MEETING REPRODUCTIVE DEMANDS IN A DYNAMIC UPWELLING SYSTEM: FORAGING STRATEGIES OF A PURSUIT-DIVING SEABIRD, THE MARBLED MURRELET

M. Zachariah Peery[1,4], Scott H. Newman[2], Curt D. Storlazzi[3], and Steven R. Beissinger[1]

[1]*Department of Environmental Science, Policy, and Management, 137 Mulford Hall #3114, University of California, Berkeley, CA 94720-3114*
[2]*Food and Agricultural Organization of the United Nations, Via Terme di Caracalla, Rome, Italy 00100*
[3]*U.S. Geological Survey, Pacific Science Center, 400 Natural Bridges Drive, Santa Cruz, CA 95060*

Abstract. Seabirds maintain plasticity in their foraging behavior to cope with energy demands and foraging constraints that vary over the reproductive cycle, but behavioral studies comparing breeding and nonbreeding individuals are rare. Here we characterize how Marbled Murrelets (*Brachyramphus marmoratus*) adjust their foraging effort in response to changes in reproductive demands in an upwelling system in central California. We radio-marked 32 murrelets of known reproductive status (9 breeders, 12 potential breeders, and 11 nonbreeders) and estimated both foraging ranges and diving rates during the breeding season. Murrelets spent more time diving during upwelling than oceanographic relaxation, increased their foraging ranges as the duration of relaxation grew longer, and reduced their foraging ranges after transitions to upwelling. When not incubating, murrelets moved in a circadian pattern, spending nighttime hours resting near flyways used to reach nesting habitat and foraging during the daytime an average of 5.7 km (SD 6.7 km) from nighttime locations. Breeders foraged close to nesting habitat once they initiated nesting and nest attendance was at a maximum, and then resumed traveling longer distances following the completion of nesting. Nonbreeders had similar nighttime and daytime distributions and tended to be located farther from inland flyways. Breeders increased the amount of time they spent diving by 71–73% when they had an active nest by increasing the number of dives rather than by increasing the frequency of anaerobiosis. Thus, to meet reproductive demands during nesting, murrelets adopted a combined strategy of reducing energy expended commuting to foraging sites and increasing aerobic dive rates.

Key words: aerobic dive limit, Brachyramphus marmoratus, *diving behavior, foraging effort, foraging range, Marbled Murrelet, radio-telemetry, upwelling.*

Alcanzando las Demandas Reproductivas en un Sistema de Surgencias Marinas Dinámicas: Estrategias de Forrajeo de *Brachyramphus marmoratus*, un Ave Marina Zambullidora

Resumen. Las aves marinas mantienen una plasticidad en sus comportamientos de forrajeo para poder con las demandas energéticas y las restricciones de forrajeo que varían durante el ciclo reproductivo. Sin embargo, los estudios sobre comportamiento que comparan individuos reproductivos y no reproductivos son raros. Aquí caracterizamos cómo los individuos de la especie *Brachyramphus marmoratus* ajustan sus esfuerzos de forrajeo en respuesta a sus demandas reproductivas en un sistema de surgencias marinas en el centro de California. Marcamos 32 individuos, de quienes conocíamos su estado reproductivo, usando radiotransmisores (9 en reproducción, 12 reproductores potenciales y 11 no reproductivos) y estimamos tanto las áreas de forrajeo como las tasas de buceo durante la época reproductiva. Los individuos de *B. marmoratus* permanecieron más tiempo buceando durante los periodos de surgencia que durante los periodos de relajación oceanográfica, aumentaron su área de forrajeo con el aumento del tiempo del periodo de relajación y redujeron sus áreas de forrajeo después de la transición al periodo de surgencias. Cuando los individuos no se encontraban incubando, se movieron siguiendo un patrón circadiano, permaneciendo durantes las horas de descanso nocturnas cerca de las rutas de vuelo que utilizan para alcanzar el hábitat de anidación y forrajeo durante el día, las que en promedio se encontraron a 5.7 km (DE 6.7 km) de las localidades de reposo nocturno. Las aves en fase reproductiva forrajearon más cerca de las áreas de anidación una vez que iniciaron la anidación y cuando la atención a los polluelos fue máxima, y luego volvieron a viajar distancias mayores una vez terminado el periodo de anidación. Las aves en fase no reproductiva presentaron distribuciones diurnas y nocturnas similares y tendieron a localizarse más lejos de las rutas de vuelo tierra adentro. Las aves en fase reproductiva aumentaron en un 71–73% el tiempo que permanecieron buceando cuando estas tenían un nido activo, aumentando el número de zambullidos sin aumentar la frecuencia de anaerobiosis. Así, para alcanzar las demandas reproductivas durante la anidación, los individuos de *B. marmoratus* adoptaron una estrategia mixta en que redujeron el gasto de engría de los vuelos hacia los sitios de forrajeo y aumentaron las tasas de zambullidos aeróbicos.

