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EFFECTS OF VESSEL ACTIVITY ON THE NEAR-SHORE ECOLOGY OF KITTLITZ'S MURRELETS (*BRACHYRAMPHUS BREVIROSTRIS*) IN GLACIER BAY, ALASKA

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Abstract.—Summer breeding populations of Kittlitz's Murrelets (*Brachyramphus brevirostris*) have declined by 80–90% in southeastern Alaska during the past 25 years. Boating activities overlap considerably in space and time with Kittlitz's Murrelets in Glacier Bay, and disturbance could affect individuals by causing them to fly away from preferred foraging sites, thereby disrupting foraging bouts or resting periods. We observed the effects of vessel activity on Kittlitz's Murrelets at sea for each of three response variables (density, group size, and behaviors) in Glacier Bay. Response variables were characterized at three time-scales of inference: immediate (instantaneous response to vessel passage), short-term (response that persisted 30 min after vessel passage), and daily (response on days with different vessel traffic rates). Group size was not affected by vessel activity. By contrast, near-shore densities were suppressed temporarily by vessel passage but recovered within the day. Density effects did not persist at the daily time-scale and, therefore, did not result in persistent loss of foraging habitat for Kittlitz's Murrelets. Also, behavior was affected at both the immediate and daily time-scales, but not at the short-term time-scale, and may have affected Kittlitz's Murrelets by increasing the amount of time spent flying, which is energetically costly. Vessel passage caused a 30-fold increase in flight behavior (from 0% to 30%). Large and fast-moving vessels caused the greatest disturbance to Kittlitz's Murrelets, which has implications for management of vessel activity. *Received 15 September 2006, accepted 17 June 2007.*

Key words: Alaska, *Brachyramphus brevirostris*, Glacier Bay National Park, Kittlitz's Murrelet, seabirds, vessel disturbance.

Efectos de la Actividad de Embarcaciones sobre la Ecología Costera de *Brachyramphus brevirostris* en Glacier Bay, Alaska

Resumen.—Las poblaciones de *Brachyramphus brevirostris* que se reproducen en el verano han disminuido en un 80–90% en el sureste de Alaska durante los últimos 25 años. Las actividades de navegación se superponen considerablemente en el espacio y el tiempo con los individuos de esta especie en Glacier Bay, y los disturbios podrían afectar a los individuos causando que vuelen alejándose de sus sitios de alimentación favoritos, lo que afectaría los períodos de alimentación y de descanso. Observamos el efecto de la actividad de embarcaciones sobre *B. brevirostris* en el mar con base en tres variables de respuesta (densidad, tamaño de grupo y comportamientos) medidas en Glacier Bay. Las variables de respuesta fueron caracterizadas en tres escalas temporales de inferencia: inmediata (respuestas instantáneas al paso de embarcaciones), de corto plazo (respuestas que persistieron 30 min después del paso de embarcaciones) y diaria (respuestas observadas en días con distintas tasas de tráfico de embarcaciones). El tamaño de los grupos no fue afectado por la actividad de las embarcaciones. En contraste, las densidades en áreas cercanas a la costa se vieron disminuidas temporalmente por el paso de embarcaciones, pero se recuperaron antes de terminar el día. Los efectos sobre la densidad no persistieron a la escala temporal diaria, por lo que no condujeron a una pérdida persistente de hábitat de alimentación para *B. brevirostris*. Además, el comportamiento se vio afectado tanto a la escala temporal inmediata como a la diaria, pero no a la de corto plazo, y podría haber afectado a las aves al aumentar la cantidad de tiempo que invirtieron en volar, lo que es energéticamente costoso. El paso de embarcaciones causó un incremento de 30 veces en el comportamiento de vuelo (de 0% a 30%). Las embarcaciones grandes y de movimiento rápido causaron los mayores disturbios sobre las aves, lo que tiene implicaciones para el manejo de la actividad de navegación.

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Wild marine and coastal habitats that were once remote and inaccessible are now frequently explored with the use of watercraft that range in size from kayaks to massive cruise ships (Hall 2001). As a result, many marine species now experience unprecedented levels of disturbance from vessel traffic, though the effects of this disturbance on most seabirds are poorly known. One such species is the Kittlitz's Murrelet (*Brachyramphus brevirostris*), a relatively rare alcid that spends much of its time at sea (Day et al. 1999).

Glacier Bay National Park (GBNP) supports a large portion of the world population of Kittlitz's Murrelets during the summer breeding season. Survey data collected during the summer from two core population areas in Alaska (Glacier Bay and Prince William Sound) indicate that the species has declined by 80–90% during the past 25 years (Kuletz et al. 2003). Currently, the Kittlitz's Murrelet is a candidate species for listing under the U.S. Endangered Species Act. Possible causes of population decline include oil pollution, gill-net mortality, change in food supply, loss of habitat from glacial recession, winter mortality, and vessel disturbance in core foraging areas (Day et al. 1999, Kuletz et al. 2003).

