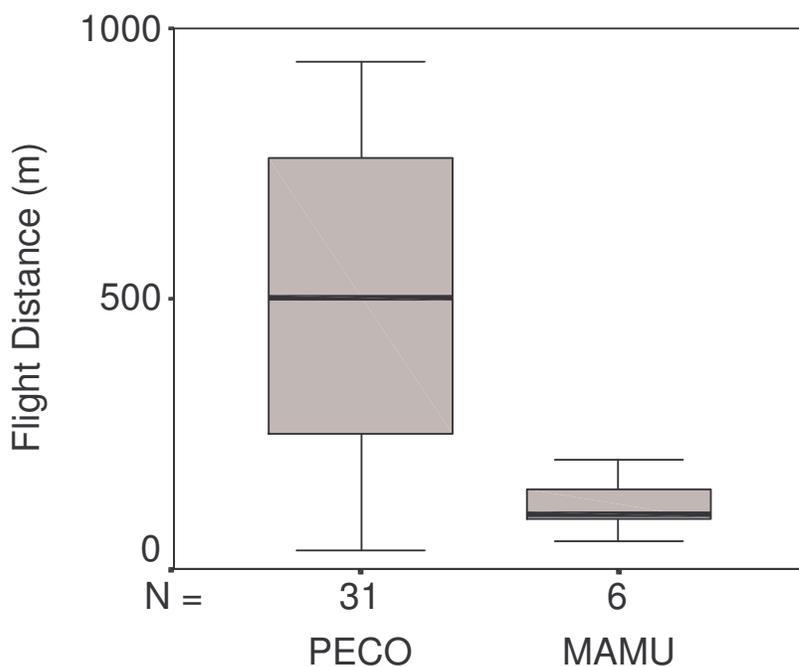


Fig. 7: Box-and-whisker plot showing median (thick line), 25 and 75% quartiles (grey box) and extreme values (whiskers) of flight distance in metres for Pelagic Cormorants (PECO) and Marbled Murrelets (MAMU) based on the theodolite observations from Carmanah Bay. Sample sizes shown are the number of observations.

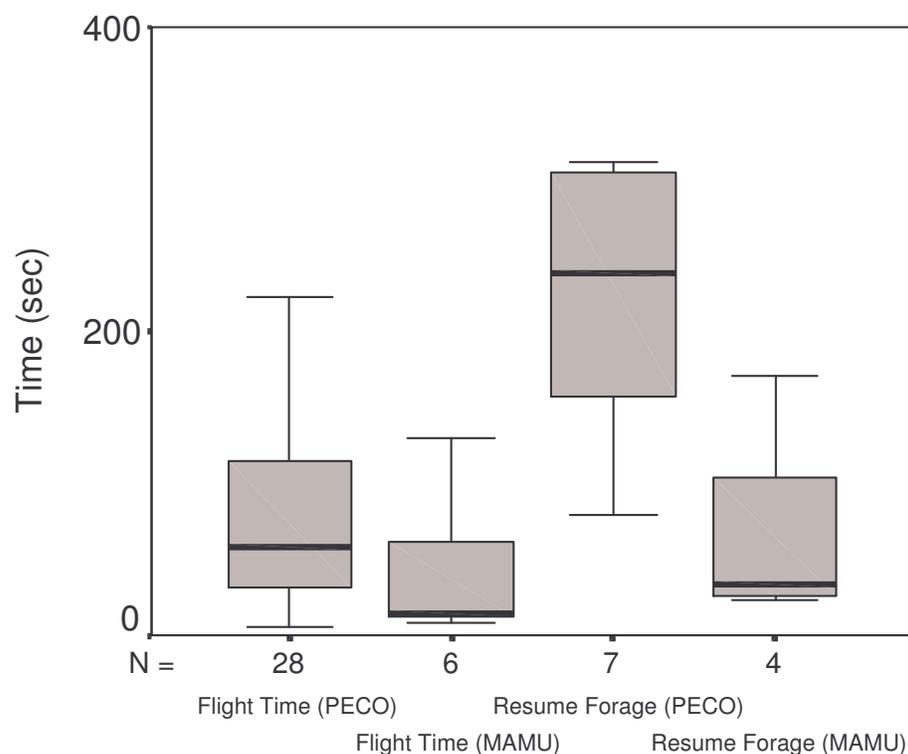


Fig. 8: Box-and-whisker plot showing median (thick line), 25 and 75% quartiles (grey box) and extreme values (whiskers) of flight times and time to resume foraging after landing from a flushing event, for Pelagic Cormorants (PECO) and Marbled Murrelets (MAMU) based on the theodolite observations from Carmanah Bay. Sample sizes shown are the number of observations.

4. Discussion

The state of an animal represents the combination of its internal and external environments as well as its perceived view of these conditions (McNamara and Houston 1996). Birds in this study were exposed to a single threat (approaching boat) that varied in its risk (e.g. angle of approach, speed) as perceived by each individual. Thus, results suggested a combination of species-specific responses and individual state was important in the decisions of birds to react to boat disturbance.

Alert distance could not be quantified in this study. In some cases, especially for Pelagic Cormorants, the alert distance of the individual may have been greater than our moment of first detection. Alert behaviours (e.g. outstretched neck) were observed in many cases indicating that risk was being assessed before a response was observed. No reaction as categorized in this study may still be considered a reaction if it alters behaviour from disturbance free conditions (i.e. lost foraging time). As a No Reaction response in this study cannot be separated from a 'no reaction' state, in which the individual was unaffected behaviourally and physiologically, this response

was assumed to have no or minimal costs to an individual. Birds that displayed a No Reaction response were still making a decision based on risk, and this risk assessment likely originated before the time of response. The dive initiation distance and flight initiation distance may represent thresholds of risk assessment in which the costs of remaining on the surface outweigh the costs of fleeing.

Habituation is a potentially confounding factor. At least in some areas murrelets seem to habituate to boat traffic (McAllister unpubl. data cited by Strachan *et al.* 1995). Within our study area habituation could not be tested, as the focal species are all highly mobile, and no data exist as to foraging site fidelity. Other studies have shown that in some species habituation to disturbance is minimal (Burger and Gochfeld 1990, Bleich *et al.* 1994), or that repeated disturbances may even increase disturbance effects (Dill *et al.* 1974). Habituation is assumed negligible in this study, though further investigation into this subject is required.