INTRODUCTION

Reproduction in seabirds is complicated by the patchy and ephemeral distribution of food resources at multiple spatial and temporal scales (Gaston and Brown 1991, Hunt et al. 1999). Garnering sufficient prey is particularly challenging during the incubation and nestling-provisioning stages when energetic requirements and constraints associated with nest attendance are greatest (Ricklefs 1983). Seabirds maintain plasticity in their activity budgets and can adjust their foraging effort in response to changes in both environmental conditions and breeding commitments (Burger and Piatt 1990, Monaghan et al. 1994, Harding et al. 2007, Piatt et al. 2007, Ronconi and Burger 2008). In general, energy expenditure is greater during the nestling-provisioning stage than the incubation stage (Chappell et al. 1993, Barlow and Croxall 2002, Shaffer et al. 2003) and increases with the energy demands of nestlings (Bertram et al. 1996, Granadeiro et al. 2000, Walker and Boersma 2003). Constraints associated with frequent nest attendance during nestling provisioning generally translate to reductions in seabirds' foraging ranges (Cairns et al. 1987, Barlow and Croxall 2002, Shaffer et al. 2003), but in some cases heightened energetic demands require that parents fly long distances to foraging sites (Weimerskirch 1998).

A rich body of literature has characterized foraging strategies of actively nesting seabirds, and the continued improvement of transmitting and miniaturized recording devices has resulted in several recent and exciting studies of seasonal changes in foraging behavior (Croxall et al. 2005, Green et al. 2005, Shaffer et al. 2006, Burger and Shaffer 2008). However, behavioral studies of individuals transitioning from pre-breeding to nesting to post-breeding stages, and comparisons of foraging strategies of breeding and nonbreeding individuals during the breeding season are rare. Nonbreeders have lower energy demands than do breeders, are less constrained by the need to attend nest sites, and have greater flexibility to range over larger areas. Whether nonbreeders exercise this flexibility is uncertain because they may be able to meet their energy requirements by making relatively small movements to foraging sites. Ultimately, comparisons of breeders and nonbreeders can improve our understanding of the interaction between behavioral plasticity and the costs and constraints of reproduction because, in a sense, nonbreeders act as controls against which the foraging strategies of breeders can be evaluated (Gaston 1985).

For both breeders and nonbreeders, locating and capturing prey underwater is constrained by the need to surface and replenish oxygen stores (Dewar 1924). The maximum time that an individual respiring aerobically can dive (aerobic dive limit; ADL) is determined by its oxygen-storage capacity and the rate at which oxygen is consumed by metabolic activity (Kooyman 1989). Dive times beyond the ADL are possible by metabolizing lactate, but anaerobiosis is disadvantageous because it results in the accumulation of lactic acid in tissues, requires longer recovery periods at the surface, and is less energy efficient (Kooyman 1989, Boyd 1997). Predictions about the frequency of anaerobic dives under different environmental conditions have been tested (Ydenberg and Clark 1989, Jodice and Collopy 1999), but whether the demands of breeding stimulate greater reliance on anaerobic diving has not been investigated.