During summer, the potential for vessel disturbance of Kittlitz's Murrelets in Glacier Bay is high. Glacial waters near tidewater glaciers and the outflow of glacial streams are preferred foraging habitat of Kittlitz's Murrelet (Day and Nigro 2000, Day et al. 2003). Kittlitz's Murrelets may prefer to forage in glacial waters because of the high forage-fish productivity of these waters (Arimitsu et al. 2008) or simply because adults nest nearby on recently deglaciated terrain (Day et al. 1999).

Tidewater glaciers are also a major draw for tourists and provide a focus for vessel activity in GBNP, which most visitors tour by cruise ship (75–84% of visitors in 1980–1992; GBNP unpubl. data). Under current (2006) regulations, 2 cruise ships, 6 large tour boats, and ≤25 private recreational motor-vessels are permitted to enter park waters each day through the summer season. Vessels overlap in space and time with Kittlitz's Murrelets in their usual foraging areas, so there is potential for adverse effects on this species.

We investigated the potential effects of vessel activity on density and behavior of Kittlitz's Murrelets in near-shore areas of Glacier Bay to evaluate whether vessel activity causes (1) a decline in the species' near-shore density, (2) a change in group size, and (3) a change in the behavior of individuals at sea.

Because of high wing-loading, flight is energetically costly in this species (Pennycuick 1987). Chick-rearing has a high energetic cost for Kittlitz's Murrelets, because of long-distance flight to inland nest sites (≤75 km inland; Day et al. 1983). Therefore, we examined whether Kittlitz's Murrelets that are provisioning chicks have different behavioral responses to vessel activity than those not engaged in provisioning. Only individuals that are rearing chicks hold a single fish crosswise in the bill for later delivery to chicks (Carter and Sealy 1987). Therefore, we considered the effects of vessel activity on the behavior of fish-holding Kittlitz's Murrelets compared with those not holding fish.

Methods

We observed density at sea, group size, and behavior with area-scan and focal-bird sampling techniques (Altmann 1974, Martin and Bateson 1986). Focal-bird samples captured time-elapsed behaviors and were more suited to analysis at longer time-scales, whereas area-scan samples captured instantaneous behaviors (Altmann 1974, Martin and Bateson 1986). Area scans were conducted each half-hour, with a mean duration of 12 min. During area scans, all murrelets were counted and data were collected on species (Kittlitz's Murrelet, Marbled Murrelet [*B. marmoratus*], or *Brachyramphus* spp. if the species could not be identified), group size, and behavior (loafing, diving, flying, fish-holding, and flying while fish-holding). Groups were defined as singles, pairs, and flocks (i.e., three or more birds in proximity that maintain formation during movement or activity; Strachan et al. 1995). Focal-bird samples were collected between area scans and required 5 min of observation on a randomly selected Kittlitz's Murrelet. Up to three focal-bird samples could be collected in a half-hour, and data recorded included the elapsed time the focal bird spent in different group sizes and behaviors.

Observations were made at seven sites in Glacier Bay (Fig. 1), and sampling occurred across available daylight hours during 41 days (9–11 h day^{-1}). Sites were selected on the basis of known concentrations of Kittlitz's Murrelets observed on boat and aerial surveys in previous years (J. F. Piatt unpubl. data). Four of the observation sites were characterized as glacial habitat (near tidewater glacier or glacier stream input), and three sites were characterized as nonglacial habitat (no glacial influence) (Fig. 1). All sampling was conducted within designated areas near shore (average area size ± SE = 3.44 ± 0.52 km^2).

One observer and one primary recorder conducted observations from land in each near-shore area. We observed with a 20–65× telescope and 10× binoculars and dictated data to recorders. Recorders used Palm m150 (Palm, Sunnyvale, California) handheld devices to record data. We created software specifically for our behavioral-sampling protocols. Additional data collected were time of day, Beaufort scale (used to describe sea state), and rain (Table 1). When Beaufort scale was >2, sampling ceased because we could no longer clearly see the birds. We acquired tide and current data (Table 1) using TIDES AND CURRENTS software (Nobeltec, Beaverton, Oregon). We also estimated breeding stage for concurrent sampling using observations of chick-rearing birds carrying fish (Agness 2006).