As all focal species were diving birds that compete for similar resources and share spatial boundaries, I would expect responses to be similar among species. This trend held for the three alcids as the majority of responses were categorized as No Reaction. Fewer birds dove, and the least flushed. Pelagic Cormorants did not display this pattern. Boat disturbance caused the majority of cormorants to flush with fewer cases of no reactions, and less diving responses being elicited. Larger species generally react sooner to disturbance events (Rodgers and Schwickert 2002; Fernández-Juricic *et al.* 2001; Cooke 1980; Humphrey *et al.* 1987; Holmes *et al.* 1993; Skagen *et al.* 1991). Smaller species may incur heavier costs to fleeing based on greater surface area to mass ratios (Holmes *et al.* 1993). Alternatively, or in conjunction, larger species may have greater perceptual ranges that allow them to detect approaching predators sooner (Kiltie 2000). Cormorants are long-necked species, indicating that detection range may play a role in reacting to boat approaches. Greater perceptual range provides a mechanism for understanding how cormorants react sooner, but not why. Availability of suitable alternate habitat plays a key role in bird reactions to human disturbance (Gill *et al.* 2001). Pelagic Cormorants may seek shelter on nearby rocks, an option not available to the other seabirds studied. Greater flushing distance in cormorants may reflect lower costs of flight, and more option in alternative sites. Common Murres had the lowest flushing frequency, despite being the largest alcid studied. Other variables are likely more important in risk assessment for murres (e.g. alternate foraging sites), and deviations from the size to reaction-distance relationship have been reported by others

(Gutzwiller *et al.* 1998; Fernández-Juricic *et al.* 2002). Thus, size *per se* is not a main factor in responses of these species to boat disturbance, but differences in reactions among species and between alcids and cormorants were evident.

Within each species the mean distance for No Reaction individuals was about the same as the flight initiation distance. In all cases dive initiation distance was the lowest. This may indicate that some flushing threshold was reached, based on a combination of internal and external conditions at which point a bird decided to flush. In other words, the mean No Reaction distance represented the distance of flushing tolerance, after which any condition(s) that may have operated to reduce that distance (e.g. angle of approach) triggered a flush response in some birds. Diving distances were about half the flushing distances, and generally occurred at larger approach angles. This may be due to the more direct approach towards birds that eventually flushed. Birds that dove may not have perceived the boat as an immediate threat, and thus a flush response would not be warranted. As the boat distance decreased towards birds not directly in front, the approach angle increased. If the distance was below some distance-threshold level, a bird would be more likely to dive, but not flush. Although this geometric correlation between angle and distance seems the most likely explanation for the lower reaction angles of flushing birds, birds are likely constantly assessing and re-assessing risk. In some cases a bird may base its reaction decision on two thresholds. The flushing threshold in which a bird chooses to remain in or leave a site, and a diving threshold in which the bird has a commitment to the location, but assessed the cost of diving as less than the costs of remaining on the surface. For example, a bird engorged with food may incur greater energy costs associated with flushing and so the flushing threshold is not triggered, but the same bird will dive once the boat approach distance crosses the diving distance-threshold. This may help explain the situation in Rhinoceros Auklets where approach angles were equal between diving and flushing birds. I refer to this interpretation as the double-threshold hypothesis.

Comparisons between model sets are confounded by different sample sizes and parameter combinations, but models predicting whether birds will abandon a site (flush) versus remain in that patch (dive or not react) were different from parameters predicting whether a reacting bird will choose to flush or dive. This suggests that a bird was constantly assessing predation risk and re-evaluating the cost-benefit dynamic.

4.1 Parameter Effects

Date

On its own date had no significance. As a variable date was supported only in the more complex models, and likely relates to temporal changes in other factors. These factors may have included chick-rearing periods or prey movement cycles. Coefficients and odds ratio confidence interval values indicated a neutral relationship with date for all models.

Sea state

Sea state when significant in a model, was often a strong predicting variable. The relationship between sea state and probability of reaction or flushing was positive, i.e., increases in sea state increased reaction and flushing responses. Since sea state and wind speed are positively correlated, increases in sea state correspond to increases in wind speed. Birds on the water may gain lift quicker and incur less energetic costs in windier conditions. Additionally, monitoring of an approaching boat may be more difficult for birds in rougher sea conditions, increasing the perceived risk to the birds.

Time of Day

Hour had both positive and negative predictive relationships depending on the model it was present in. When hour was positively related to disturbance or flushing events, birds might have been reacting under a heightened awareness state due to diurnal predators (e.g. Bald Eagle (*Haliaeetus leucocephalus*), Peregrine Falcon *Falco peregrinus*), or because they had acquired enough prey resource earlier in the day that reacting was not as energetically stressing. Birds that reacted less later in the day may have done so due to energetic demands. A bird that had lost foraging opportunities earlier in the day, had not located adequate resources, or was trying to locate fish before returning to a nest site may have appeared more tolerant to boat disturbance as the day progressed.

Group Size

In all models that included group size, it was a significant predictor of a reaction or Flush response. In those cases reaction or flushing response decreases with increasing group size. Decreased vigilance per individual with increasing group size has been well documented for many social animals (reviews by Elgar 1989; Lima and Dill 1990; Quenette 1990; Roberts 1996). Pulliam (1973) suggested that predator detection likelihood increases with increased

flock size, and this has been demonstrated in field experiments (Elgar 1989). Roberts (1996) reviewed cases in which individual risk was less in larger groups (in part through greater predator detection), such as through dilution effects. Group size may be associated with prey concentrations in Marbled Murrelets (Strachan *et al.* 1995) and other seabirds off Vancouver Island (Porter and Sealy 1981, 1982). Although larger groups of seabirds may congregate in areas of higher prey abundance, decreased vigilance rates do not necessarily confer greater successful foraging rates (Cresswell 1994; Roberts 1996). Groups of birds may flush less if the individuals in the group wish to remain together (e.g. mated pairs). Individuals in groups could flush simultaneously, but the separation of birds after flight was sometimes observed (potentially a predator avoidance strategy). Increased predator detection rate and decreased predation risk to the individual may explain the reduced reaction rates of groups of birds. As flushed birds could fly together, high patch quality may be the cause of reduced flushing rates for groups of birds in this study.

Distance

The effects of distance between the birds and the approaching boat showed contradicting results. Intuitively a closer distance should cause a bird to react more strongly (either a reaction in the Reaction-No reaction models, or a flush in the Dive-Flush or Flush-Stay models), as predation risk would be greater. This was supported in all of the Reaction-No reaction models, and by previous studies (e.g. Pierce *et al.* 1993; Ronconi and St. Clair 2002). Increases in distance conversely increase flushing probability in all of the dive-flush models. This can be interpreted based on greater distances having lower approach angles. Alternatively, the double-threshold hypothesis may be considered, where a bird that was stimulated by the first distance-threshold (which occurs at greater distances) would be more likely to have flushed than a bird that decided to remain. Birds that remained might have had greater investment in the site, decreasing the probability of fleeing, even as approach distances decreased.