In this study, we used radio-telemetry to study how the Marbled Murrelet (*Brachyramphus marmoratus*), a pursuit-diving seabird in the family Alcidae, adjusts the effort it invests in foraging in order to cope with the constraints and energy demands of reproduction. We also characterize changes in the murrelet's foraging behavior in response to short-term variation in physical oceanographic processes that likely influence the distribution of prey. In our study area, murrelets nest in remnant old-growth redwood–Douglas fir (*Sequoia sempervirens–Pseudotsuga menziesii*) forests in the Santa Cruz Mountains in central California and are listed as a threatened species under the U. S. Endangered Species Act. Murrelets lay a single egg that takes females approximately 14 days to form (McFarlane-Tranquilla et al. 2003b) at nests located, in central California, an average of 9 km inland (Baker et al. 2006). Parents share incubation duties equally over an incubation period of about 30 days, each taking 24-hour incubation shifts and switching duties near dawn (Nelson 1997). Thus, incubating individuals forage at sea every other day and only have about half as much time available for foraging as nonincubating individuals. Parents fly inland to provision nestlings for about 30 days until fledging (Nelson 1997). Nonbreeding individuals that are physiologically in breeding condition also regularly fly inland to visit nesting habitat, but nonbreeders not in breeding conditions are rarely detected inland (Peery et al. 2004b).

Murrelets in our study population forage on small fish and invertebrates near shore in the shallow waters of the California Current (Henkel and Harvey 2006, Becker et al. 2007). Seasonal meso-scale upwelling of cold, nutrient-rich water generates a high level of primary productivity and is an important factor structuring seabird communities in the region (Ainley et al. 2005). At finer spatial and temporal scales, upwelling and the relaxation of upwelling affects the distribution of forage fish and invertebrates via aggregative processes. Mechanisms include the development of horizontal thermal fronts at the boundaries of water masses with different properties (Bjorkstedt et al. 2002, Shanks and McCulloch 2003), the development of vertical stratification in the water column (Husby and Nelson 1982, Simpson 1987), and the advection of coastal waters offshore (Ainley et al. 1993, Larson et al. 1994). In concert, these processes result in a patchily and ephemerally distributed prey base for Marbled Murrelets in the region (Becker and Beissinger 2003).

We addressed several questions about how Marbled Murrelets adjust their diving behavior and movements at sea in response to individual differences in breeding commitments and ocean conditions. First, we tested whether breeders travel shorter distances to and among foraging sites than do nonbreeders, as might be expected from the need to attend

nest sites, or whether breeders range over larger areas, as might be expected from their greater energetic requirements. Second, we tested whether breeders spend a greater proportion of time at sea diving for prey than do nonbreeders. Third, we determined whether breeders forage above their aerobic capacity more often than do nonbreeders. Finally, we explored the relationship between upwelling processes and murrelets' foraging strategies by comparing diving behavior and foraging ranges during periods of upwelling versus relaxation that varied on daily to weekly time scales.

METHODS

RADIO-MARKING, RADIO-TRACKING, AND ASSESSING BREEDING STATUS

We captured and radio-marked 46 Marbled Murrelets at the beginning of the breeding season (25 April–16 May) in 2000 and 2001 in Año Nuevo Bay, California, adjacent to nesting habitat in the Santa Cruz Mountains (Fig. 1). Murrelets were captured at sea by being spotlighted and dip-netted from a small inflatable vessel (Peery et al. 2004a). Radio-telemetry transmitters (model BD-2G; Holohil Systems Ltd., Woodland, Ontario, Canada) were attached with a subcutaneous anchor, glue, and suture (Newman et al. 1999) and weighed 2.3 g, approximately 1% of the murrelet's mean body mass. We determined the presence or absence of a brood patch and took a 0.25- to 1.5-mL blood sample from the medial metatarsal vein to determine sex (Zoogen™ sex analysis, Celera AgGen, Davis, CA) and for physiological analyses. Physiological analyses included estimating plasma vitellogenin and calcium concentrations, both of which become elevated in females during egg production, to assess reproductive status (McFarlane-Tranquilla et al. 2003b, Peery et al. 2004a).