When a vessel entered an observation area, the land-based observer characterized responses of loafing Kittlitz's Murrelets on either side and in front of the vessel (≤1,000 m). If behavior changed as the vessel approached, we recorded the distance between the vessel and the bird when the behavioral response occurred, the change in behavior (dive or fly), and species identification. We also collected data on the vessel (speed and size; Table 1). If behavior did not change as the vessel approached, we recorded the vessel's closest approach to the sampled Kittlitz's Murrelet and recorded the response as loafing behavior, which indicated no response. Ship-based observations were conducted to supplement land-based efforts and to increase the sample size for vessel factors (speed and size) that were under-represented by our opportunistic land-based effort. Vessel-speed, vessel-size, and approach-distance estimates were calibrated with known measures and recorded in three, five, and three categories, respectively (Table 1).

Analytical methods.—Three hierarchical time-scales of vessel activity were defined for our data: immediate (instantaneous

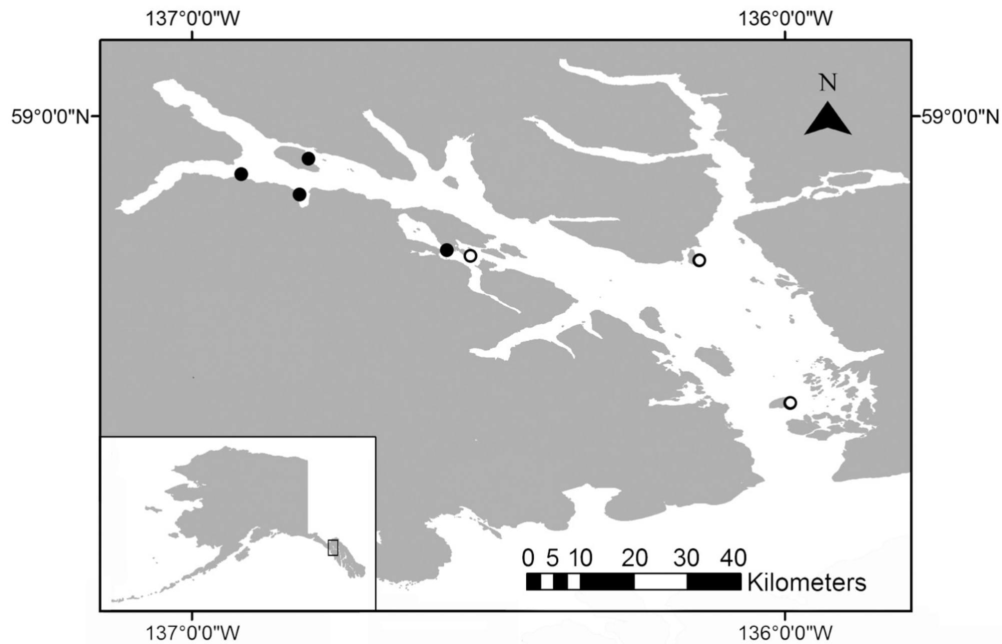

FIG. 1. Location of field sites in Glacier Bay, Alaska. The four sites marked with black circles were glacial, and the three sites with open circles were nonglacial.

response to vessel passage), short-term (response persisted 30 min after vessel passage), and daily (variable responses on days with differing vessel traffic rates). At the daily time-scale, vessel activity was considered as one of many potential explanatory variables for changes in murrelet density, group size, and behavior, whereas vessel activity alone was considered when investigating effects at immediate and short-term time-scales. Taken together, these three time-scales were superior to a single scale in evaluating effects of vessel activity.

Short-term and daily time-scales were used to test the effects of vessel activity on density near shore and group size. We used all three time-scales to test the effects of vessel activity on murrelet behavior. Cross-correlation plots (SYSTAT, version 7.0; Systat Software, San Jose, California) confirmed independence of daily scan and focal series. Our sampling unit was, therefore, an individual scan or focal sample. We assigned unidentified murrelets to species (Kittlitz's or Marbled murrelet) by multiplying the number of unidentified individuals in a given scan by the proportion of each identified species (where identified species proportions sum to 1) and added these numbers to the identified species counts. On average, unidentified species made up <5% of total murrelets per scan. We investigated group size by testing the effect of vessels on mean group size per scan and investigated density near shore by testing the effect of vessels on Kittlitz's Murrelets km^{-2} per scan. We tested the effect of vessels on the proportion of total Kittlitz's Murrelets engaged in different behaviors per scan to investigate

TABLE 1. Sources of variability included in daily-time-scale analysis (tide height through vessel rate) and vessel characteristics included in immediate-time-scale analysis (vessel speed, size, and approach distance).