Some birds reacted to an approaching boat by moving away from the boat without diving or flushing. They may have been moving to a distance considered safe. Distance is not necessarily independent of reaction, but rather the distance from the boat may cause the response chosen by the bird.

Speed

The influence of boat speed as a predicting variable was weak at best. This may be due to the heavy bias towards sampling at 10 km/hr. Previous work has shown that disturbance effects of boats increase with increasing speed (Burger 1998). There was a very weak negative relationship between speed and reaction probability, but interpreting this result in terms of predicting bird reaction would likely be erroneous. The interactions between speed and approach distance were found to be significant, even when boat speed alone was not a significant predictor. This result suggests that speed increased reaction probability, but this increase was greatest at closer approach distances. This mirrors the result found for Black Guillemots (*Cephus grille*) by Ronconi and St. Clair (2002). Lafferty (2001) found that faster approach speeds (i.e. joggers) were less disturbing to Snowy Plovers than slower approach speeds (i.e. walkers). Slower speeds may indicate active prey searching or pursuit (i.e. stalking) by the predator to some species (Frid and Dill 2002).

Bird Density

High bird density among the 21 coastal sectors in our study area should reflect areas of higher foraging or resting suitability. Although weak, higher bird density increased the probability of both reactions and flush response. This may have been due to density-dependent factors, such as competition between individuals, which reduces the quality of the site. Alternatively birds in high density areas may have been in better condition, and thus could afford to flee the site more readily (Gill *et al.* 2001; Beale and Monaghan 2004), or may have been reacting based on other birds being disturbed in the same area. Bird densities for Marbled Murrelet, Common Murre, and Rhinoceros Auklet were calculated based on averages of previous years' surveys. Lack of predictive power may either reflect truly on bird density effect, or a difference in density or distributions of birds between the study period and previous survey years.

Location

Location as a variable tested for coarse spatial differences in reactions along the survey routes. Location was entered based on sector codes, though sectors differed in length. A positive relationship suggests that reaction or flushing response increases as one moves from south to north along the study area. Northern regions often had rougher sea conditions, and may be correlated with parameters previously described. Spatial effects varied among species and

models, though location was only significant on its own in three cases. Marbled Murrelets were more likely to react, but less likely to flush, and Pelagic Cormorants were less likely to react, in the northern locations.

Average Prey Density

Average prey density could only be incorporated into the Flush-Stay model as echosounder use was limited to a constant low speed of travel. Prey density was an index of patch quality. Negative relationships between flushing from a site and prey density may reflect the benefit to an individual of remaining in a patch of high quality. This may be especially apparent for species that feed on highly mobile or concentrated prey (Gill *et al.* 2001), as was the case for these waterbirds. Positive relationships may reflect the greater physical condition of individuals within high quality patches allowing an escape response without detriment to the fitness of that individual. Because seabird-prey associations are sensitive to scale (Burger *et al.* 1994), analyses on different scales may have yielded different results. Prey density was not significant on its own for any species, and had a negative relationship only with Common Murre. The inclusion of this term in many of the top candidate models for all species indicates that in combination with other factors, prey density is an important variable, though its effects are difficult to interpret.

Angle

Angle of approach can influence reaction and more direct approaches should purvey greater predation risk, and therefore trigger greater flight initiation distances (Burger and Gochfeld 1990; Burger and Gochfeld 1981; Walther 1969). Angles of 0° necessarily caused a reaction (failure to react would have led to collision), while all no reactions were default to 90° angles of approach. Without variation in angle for non-reacting birds, it could only be included in the dive-flush model. Shallower angles were expected to elicit more energetically costly responses due to assumed increase in predation risk. Angle was not found in any top model. Its occurrence in models within 2 AIC_c scores of top-models indicates that it does have some influence. As approach angle increased, individuals were less likely to flush. Its use in the models was confounded by the geometric correlation with approach distance (i.e. angle increases as approach distance decreases) (Bulova 1994; Frid and Dill 2002). An individual may assess

angle during an initial response decision, and angle could be significant in that decision, despite its lack of importance in these results and geometrical correlation with distance.

4.2 *Species-Specific Responses*

4.2.1 *Marbled Murrelets*

Marbled Murrelets appear to base their decision to react on a combination of all parameters and interactions tested. Of birds that reacted to an approaching boat, all parameters and interactions except murrelet density applied. In deciding to leave or stay at a site, bird density, sea state and group size are important predictors.

Sea state and group size were the strongest univariate predictors in all three model-sets. In all cases Dive and/or Flush responses increased with increasing sea state and decreasing group size. The few flushing events that were tracked in Carmanah Bay with the theodolite suggested that Marbled Murrelets were not flying far, and generally resumed foraging fairly quickly. Although the sample size for those results was small, it may indicate that flushed birds still had a commitment to the site they were at.

Our results of reaction proportions were similar to those reported by others (C. Strong, unpubl. data cited by Strachan *et al.* 1995). Strong found 23.4% of birds dove and 15.4% flushed, versus 31% and 9.2% in our study, respectively.

A recent study has suggested that single foraging Marbled Murrelets may represent breeding individuals during the incubation phase (Mack *et al.* 2004). If the hypothesis of group size as an index of productivity was true, then boat disturbance could have disproportionate fitness costs affecting reproductive individuals, especially as our study found that single birds were more likely to react to boat disturbance.

Carter and Sealy (1990) reported that foraging groups of three or more birds did not dive together in any coordinated pattern. The observations in this study of synchronous diving by groups of Marbled Murrelet supports the assumption that birds were diving in response to the boat disturbance as opposed to regular foraging dives.

4.2.2 *Common Murre*

According to the models, Common Murres seem to react based on many of the parameters tested, but specific variables in determining their flush response (distance and speed in the Dive-Flush model). Reacting birds were more likely to flush at greater distances than dive. Average prey density best predicted site abandonment with higher prey density reducing

flushing probability. Caution should be used in interpreting these results. Only 1.2% (or 9 individuals) of Common Murres flushed. Average prey density may partially explain why Common Murre flush, but further research on this question would be needed.

Group size and distance are the most significant univariate parameters predicting reaction, though single murrelets have a much lower reaction probability than single birds of the other species. Reaction responses generally stopped at distances greater than 100 m.