Surveys from fixed-wing aircraft and ground-based vehicles were conducted every day from radio-marking through July along the coast from approximately 10 km south of Santa Cruz to 10 km north of Half Moon Bay, California, to (1) locate murrelets at sea and (2) locate and monitor murrelet nests in the Santa Cruz Mountains (Fig. 1). Occasional aerial telemetry surveys extended as far south as Point Conception, California, and as far north as the California–Oregon border. Mean tracking duration was approximately 63 days. Universal Transverse Mercator coordinates of murrelets at sea were obtained by triangulation from two or three locations from ground vehicles and by circling the radio signal with the aircraft. Error in telemetry locations was estimated to be <1 km. We acquired at least one location, but usually estimated several locations, for each murrelet on >90% of each 24-hour period starting at sunrise. Daytime locations at sea were considered to represent foraging locations and nighttime locations were assumed to represent resting locations because murrelets forage frequently throughout the day but not at night (Jodice and Collopy 1999, Henkel et al. 2003). When more than one location was obtained during a given day or night, a single location was randomly selected for statistical analyses.
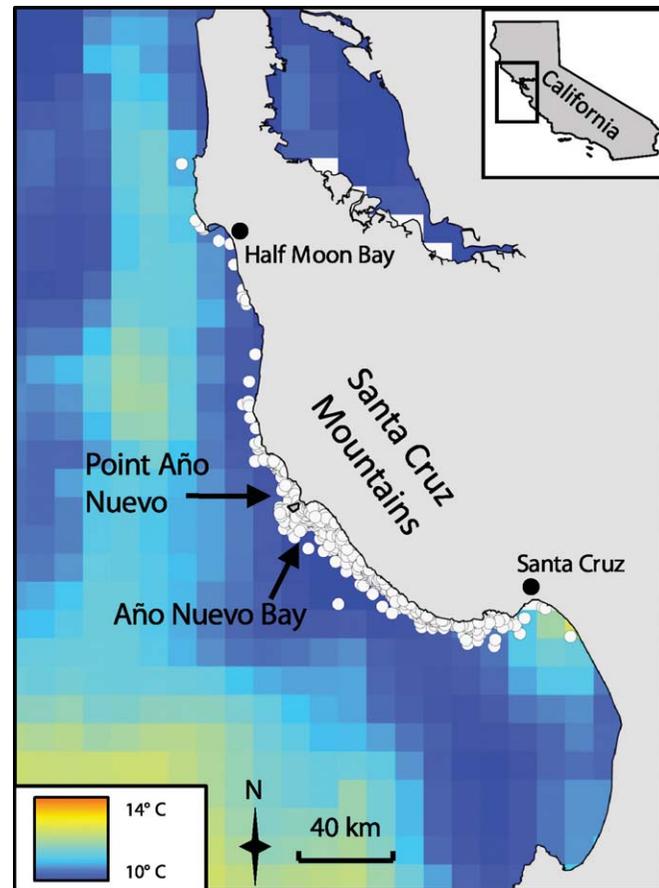

FIGURE 1.   At-sea radio-telemetry locations for 32 Marbled Murrelets (white circles; n = 2207 locations) radio-marked in central California in 2000 and 2001. Shaded squares at sea represent sea-surface temperatures derived from a 1-month composite of AVHRR satellite images taken in May of 2000 (http://las.pfeg.noaa.gov/oceanWatch/oceanwatch.php). Note the plume of cold, upwelled water originating from Point Año Nuevo.