Variable	Description
Tide height	Higher-high, high, lower-low, low
Tide current	Ebb, slack, flood
Tide magnitude	Spring, neap, transition tide series
Beaufort scale (sea state)	0, 1, 2
Rain	Yes, no
Near-shore habitat type	Glacial, nonglacial
Time of day	Morning (0400–0900 hours), midday (0900–1800 hours), evening (1800–2300 hours)
Breeding stage	Egg-lay, hatch (chick-rear and fledge)
Vessel rate (vessels h^{-1})	None (0.00), low (0.01–0.30), moderate (0.31–0.60), high (0.61–1.50)
Vessel speed (km h^{-1})	Slow (0–16), moderate (17–32), fast (33–48)
Vessel size (m)	Small (<6), medium (6–18), large (19–29), tour boat (30–50), cruise ship (generally ≥300)[a]
Approach distance (m)	Close (0–100), moderate (101–400), far (401–1,000)

[a]We did not observe vessels in the size range of approximately 51–299 m.

behavioral effects at short-term and immediate time-scales and used time spent per behavior (per focal sample) to test effects of vessels on behavior at the daily time-scale.

We evaluated the short-term effects of vessels with "before" and "after" samples. For example, to investigate effects of vessels on density, group size, and behavior, we paired these parameters from scans taken 30 min before and 30 min after vessel activities. We tested the significance ($\alpha = 0.05$) of the mean response variable (as difference and ln transformed proportion) with paired t-tests (SPSS, version 12.0; SPSS, Chicago, Illinois). We back-transformed proportion values after analysis to represent results.

We tested the effects of vessels on density, group size, and behaviors at the daily time-scale using all scan or focal samples to ensure coverage across daylight hours and to allow us to comprehensively represent the daily time-scale. We used a daily vessel rate (vessels h^{-1}) to capture variation in vessel activity at the daily time-scale. To ensure that the vessel rate accurately reflected daily vessel activity, only data from 36 full sampling days (≥9 h day^{-1}) were used. Because the period of a day was longer than our immediate or short-term time-scales of inference, we incorporated other likely sources of variability in our response variables at a daily time-scale (Table 1).

We modeled the effect of potentially influential variables at the daily time-scale with regression trees. Methods for regression-tree analysis followed those described in detail by Breiman et al. (1984), De'ath and Fabricius (2000), and De'ath (2002). We used univariate regression-tree analysis (SPLUS, version 7.0; Insightful, Seattle, Washington) for the response variables "density" and "group size" (De'ath and Fabricius 2000) and multivariate regression-tree analysis (R, version 2.1.1; R Foundation for Statistical Computing, Vienna, Austria) for behavioral response variables (De'ath 2002). Univariate regression trees are used for a single response variable (i.e., density or group size), whereas multivariate regression trees are used for more than one response variable (i.e., behaviors). We needed to use multivariate trees to evaluate behavior variables because of the intradependence of multiple behaviors in a single focal sample. For example, a bird can behave in multiple states during a sample, such that multiple behavior categories were response variables in the same sampling period. Hence, the bird's behaviors are intradependent within a sampling unit, and values for each behavior state in a given sampling unit sum to 1. However, this is not problematic, because, unlike standard regression analysis, regression-tree models do not require underlying assumptions about error distribution, form, or covariance (De'ath 2002).

For each model run, the measure of variability that defined splitting criteria was sums of squares. The deviance explained by a node, therefore, is the proportion of total sums of squares of the mean per node, and overall deviance is the sum across all leaves (De'ath and Fabricius 2000). We used 10-fold cross-validation techniques and the 1-SE rule to determine the best tree size (Breiman et al. 1984, De'ath and Fabricius 2000). Each model was run 50 times, and the modal best tree size was chosen (De'ath and Fabricius 2000). In regression-tree analysis, the importance of explanatory variables is indicated by the split number, or branch location. Branches closer to the tree root (top of the tree diagram) represent more important predictor variables than branches closer to the terminal nodes (ends of the tree).

Using presence-and-absence sampling, we investigated effects of vessels on behavior at the immediate time-scale. We compared behavioral-proportion data from scans conducted in the absence of vessels with behavioral-proportion data conducted during vessel activity. Mood's median test (SPSS) was used to evaluate whether behaviors in the absence of vessels were significantly different from behaviors in the presence of vessels. We also used multivariate regression-tree analysis to evaluate whether all vessel events were equally disturbing to Kittlitz's Murrelets, by including vessel variables as potential explanatory variables in the analysis (speed, size, and approach distance; Table 1). All variables included in analyses of the daily time-scale (with the exception of vessel rate) were also included in regression-tree analysis for immediate effects.