4.2.3 Rhinoceros Auklet

Distance and speed were the best predictors in auklet reaction behaviour according to the models. There was an increase in reaction probability as distance decreases. Among reacting birds increased distance predicted increased flushing probability. Again, either the geometric correlation between angle and distance, or the double-threshold hypothesis could be invoked to explain this. Approach angles were equal between diving and flushing birds, supporting the double-threshold explanation in this case. Rhinoceros Auklets appear to have based site abandonment decisions on a greater number of variables, including group size and average prey density than the other species considered in our study. Although little confidence exists for those two parameters individually, auklets appear to abandon sites more often when in smaller groups, or where there is greater prey density

As with the other alcids, Rhinoceros Auklets reaction probability declined to 10% at 70 m from our boat. Similarly, all reaction responses seem to stop at distances of more than 100 m.

4.2.4 Pelagic Cormorants

As with murrelets and murrelets, Pelagic Cormorants appear to be influenced by a large number of parameters in reacting to an approaching boat. Most Pelagic Cormorants reacted to an approaching boat (76.8%). The high proportion of reactions might indicate that the threshold level at which these parameters elicit a response was much lower than in alcids. However, dive distance was still about half that of flush distance, as was true for alcids. The angle-distance relationship is the most parsimonious explanation for this trend for this species, especially as only 3.5% of cormorants dove.

As time of day increased, the probability of flushing decreased. Time of day did not predict if a cormorant would abandon a site in comparison with remaining (diving or not reacting). Sea State, prey density and group size were among the factors that did. Of these,

group size was the greatest predictor. Prey density increases may increase probability of patch abandonment. Again this may be a function of individual condition.

Unlike the alcids, reaction probability remained high even at large distances. Diving rates became negligible at distances greater than 50 m, but flushing rate remained greater than 70% even at distances greater than 100 m.

As well as flushing more and reacting at greater distances, cormorants tracked in Carmanah Bay flew much further distances (667 m) than Marbled Murrelets, and took longer to resume foraging (longer than 4 mins). Some cormorants landed on rocks after flushing. Disturbance effects are greater for Pelagic Cormorants than any of the alcid species studied.

4.3 Conservation Implications

Traditionally buffer zones and set-back distances have been applied to some areas where boat disturbance occurs (Erwin 1989; Rodgers and Smith 1995, 1997; Rodgers and Schwikert 2002; Carney and Sydeman 1999; Blumstein *et al.* 2002). These buffers are calculated based on the tolerance to disturbance as measured by flight initiation distance. Improved buffer zones incorporate alert distance as a more conservative measure of disturbance, further reducing any potential fitness (and population-level) consequences of disturbance (Rodgers and Smith 1995, 1997; Fernández-Juricic *et al.* 2001). The expanding literature suggests that traditional methods of quantifying disturbance may not accurately reflect disturbance impacts (Gill *et al.* 2001; Beale and Monaghan 2004). Thorough investigation into individual energy costs and population-level responses is encouraged for a complete understanding of disturbance impacts on these species. Such data do not yet exist for Pacific alcids or Pelagic Cormorants, or indeed most waterbirds at sea. Recreational boat-disturbance impacts are not even acknowledged in most literature describing potential conservation concerns for this group of birds. This remains an important data gap as human populations increase along the coast, along with increased recreational boat use.

The large difference in predictive parameters among and within species depending on reaction of the birds was indicative that individuals assess risk based not only on the perceived threat, but also on environmental conditions, site characteristics, and probably also individual state. These conditions will vary spatially and temporally. A number of recommendations can be made based on the data from this study.

All alcids have a 10% probability of reaction at 70 m from our boat, and appear to stop reacting at about 100 m. The predictive equation predicts reaction probability approaches 0% at 120 m. Buffers of a minimum distance of 100 m would be effective in reducing the boat disturbance effects to birds. In rougher sea conditions (Beaufort scale 3 or higher) an increased buffer distance of 150 m may be necessary. In cases, such as for Pelagic Cormorants, birds may react before visual detection by a boat-based human observer is possible. At 150 m over 60% of cormorants were still predicted to react. For this species keeping a maximum distance (minimum 200 m) from cormorants would be the best buffer distance. For all species, and especially when a buffer distance is not met, direct approaches should be avoided, specifically approach angles less than 45°.

As there was little evidence that speed on its own had an impact, limits to this parameter would not be necessary. The interaction of speed by distance was significant in most cases. If buffer zones were met, speed again would not be a strong disturbance factor, but birds may react more to faster boats at close distances. Date, hour and location, though included in some models, are also weak predictors of disturbance. Time of day, time of year, or location restrictions would also not be necessary based on these data. However, time of year should still be considered in management recommendations, to reduce impacts during the breeding phase.

Although groups of birds react less to boat disturbance, the buffer zone should be the same as for individual birds. This reduces the boat disturbance effects in areas of high patch quality, eliminates the need for multiple buffer zones which may be difficult for the public to remember, and is a protective measure for these birds if the bird disturbance effects do not adequately reflect the disturbance impacts (Gill *et al.* 2001).

The consistency of pattern between all species indicates that a constant management plan can be invoked for all species studied, and that this recommendation should be based on the most sensitive species. A general buffer of 200 m would eliminate most boat disturbance effects on alcids, and reduce the effects on cormorants. Without thorough knowledge of the impacts of disturbance at the population-level, these guidelines would reduce effects to individuals, which would likely have population-level benefits.

A more conservative approach would be to implement exclusion zones for recreational boat traffic. As areas of high patch quality may vary temporally and spatially (e.g. shift due to sea surface temperature changes), defining one or few set areas would be difficult. An exclusion

zone running along the length of the shoreline of the West Coast Trail out to 1 km offshore would be adequate. Outside this zone individual buffer zones could still be set in place. Beyond 1 km from shore Common Murre was the most commonly encountered species studied, and is also the most tolerant to boat disturbance. This exclusion zone could be seasonal, occurring during periods of greater stress to the birds (i.e. breeding season), and/or during seasons of high boat traffic, as occurs off southwestern Vancouver Island during the summer months.