If a radio-marked murrelet was not located at sea, we flew over all potential nesting habitat in the Santa Cruz Mountains to determine if it had initiated incubation. When a bird was detected inland, we immediately visited the forested area from which the signal originated to locate the nest tree. We returned early the following morning to observe the pair exchanging incubation duties to locate the actual nest site. Nests were monitored regularly with a combination of aerial telemetry surveys and visual observations. Hatching was assumed to have occurred when the 24-hour on/off pattern of incubation ended and murrelets were observed delivering prey to nestlings. We climbed the nest tree to confirm nest failure when parents stopped attending the nest prior to the expected fledging date. Using these methods, we were generally able to identify the exact date of nest initiation, hatching, and nest failure.

On the basis of behavioral and physiological criteria we classified the reproductive status of 32 radio-tagged

murrelets into five breeding categories: pre-breeding, nesting, post-breeding, potentially breeding, and nonbreeding. Because of early radio failure or mortality, 14 of the 46 radio-marked murrelets were not tracked long enough for their breeding status to be assessed. We categorized murrelets that initiated nesting at some point in the tracking period ($n = 9$) as breeders. Some breeders were tracked across multiple stages of the nesting cycle, so sample sizes in these stages exceeded the total number of breeders ($n = 6$ pre-breeders, $n = 7$ nesters, $n = 5$ post-breeders). Breeders were assigned to the pre-breeding, nesting, or post-breeding stages by their activity patterns at the time of the telemetry location or dive sample. Murrelets that were incubating or provisioning nestlings were pooled into a single "nesting" category because of small samples sizes (only two murrelets reached the nestling-provisioning stage, and all nests failed). Potential breeders ($n = 12$) were birds that did not initiate nesting but were physiologically in breeding condition at the time of capture. Physiological characteristics indicating breeding were (1) the presence of a brood patch, which can be developed in both sexes (McFarlane-Tranquilla et al. 2003a), and (2) elevated plasma calcium or vitellogenin concentrations; Peery et al. (2004b) described criteria for determining if calcium and vitellogenin levels are elevated. Nonbreeders ($n = 11$) were birds that did not initiate nesting and were not in breeding condition at the time of capture. Unlike that of breeders, the status of nonbreeders and potential breeders did not change through the tracking period. Thus, a total of 41 combinations of individuals by breeding status were available for analysis (6 pre-breeders, 7 nesters, 5 post-breeders, 12 potential breeders, and 11 nonbreeders).

QUANTIFYING DIVING BEHAVIOR

The duration of individual dives, pauses on the surface after dives, and the proportion of time murrelets spent diving were estimated by radio-telemetry from ground-based vehicles, as signals are inaudible when transmitters are submerged under water. The pulse rate of radio-transmitters was set to one pulse per second, such that individual dive and surface times were probably estimated with ≤1 sec of error. Diving behavior was characterized during intervals of 1 hr (dive samples), which were initiated and terminated independently of whether the murrelet was diving and often started and stopped during a bout of diving. Therefore, sampling was designed primarily to estimate and characterize factors affecting the proportion of time radio-marked murrelets spent diving rather than to quantify the duration and nature of individual bouts of diving. As many dive samples were taken as possible each day, and the order in which individuals were sampled was randomized. Surveys were not randomized with respect to time of day for logistical reasons, and time was therefore used as a covariate in statistical analyses (see below). We never observed murrelets foraging at night and restricted dive sampling to 06:00 to 21:00 hrs (PST). The proportion of time a murrelet

spent diving was expressed as the number of minutes it was under water during the dive sample divided by 60 min (the duration of dive samples). The proportion of time spent diving applied only to daytime hours on days in which individuals were at sea (i.e., not incubating or flying inland).