Results

Near-shore density.—Vessel activity caused a decline in near-shore density at the short-term time-scale ($\bar{x}$ test values: difference = 2.79 ± 1.29, $t = 2.16$, df = 61, one-tailed $P = 0.0017$; proportion = 0.40 ± 0.12, $t = -5.75$, df = 61, $P < 0.0001$). To evaluate effects on murrelet density at the daily time-scale, we first ran regression-tree analysis for factors other than vessel traffic, and then we reran the model including the vessel factor to evaluate its importance in the model hierarchy. Without considering vessel effects, natural environmental and biological factors ($r^2 = 0.20$) contributed to variability in density. The greatest densities of Kittlitz's Murrelets occurred during morning and midday hours ($\bar{x} = 6.5$ birds km^{-2}, $n = 706$ scans), during spring tide series ($\bar{x} = 17.2$ birds km^{-2}, $n = 35$), and during the egg-laying stage ($\bar{x} = 73.6$ birds km^{-2}, $n = 13$). The lowest densities occurred during the evening hours ($\bar{x} = 2.5$ birds km^{-2}, $n = 198$), during neap and transition tide series ($\bar{x} = 2.1$ birds km^{-2}, $n = 182$), during higher-high-tide and low-tide states ($\bar{x} = 1.7$ birds km^{-2}, $n = 141$), and during ebb and slack current states ($\bar{x} = 1.0$ birds km^{-2}, $n = 81$).

When vessel effects were considered, model fit improved, which indicates that vessel rate helped predict murrelet density ($r^2 = 0.30$; Fig. 2). Although daily vessel rate was a more important predictor variable during the evening hours (second split) than during the morning and midday hours (fifth split), it remained important regardless of time of day, being positively correlated with density (i.e., murrelet density was lower when the vessel rate was none or low, and greater when the vessel rate was moderate or high; Fig. 2). Therefore, vessel activity did not result in a decrease in near-shore density at the daily time-scale.

Group size.—Vessel activity did not change group size at the short-term time-scale (difference test, $t = 0.653$, df = 61, two-tailed $P = 0.561$). Regression-tree analysis showed that daily vessel rate was not a good predictor of group size, because vessel rate was not selected as a predictor variable in the "best" model ($r^2 = 0.48$) of group size. We concluded that vessel activity did not change group size at the daily time-scale. However, the analysis provides information about variables that predicted important variation in group size, including species identity. Kittlitz's and Marbled murrelet groupings were similar, and both single-species groups were smaller ($\bar{x} = 1.73$ birds, for both single-species groups) than mixed groups ($\bar{x} = 5.33$ birds). Additionally, breeding stage (second split) and tidal magnitude (third split) were important predictors of murrelet group size.