Most boat traffic off the West Coast Trail is due to recreational fishers. Three Rockfish Conservation Areas already exist along the West Coast Trail (Fisheries and Oceans Canada 2006) that exclude most recreational fishing (though not boating). Some of these conservation areas extend greater than 1 km offshore. Thus, a further closure should not greatly disrupt recreational fishing. As this study took place within and near the boundaries of a national park, exclusion zones could be implemented in accordance with the Parks Canada Agency Act to “manage visitor use and tourism to ensure...the maintenance of ecological integrity...” (Parks Canada Agency Act 1998). Furthermore, Marbled Murrelets are protected under the Canada Species at Risk Act (SARA), and nest in watersheds adjacent to the Pacific Rim National Park Reserve. Buffer or exclusion zones thus can be established for the conservation of species, and in meeting of Department of Fisheries and Oceans, Parks Canada, and endangered species legislations in waters off the West Coast Trail unit of Pacific Rim National Park Reserve.

5. Conclusion

This study provides the first in-depth examination of boat disturbance *effects* of Pacific alcids and at-sea Pelagic Cormorants. The dive initiation distance was proposed as a complementary measure to flight initiation distance for diving birds. Results of this study are a good benchmark for future, more explanatory studies, into boat disturbance *impacts*. Species appear to react to boat disturbances based on different combinations of parameters. Response trends still hold among species, with alcids reacting similarly, and cormorants reacting at much greater distances. Responses seem to increase in rougher sea conditions and in lower group sizes. A buffer distance of 150 m would reduce most disturbance effects to alcids, especially in rougher seas or to lone birds. Minimum distances of 200 m are necessary for cormorants. Approach angles less than 45° should also be avoided. As cormorants may react to boats before detection by human observers, exclusion zones may more adequately reduce disturbances to cormorants and other species.

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Appendix A: Predictive Equation Graphs

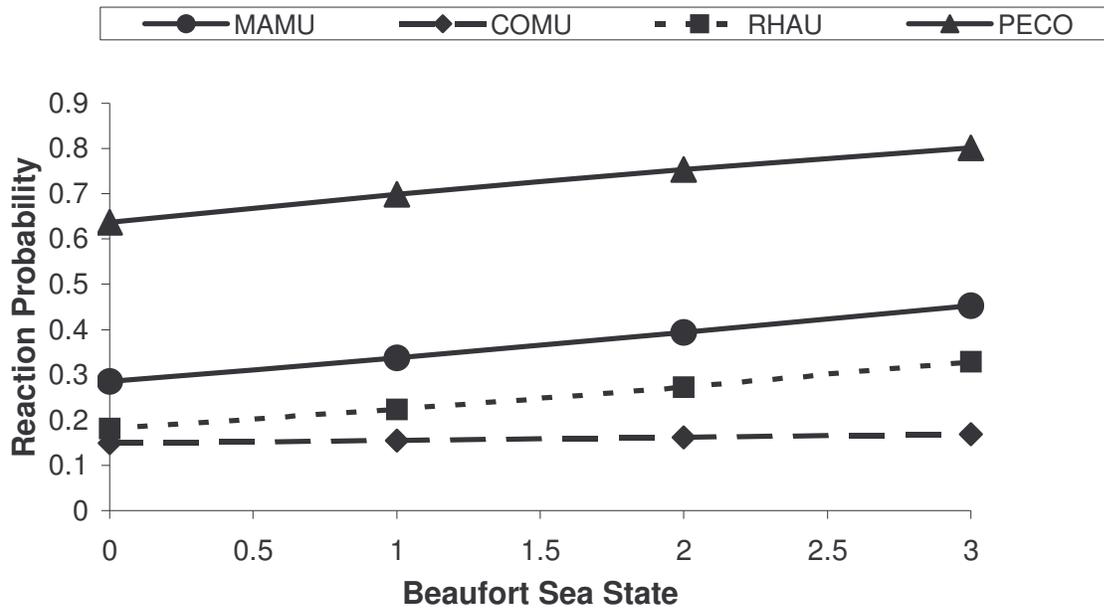


Fig. 4: Reaction (dive/flush) probability as a function of approach distance based on a predictive logistic regression equation (see methods) for the four focal species: Marbled Murrelet (MAMU), Common Murre (COMU), Rhinoceros Auklet (RHAU) and Pelagic Cormorant (PECO). Increased sea state increased reaction probability for all species, except Common Murre, which remained constant.

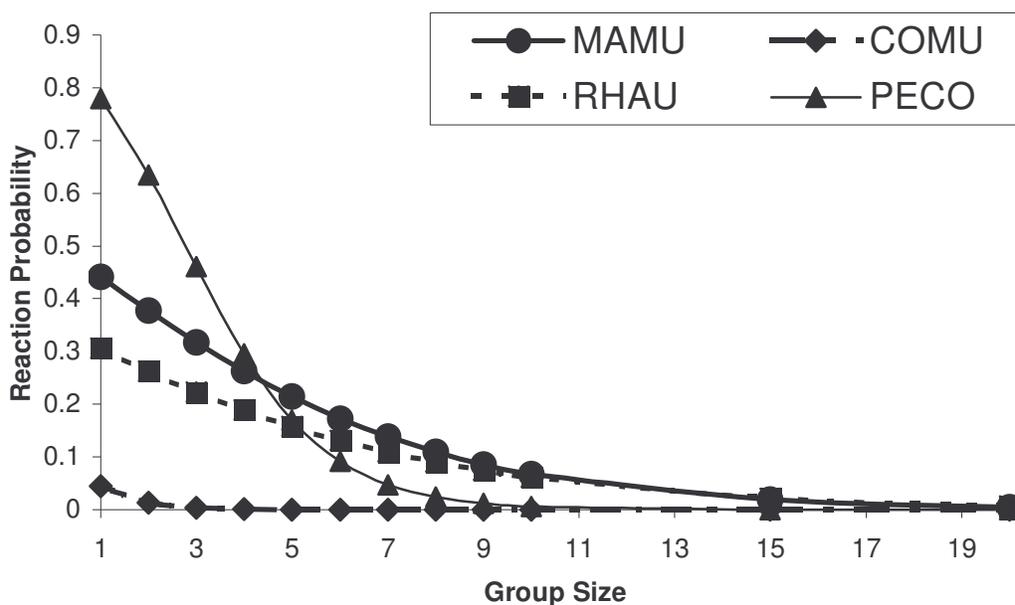


Fig. 5: Reaction (dive/flush) probability as a function of group size based on a predictive logistic regression equation (see methods) for the four focal species: Marbled Murrelet (MAMU), Common Murre (COMU), Rhinoceros Auklet (RHAU) and Pelagic Cormorant (PECO). Cormorants have a greater rate of decline in reaction probability with increased group size than do the alcids.