CHARACTERIZING OCEANOGRAPHIC CONDITIONS

Upwelling conditions were characterized with daily estimates of the Bakun Upwelling Index (Bakun 1973) at 36° N′ 122° W′ obtained from the National Oceanic and Atmospheric Administration's Pacific Fisheries Environmental Laboratory website (http://www.pfeg.noaa.gov). The upwelling index is derived from the intensity of atmospheric pressure gradients that generate upwelling-favorable (i.e., northwesterly) winds and is expressed as the volume (m^3) of water transported offshore per second per 100 m of coastline. Upwelling is episodic in that it generally lasts several days and is preceded and followed by relaxation, often of shorter duration. Thus, we subjectively categorized each day that radio-marked murrelets were tracked as (1) "upwelling" if the upwelling index was ≥150 or (2) "relaxation" if the upwelling index was <150 (Fig. 2). This criterion seemed reasonable because it resulted in a roughly even number of days in both categories and because the upwelling index was usually well over 150 during upwelling and well under 150 during relaxation (Fig. 2).

STATISTICAL ANALYSES

Factors affecting foraging ranges and diving rates. We first presented a graphical and qualitative description of murrelet movements at sea, particularly relative to flyways used to reach nesting habitat in the Santa Cruz Mountains. We then conducted a series of statistical analyses to test hypotheses about the effect of breeding status and oceanographic conditions on murrelet diving and movement patterns. Separate analyses were conducted for (1) the Euclidean distance between nighttime locations and locations the following day, (2) the Euclidean distance between daytime locations on consecutive days, and (3) the proportion of time murrelets spent diving. Mixed general linear models were used to model variation in foraging behavior as a function of reproductive demands and oceanographic conditions. Breeding status (nonbreeders, potential breeders, pre-breeders, nesters, and post-breeders), sex, upwelling state (upwelling or relaxation), and year (2000 or 2001) were treated as fixed effects and tested with *F*-tests. Individual was treated as a random effect nested within breeding status to accommodate multiple observations of foraging behavior for the same individual, in other words, to avoid pseudo-replication of foraging observations. We also included the number of days that upwelling or relaxation had lasted prior to the behavioral observation as a linear covariate. Foraging observations >8 days since the transition were rounded to 8 days because relatively few episodes of upwelling or relaxation
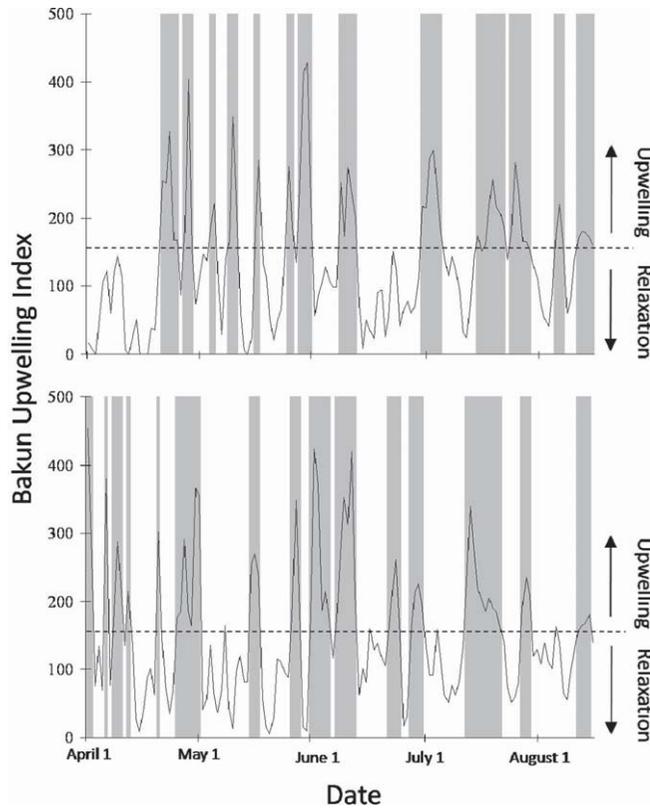
FIGURE 2. Bakun Upwelling Index (Bakun 1973) calculated at the National Oceanic and Atmospheric Administration's Buoy 46042 (36° N, 122° W) in the spring and summer of 2000 and 2001. The upwelling index was derived from the intensity of atmospheric pressure gradients that generate upwelling-favorable (i.e., northwesterly) winds and was measured as the volume (m^3) of water transported offshore per second per 100 m of coastline. Days with an upwelling index >150 are shaded grey and assigned to "upwelling" events; days with an index <150 are shaded white and assigned to "relaxation" events.