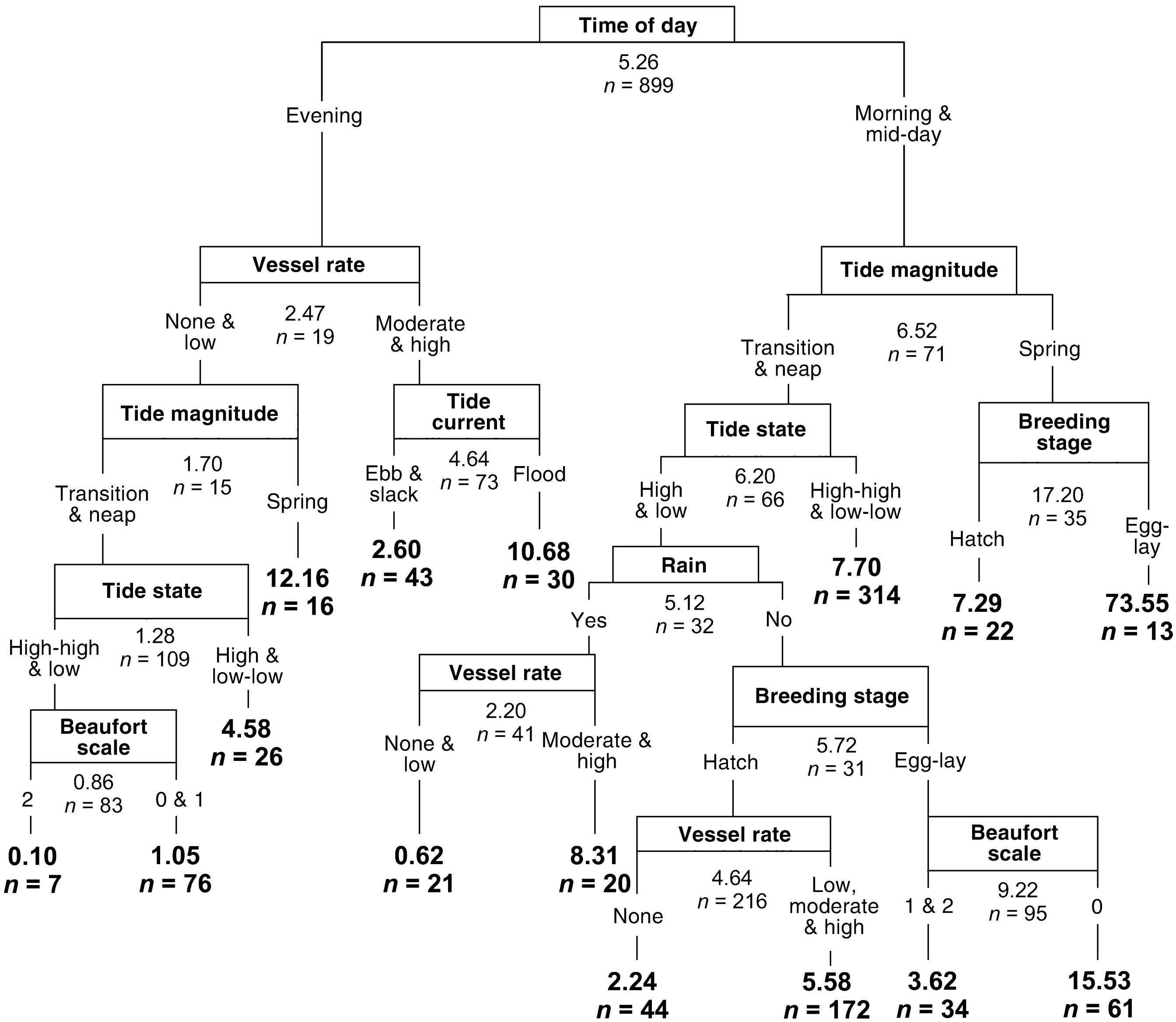

FIG. 2. Best regression-tree model of biological, environmental, and vessel variables included in analysis of the daily time-scale for density of Kittlitz's Murrelets. For each node, the first numeric value indicates mean density (birds km^{-2}). Lengths of branches indicate the amounts of variance explained. Terminal nodes are in bold.

Behaviors.—At the immediate time-scale, we found that Kittlitz's Murrelets changed behavior in the presence of vessels (Fig. 3), such that the proportion of individuals flying increased, loafing decreased, and diving behavior did not immediately change (Mood's median: $\chi^2 = 102.6$, df = 1, $P < 0.0001$; $\chi^2 = 325.9$, df = 1, $P < 0.0001$; and $\chi^2 = 1.160$, df = 1, $P = 0.322$, respectively). Behaviors of Kittlitz's Murrelets did not change at the short-term time-scale for vessel activity (loafing: $t = -0.012$, $P = 0.983$; diving: $t = -0.109$, $P = 0.914$; flying: $t = 1.357$, $P = 0.180$).

Kittlitz's Murrelets not holding fish (i.e., nonbreeders) had greater flight response (proportion, $\bar{x} = 0.55$) from cruise ships and tour boats than from small, medium, or large recreational vessels ($\bar{x} = 0.26$). Vessel size was the only split included in the best regression model for non-fish-holders ($r^2 = 0.10$; Fig. 4). Fish-holders (i.e., breeders) had the greatest flight response (proportion, $\bar{x} = 0.54$) from slow vessels with "far" (400–1,000 m) approach distance ($r^2 = 0.50$; Fig. 5). The mean flight response of Kittlitz's Murrelets to vessels of fast or medium speed, however, was very low (proportion, $\bar{x} = 0.01$). Fish-holders most commonly responded to vessels by diving, regardless of vessel speed, approach distance, or vessel size (Fig. 5). Variables other than vessel-related factors (i.e., biological and environmental) were not found in the best regression models and, therefore, did not influence variability in the behavioral response of fish holders or non-fish-holders during vessel activity.

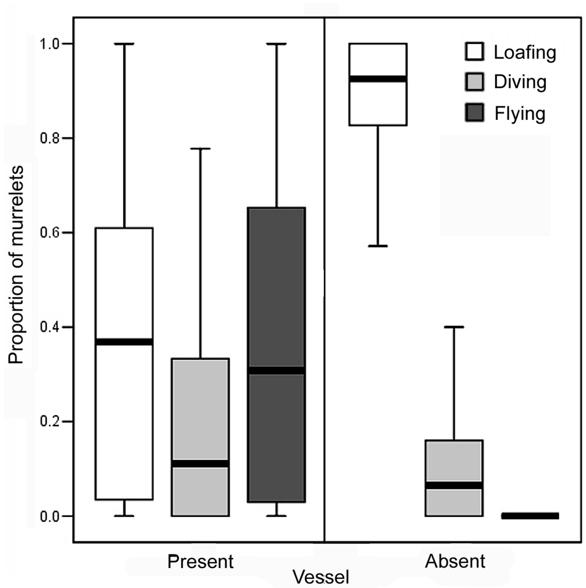

FIG. 3. Median and quartile plots of Kittlitz's Murrelet behaviors (proportions of Kittlitz's Murrelets loafing, diving, or flying) summarized in the presence and absence of vessels. Box includes lower quartile of observations, black line indicates the median, and whiskers indicate range. Significant behavioral change was detected for loafing (decrease) and flying (increase) in the presence of vessels.