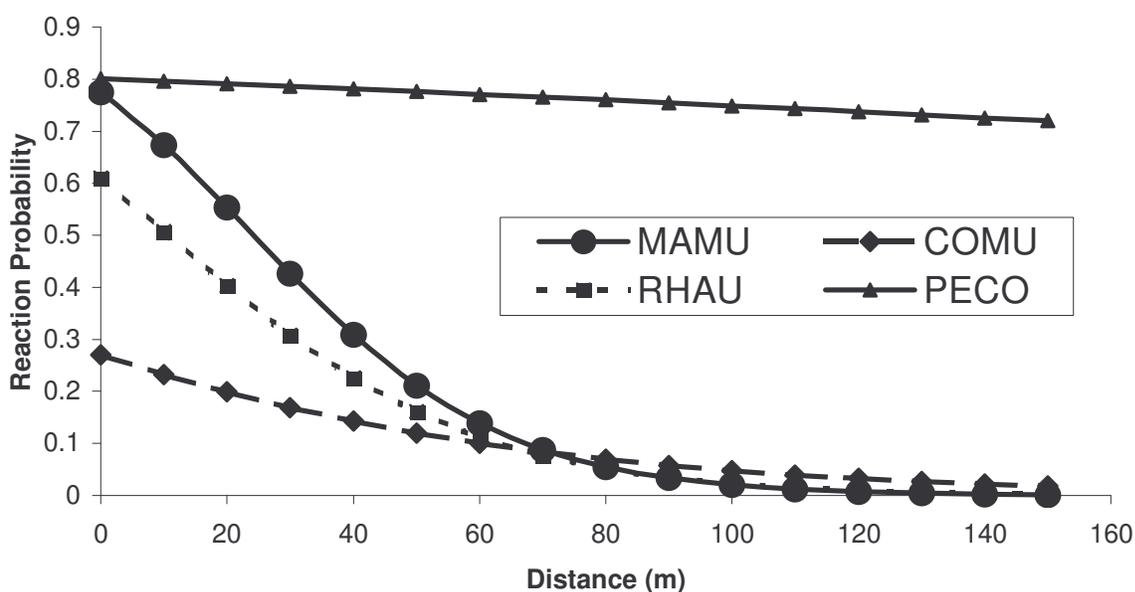


Fig. 6: Reaction (dive/flush) probability as a function of approach distance based on a predictive logistic regression equation (see methods) for the four focal species: Marbled Murrelet (MAMU), Common Murre (COMU), Rhinoceros Auklet (RHAU) and Pelagic Cormorant (PECO). Alcids all follow a similar trend and reach 10% reaction probability at 70 m. Cormorants retain high reaction probabilities at long distances.

Appendix B: Top 5 Candidate Models for the Three Model-Sets for Each Species

Table 2: Top 5 candidate logistic regression models for predicting reaction behaviour (Reaction-No Reaction model) in Marbled Murrelets, Common Murres, Rhinoceros Auklets, and Pelagic Cormorants.

Model Parameters ^a	-2 Log likelihood	κ^b	w_i^c	ΔAIC_c
A) Marbled Murrelet				
SS + Dist + Grp + Spd + Date + Hr + Bird + Loc + Dist x Spd + Grp x Dist + Spd x Grp*	3429.53	11	0.71	0
SS + Dist + Grp + Spd + Date + Hr + Bird + Dist x Spd + Grp x Dist + Spd x Grp	3433.38	10	0.28	1.84
SS + Dist + Grp + Spd + Date + Dist x Spd + Grp x Dist + Spd x Grp	3445.28	8	0.0077	9.71
Dist + Grp + Spd + Date + Dist x Spd + Grp x Dist	3463.12	6	0.0031	11.53
SS + Dist + Grp + Spd + Date + Hr + Loc + Dist x Spd + Grp x Dist + Spd x Grp	3443.26	10	0.0028	11.71
B) Common Murre				
SS + Grp + Dist + Spd + Hr + Date + Bird	539.04	7	0.40	0
SS + Grp + Dist + Spd + Hr + Date + Loc + Bird	533.77	8	0.17	1.67
SS + Grp + Dist + Spd + Date + Hr + Loc + Dist x Spd + Grp x Dist + Spd x Grp	529.83	10	0.16	1.85
SS + Grp + Dist + Spd + Date + Hr + Loc + Bird + Dist x Spd + Grp x Dist + Spd x Grp*	529.39	11	0.07	3.48
SS + Grp + Dist + Spd + Date	542.50	5	0.05	4.27
C) Rhinoceros Auklet				
SS + Dist + Grp + Spd + Date	271.01	5	0.28	0
Dist + Spd	277.24	2	0.27	0.05
Dist + Grp + Spd	277.22	3	0.10	2.08
Dist + Grp + Spd + Date + Grp x Dist + Dist x Spd	271.24	6	0.09	2.33
SS + Dist	281.02	2	0.04	3.83
D) Pelagic Cormorant				
SS + Dist + Grp + Spd + Date + Hr + Loc + Dist x Spd + Grp x Dist + Spd x Grp*	674.63	10	0.32	0
SS + Grp + Hr + Loc + Grp x Dist + Spd x Grp	681.23	7	0.26	0.44
SS + Dist + Grp + Spd + Date + Hr + Dist x Spd + Grp x Dist + Spd x Grp	677.30	9	0.24	0.61
SS + Dist + Grp + Spd + Date + Dist x Spd + Grp x Dist + Spd x Grp	681.00	8	0.10	2.25
Dist + Grp + Spd + Date + Grp x Dist + Dist x Spd	686.66	6	0.05	3.82

^a Model Parameters: **SS** = sea state, **Dist** = distance at moment of reaction, **Grp** = group size, **Spd** = boat speed, **Date** = Julian date, **Hr** = hour of day, **Bird** = average bird density per sector, **Loc** = location, Dist x Spd, Grp x Dist, and Spd x Grp were interaction terms of those variables.

^b Number of parameters in model.

^c Akaike model weight.

* Global Model.

Table 4: Top 5 candidate logistic regression models for predicting flushing behaviour from reacting birds (Dive-Flush model) in Marbled Murrelets, Common Murres, Rhinoceros Auklets, and Pelagic Cormorants.

Model Parameters ^a	-2 Log likelihood	κ^b	w_i^c	ΔAIC_c
A) Marbled Murrelet				
SS + Dist + Grp + Spd + Date + Hr + Loc + + Dist x Spd + Grp x Dist + Spd x Grp	1025.738	10	0.73	0
SS + Dist + Grp + Spd + Ang + Date + Hr + Loc + Bird + Dist x Spd + Grp x Dist + Spd x Grp*	1024.883	12	0.15	3.22
SS + Dist + Grp + Spd + Date + Dist x Spd + Grp x Dist + Spd x Grp	1035.61	8	0.04	5.81
SS + Dist + Grp + Spd + Date + Hr + Bird + Dist x Spd + Grp x Dist + Spd x Grp	1031.87	10	0.03	6.13
SS + Bird + Grp + Ang + Dist x Spd + Grp x Dist + Grp x Spd	1039.335	7	0.02	7.51
B) Common Murre				
Dist + Spd	53.82	2	0.098	0
Dist + Grp + Spd	51.84	3	0.091	0.15
Spd + Grp + Dist x Grp	51.84	3	0.091	0.15
Dist + Ang	54.10	2	0.085	0.28
Dist	56.93	1	0.058	1.04
C) Rhinoceros Auklet				
Dist + Spd	73.51	2	0.142	0
Spd + Grp + Dist x Grp + Grp x Spd + Dist x Spd	66.85	5	0.139	0.03
Dist	75.94	1	0.12	0.32
Dist + Ang	74.98	2	0.07	1.47
SS + Grp + Spd x Dist	72.83	3	0.07	1.49
D) Pelagic Cormorant				
Hr + Loc + Dist x Grp	147.67	3	0.21	0
SS + Grp + Spd + Ang x Dist + Dist x Grp	144.61	5	0.13	1.01
Dist + Loc + Hr + Dist x Grp	147.25	4	0.09	1.62
Dist + Grp	151.84	2	0.07	2.15
SS + Grp + Dist + Spd + Hr	147.57	5	0.03	3.97

^a Model Parameters: **SS** = sea state, **Dist** = distance at moment of reaction, **Grp** = group size, **Spd** = boat speed, **Date** = Julian date, **Hr** = hour of day, **Bird** = average bird density per sector, **Loc** = location, **Ang** = approach angle at moment of reaction, Dist x Spd, Grp x Dist, and Spd x Grp were interaction terms of those variables.

^b Number of parameters in model.

^c Akaike model weight.

* Global Model.

Table 6: Top 5 candidate logistic regression models for predicting site abandonment behaviour (Flush-Stay model) in Marbled Murrelets, Common Murres, Rhinoceros Auklets, and Pelagic Cormorants.

Model Parameters ^a	-2 Log likelihood	κ^b	w_i^c	ΔAIC_c
A) Marbled Murrelet				
SS + Grp + Bird	1043.45	3	0.32	0
SS + Grp + Prey + Bird	1042.42	4	0.20	0.97
SS + Grp + Hr + Bird	1043.39	4	0.121	1.94
SS + Grp + Bird + Dist x Grp	1043.43	4	0.196	1.99
SS + Grp + Bird + Prey + Dist x Grp	1042.40	5	0.07	2.97
B) Common Murre				
Prey	40.01	1	0.21	0
SS + Prey	39.85	2	0.09	1.79
Dist + Prey	39.96	2	0.0813	1.909
Loc + Prey	39.97	2	0.0811	1.914
Grp + Prey	39.97	2	0.0810	1.916
C) Rhinoceros Auklet				
Dist + Grp + Prey + Date + Dist x Grp	60.63	5	0.16	0
Grp + Prey	67.69	2	0.112	0.72
SS + Dist + Grp + Prey + Date + Dist x Grp	59.28	6	0.107	0.82
Grp + Prey + Dist x Grp	66.39	3	0.08	1.51
SS + Grp + Prey	67.47	3	0.04	2.59
D) Pelagic Cormorant				
SS + Dist + Grp + Prey + Date + Dist x Grp	401.32	6	0.31	0
Dist + Grp + Prey + Date + Dist x Grp	403.70	5	0.27	0.30
SS + Dist + Grp + Date + Hr + Prey + Dist x Grp	401.32	7	0.11	2.09
SS + Dist + Grp + Date + Hr + Loc + Dist x Grp	402.22	7	0.07	2.99
Date + Grp	414.03	2	0.03	4.49

^a Model Parameters: **SS** = sea state, **Dist** = distance at moment of reaction, **Grp** = group size, **Date** = Julian date, **Hr** = hour of day, **Bird** = average bird density per sector, **Loc** = location, **Prey** = average prey density, Grp x Dist was an interaction term of those variables.

^b Number of parameters in model.

^c Akaike model weight.

Appendix C: Univariate Parameter Estimates for the Three Model-Sets for Each Species

Table 3. Univariate parameter estimates of the Reaction-No Reaction model for Marbled Murrelet ($n = 3063$), Common Murre ($n = 652$), Rhinoceros Auklet ($n = 268$), and Pelagic Cormorant ($n = 670$).

Parameter	β	SE	P	Exp β (odds ratio)	Exp β 95% C.I.	
					Lower Bound	Upper Bound
A) Marbled Murrelet						
Julian Date	-0.007	0.002	<0.001	0.993	0.989	0.997
Sea State	0.243	0.048	<0.001	1.274	1.161	1.490
Hour	0.027	0.013	0.035	1.028	1.002	1.054
Group Size	-0.264	0.043	<0.001	0.768	0.706	0.835
Distance	-0.051	0.002	<0.001	0.950	0.946	0.955
Speed	-0.012	0.005	0.007	0.988	0.979	0.997
Bird Density	0.007	0.002	0.004	1.007	1.002	1.012
Location	0.018	0.008	0.019	1.018	1.003	1.034
B) Common Murre						
Julian Date	-0.012	0.005	0.012	0.988	0.978	0.997
Sea State	0.051	0.114	0.654	1.052	0.802	1.308
Hour	0.061	0.030	0.041	1.063	1.005	1.145
Group Size	-1.210	0.339	<0.001	0.298	0.172	0.648
Distance	-0.018	0.005	<0.001	0.982	0.974	0.993
Speed	-0.009	0.012	0.452	0.991	0.973	1.023
Bird Density	-0.013	0.011	0.256	0.987	0.966	1.009
Location	0.013	0.015	0.401	1.013	0.950	1.026
C) Rhinoceros Auklet						
Julian Date	-0.013	0.007	0.061	0.987	0.974	1.001
Sea State	0.307	0.159	0.054	1.359	0.994	1.858
Hour	0.023	0.042	0.579	1.024	0.843	1.112
Group Size	-0.174	0.125	0.162	0.840	0.658	1.072
Distance	-0.042	0.008	<0.001	0.959	0.947	0.975
Speed	-0.03	0.017	0.081	0.970	0.938	1.004
Bird Density	-0.023	0.031	0.463	0.977	0.919	1.039
Location	0.008	0.022	0.721	1.008	0.966	1.051
D) Pelagic Cormorant						
Julian Date	0.010	0.004	0.022	1.010	1.002	1.020
Sea State	0.272	0.110	0.013	1.313	1.058	1.627
Hour	-0.079	0.034	0.019	0.924	0.865	0.987
Group Size	-0.763	0.214	<0.001	0.466	0.306	0.710
Distance	-0.003	0.003	0.247	0.997	0.992	1.002
Speed	0.017	0.010	0.087	1.017	0.998	1.038
Location	-0.045	0.017	0.009	0.956	0.924	0.989

Table 5. Univariate parameter estimates of the Dive-Flush model for Marbled Murrelet ($n = 1206$), Common Murre ($n = 105$), Rhinoceros Auklet ($n = 75$), and Pelagic Cormorant ($n = 514$).