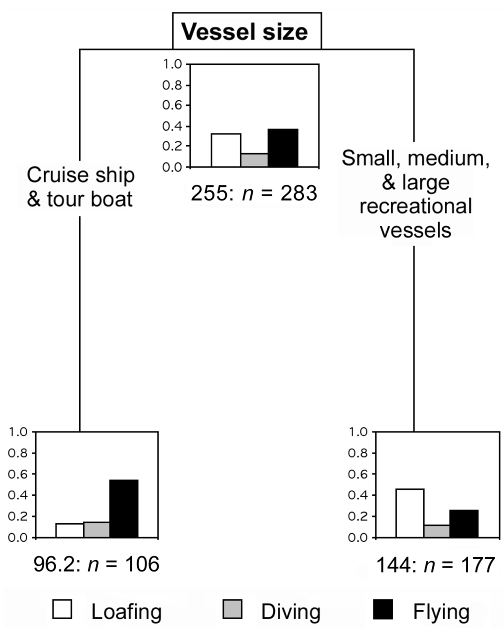

FIG. 4. Best regression-tree model of environmental, biological, and vessel variables (vessel size, speed, and approach distance) included in the immediate-time-scale analysis for behavioral response of non-fish-holding Kittlitz's Murrelets. The first numeric at the tree root (top of tree) is the amount of overall variation in the response, expressed as variance. For each node, the first numeric indicates the amount of unexplained variance remaining. The *y*-axis of individual branch plots is the mean proportion of birds engaged in each behavior category. Lengths of branches indicate the amounts of variance explained.

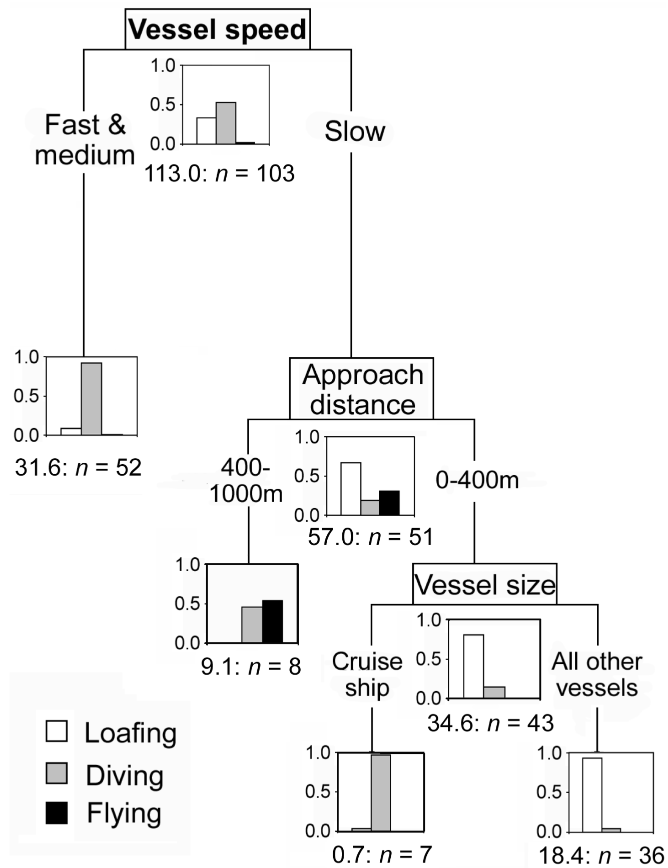

FIG. 5. Best regression-tree model of environmental, biological, and vessel variables (vessel size, speed, and approach distance) included in the immediate-time-scale analysis for behavioral response of fish-holding Kittlitz's Murrelets. The first numeric at the tree root (top of tree) is the amount of overall variation in the response, expressed as variance. For each node, the first numeric indicates the amount of unexplained variance remaining. The *y*-axis of individual branch plots is the mean proportion of birds engaged in each behavior. Lengths of branches indicate the amounts of variance explained.

For the daily time-scale, the best regression-tree model (not illustrated) included vessel rate as the second of two splits accounting for variability in behaviors ($r^2 = 0.20$). Therefore, vessel activity caused changes in behavior at the daily time-scale. Individuals spent more time loafing and less time diving when there was no vessel traffic on a given day than when vessel traffic was low, moderate, or high. The primary variable influencing variation in behavior was breeding stage. All other variables in the regression analysis did not contribute to the variation in behavior and, therefore, were excluded from the best model.

DISCUSSION

Environmental and biological factors had more influence than vessels on density near shore, group size, and behavior of Kittlitz's Murrelets. Vessels did not influence group size. Nevertheless, vessels influenced density near shore and behavior, but they were not the sole or the most influential factor. In the following, we discuss vessel effects in more detail.