Parameter	β	SE	P	Exp β (odds ratio)	Exp β 95% C.I.	
					Lower Bound	Upper Bound
A) Marbled Murrelet						
Julian Date	-0.009	0.004	0.012	0.991	0.984	0.998
Sea State	0.360	0.084	<0.001	1.434	1.217	1.690
Hour	-0.022	0.025	0.386	0.979	0.932	1.028
Group Size	-0.193	0.095	0.043	0.824	0.684	0.994
Distance	0.066	0.005	<0.001	1.068	1.057	1.079
Speed	-0.021	0.009	0.025	0.979	0.961	0.997
Bird Density	0.006	0.005	0.224	1.006	0.997	1.015
Angle	-0.004	0.002	0.051	0.996	0.991	1.000
Location	-0.047	0.015	0.002	0.954	0.926	0.983
B) Common Murre						
Julian Date	0.007	0.016	0.646	1.007	0.977	1.039
Sea State	-0.335	0.438	0.444	0.715	0.303	1.688
Hour	-0.111	0.117	0.344	0.895	0.711	1.127
Group Size	0.936	0.696	0.167	2.62	0.669	10.251
Distance	0.032	0.015	0.031	1.032	1.003	1.062
Speed	0.042	0.037	0.253	1.043	0.970	1.122
Bird Density	-0.007	0.040	0.855	0.993	0.917	1.075
Angle	-0.014	0.011	0.193	0.986	0.965	1.007
Location	0.097	0.081	0.233	1.102	0.940	1.292
C) Rhinoceros Auklet						
Julian Date	-0.007	0.013	0.583	0.993	0.968	1.108
Sea State	-0.315	0.290	0.277	0.730	0.414	1.287
Hour	-0.005	0.077	0.951	0.995	0.855	1.158
Group Size	-0.045	0.246	0.856	0.956	0.590	1.549
Distance	0.049	0.016	0.003	1.050	1.017	1.085
Speed	0.048	0.034	0.155	1.050	0.982	1.122
Bird Density	0.093	0.062	0.132	1.098	0.972	1.239
Angle	-0.001	0.009	0.875	0.999	0.982	1.016
Location	-0.036	0.043	0.408	0.965	0.886	1.050
D) Pelagic Cormorant						
Julian Date	0.011	0.010	0.279	1.011	0.991	1.03
Sea State	-0.100	0.239	0.675	0.905	0.567	1.445
Hour	-0.163	0.079	0.039	0.850	0.728	0.992
Group Size	17.513	5803.84	0.998	4×10^7	0	v. large
Distance	0.061	0.012	<0.001	1.062	1.038	1.087
Speed	-0.014	0.022	0.505	0.986	0.945	1.028
Angle	-0.021	0.008	0.009	0.979	0.963	0.995
Location	0.003	0.040	0.939	1.003	0.928	1.084

Table 7. Univariate parameter estimates of the Flush-Stay model for Marbled Murrelet ($n = 1690$), Common Murre ($n = 372$), Rhinoceros Auklet ($n = 152$), and Pelagic Cormorant ($n = 335$).

Parameter	β	SE	P	Exp β (odds ratio)	Exp β 95% C.I.	
					Lower Bound	Upper Bound
A) Marbled Murrelet						
Julian Date	-0.010	0.005	0.029	0.990	0.981	0.999
Sea State	0.490	0.103	<0.001	1.632	1.333	1.998
Hour	0.028	0.029	0.347	1.028	0.971	1.089
Group Size	-0.398	0.119	0.001	0.672	0.532	0.848
Distance	-0.003	0.004	0.398	0.997	0.990	1.004
Bird Density	0.018	0.006	0.001	1.018	1.007	1.030
Prey Density	0.023	0.031	0.448	1.024	0.964	1.087
Location	-0.017	0.017	0.311	0.983	0.950	1.016
B) Common Murre						
Julian Date	-0.014	0.024	0.542	0.986	0.941	1.032
Sea State	-0.249	0.616	0.686	0.780	0.233	2.610
Hour	-0.053	0.161	0.741	0.948	0.691	1.300
Group Size	0.004	0.172	0.981	1.004	0.717	1.407
Distance	0.009	0.017	0.614	1.009	0.976	1.043
Bird Density	0.004	0.051	0.941	1.004	0.908	1.109
Prey Density	-2.992	2.316	0.196	0.050	0.001	4.700
Location	0.038	0.095	0.689	1.039	0.862	1.251
C) Rhinoceros Auklet						
Julian Date	-0.025	0.018	0.176	0.975	0.941	1.011
Sea State	0.020	0.344	0.953	1.021	0.520	2.004
Hour	0.240	0.107	0.026	1.271	1.030	1.569
Group Size	-0.405	0.474	0.393	0.667	0.264	1.689
Distance	0.002	0.012	0.855	1.002	0.979	1.026
Bird Density	-0.031	0.081	0.703	0.970	0.827	1.136
Prey Density	0.690	0.377	0.068	1.993	0.951	4.176
Location	0.007	0.052	0.899	1.007	0.909	1.115
D) Pelagic Cormorant						
Julian Date	0.011	0.006	0.051	1.011	1.000	1.023
Sea State	0.043	0.150	0.776	1.044	0.777	1.402
Hour	-0.017	0.043	0.693	0.983	0.903	1.070
Group Size	-0.534	0.245	0.029	0.586	0.363	0.947
Distance	-0.004	0.003	0.296	0.996	0.990	1.003
Prey Density	0.068	0.059	0.249	1.070	0.954	1.201
Location	-0.001	0.020	0.967	0.999	0.960	1.040