At the short-term time-scale, near-shore density of Kittlitz's Murrelets declined substantially (difference of 2.79 birds km^{-2}, or a 40% average decrease) because of vessel disturbance. Vessel activity did not cause declines to persist at the daily time-scale, where environmental and biological factors had the greatest influence, which suggests only temporary disturbance of murrelets by vessels. Kittlitz's Murrelets likely returned to the disturbed areas over a short period, within the day. In fact, vessel activity was positively related to murrelet density at the daily time-scale, regardless of other interactions among variables. Although Kittlitz's Murrelets moved an unknown distance away to accommodate vessel traffic, they eventually returned within the day in greater numbers, which led to an overall influx of Kittlitz's Murrelets to the near-shore system for reasons that remain unclear to us. Other studies suggest that vessel traffic can cause loss of suitable habitat if displaced birds do not return to areas disturbed by vessels (Green-backed Heron [*Butorides striatus*]: Kaiser and Fritzell 1984; waterfowl: Knapton et al. 2000, Kenow et al. 2003). Our results show that the Kittlitz's Murrelet is displaced from habitat temporarily; however, birds returned to the same spatial habitat after disturbance ceased (within a day). We conclude that vessel activity does not constitute a loss of suitable habitat for the Kittlitz's Murrelet, because density rebounded over the course of a day.

Group size may be important to foraging success in murrelets. For instance, it appears that the Marbled Murrelet uses a cooperative foraging strategy, whereby a small group (typically two birds) herds a school of fish underwater to increase the time during which schools remain available as prey (Strachan et al. 1995, Speckman et al. 2003). Foraging behavior of the Kittlitz's Murrelet is probably similar to that of the closely related Marbled Murrelet. Nevertheless, we did not detect effects of vessel activity on the group size of Kittlitz's Murrelets at short-term or daily time-scales, which indicates that group dynamics were not affected.

Although behavior of Kittlitz's Murrelets was not influenced at the short-term time-scale, the cumulative effects of vessel events at the daily time-scale led to a threefold increase in diving behavior on days with higher rates of vessel traffic. This change in daily time-budget (more diving on days with higher rates of vessel traffic) does not represent a flee response of murrelets to individual vessels. Change in diving behavior was not detected at the short-term or immediate time-scales, which would be more representative of behavioral changes resulting from individual vessels. Thus, it is likely that increased diving behavior on days with higher rates of vessel traffic may help Kittlitz's Murrelets regain energy lost in flight during vessel activity if diving results in prey capture. Although Kittlitz's Murrelets increased diving effort on days with vessel activity by a factor of three ($\bar{x}$ increase in proportion of time from 0.04 to 0.12), flying effort during vessel activity increased more than 30-fold (mean increase from 0% to 30% of birds). Negative effects on the birds' daily energy budgets can occur when vessel activity reduces foraging behavior and increases energetically costly behavior such as flight. Other studies have shown that such behavioral changes may constitute significant energy loss at high rates of vessel traffic (diving ducks: Korschgen et al. 1985; American Coot [*Fulica americana*]: Schummer and Eddleman 2003). Therefore, it is possible that Kittlitz's Murrelets suffer a net energy loss as a consequence of vessel activity.

Our finding that vessel speed and size resulted in behavioral changes during vessel activity has some management implications. For example, non-fish-holders had the greatest flight response from large vessels (i.e., large tour boats or cruise ships). Few cruise ships (two per day) and large tour boats (six per day) are currently permitted to enter GBNP. Given that large vessels cause the greatest disturbance (i.e., flight response) to non-fish-holders, we recommend that large vessels continue to be regulated at low numbers in GBNP.

Fish-holders generally do not deviate from loafing behavior until flight is initiated to carry fish to their inland nest (Carter and Sealy 1987). The combination of high investments of time and effort in holding the fish, greater flight lift-off cost (due to fish mass), and unwillingness of the bird to expend energy by taking off likely influenced the low probability of flight for fish-holders under most vessel conditions (overall, 1% of fish-holders flew from vessels), with the exception of slow vessels with far approach (potentially allowing enough reaction time to respond in flight). Dive response may be a better indicator of disturbance for fish-holders. Dive behavior was not observed among fish-holders in the absence of vessels, and the limited warning of vessel approach under high-speed conditions may make dive response the only prudent option. Given that fast vessel speed caused the greatest disturbance (i.e., dive response) for fish-holders (95% of fish-holders dove from vessels at fast to moderate speed), vessel travel at slower speeds enforced with speed limits (i.e., ≤16 km h^{-1}) could prevent disturbance of fish-holders. In a study of the Marbled Murrelet (Speckman et al. 2004), small boats caused fish-holders to dive, and some birds then ate their held fish if repeatedly disturbed by the approaching vessel. The biological effects of this behavior could be significant to both the adult murrelet that expends additional energy to catch another fish and to its chick if a meal is not delivered (Speckman et al. 2004).

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