exceeded this duration. Day of year was included in the model as a covariate to account for temporal variation in foraging not described by changes in ocean conditions. For the analysis of diving, we also modeled the effect of time of day (assigned to one of five 3-hr blocks) and sea-surface conditions at the time the dive sample was conducted. Sea-surface conditions were classified as calm (no white caps), moderate (light white caps), or rough (heavy white caps) by visual observation from the telemetry platform.

Two-way interactions between main effects were considered if there was *a priori* biological justification to do so. These included interactions between breeding status and upwelling state to determine if individuals with reproductive commitments responded differently to ocean conditions. We also considered the interaction between upwelling state and upwelling duration to test whether the response to an upwelling or relaxation depended on the duration of the episode. The statistical significance of all fixed effects was initially tested with a global model including all terms, and nonsignificant effects

were removed sequentially starting with interactions until only significant effects remained. The denominator appropriate for testing the significance of a given fixed effect is the interaction between the fixed effect and the random effect for a mixed model with a single random effect (i.e., the "individual" term in our model; Hicks 1993). Like almost all ecological datasets, however, ours was not large enough for all interaction terms between the random individual effect and the fixed effects to be included in the model (Newman et al. 1997). Instead, we used the error mean square as the denominator for all tests of fixed effects (except breeding status for which the random individual term provided the appropriate denominator), because there was no evidence for significant interactions between fixed effects and the random individual effect when interactions where tested individually. Post-hoc *t*-tests of least-squares (model-adjusted) means were used to test for differences among the levels of statistically significant fixed effects. A critical value of 0.05 was used for all tests. We used PROC MIXED of program SAS for mixed-model analyses (Littell et al. 1996).

Testing for anaerobic diving. We evaluated the extent to which murrelets made use of anaerobic diving by estimating how many dives exceeded both behavioral and calculated aerobic dive limits (bADL and cADL, respectively). To estimate bADL, we modeled the relationship between the time individuals spent under water (dive time) and on the surface after a dive (post-dive surface time). Surface times are expected to increase linearly with dive times when individuals dive aerobically (i.e., forage below their ADL). However, post-dive surface times are expected to increase at a comparatively faster rate when dive times exceed the individual's ADL because longer surface times are needed to metabolize lactate accumulated during dives fueled by anaerobic respiration (Kooyman and Kooyman 1995, Boyd 1997). We tested for anaerobic diving by evaluating the level of support for competing one- and two-slope linear regression models where dive time and post-dive surface time were the independent and dependent variables, respectively. If the data for a given individual supported the one-slope model better, we inferred that the individual primarily used aerobic respiration when diving. If they supported the two-slope model better, we inferred that the individual respired both aerobically and anaerobically. We fit the two competing models to the data by using maximum-likelihood methods implemented in PROC NLMIXED in SAS (Littell et al. 1996) for each individual independently. The two-slope model took the form:

$$S = aD + b \qquad \text{if } 0 \le D < k \qquad (1)$$

$$S = cD + k(a - c) + b \qquad \text{if } D > k \qquad (2)$$

where S = post-dive surface time, D = dive time, a = the slope of S against D when $0 \le D < k$, b = the S intercept for $D = 0$, c = the slope of S against D when $D \ge k$, and $k = D$ at the value where slope a ends and slope c begins (and is thus an estimate of ADL). The one-slope model was formulated with equation

1 only. The level of support for the two competing models was evaluated by means of AIC$_c$ (Burnham and Anderson 2002). We considered the two-slope model (indicative of anaerobic diving) to be better supported if (1) the AIC$_c$ for the two-slope model was >2 values lower than the AIC$_c$ for the one-slope model and (2) $c > 0$ and $c > a$. Our method of looking for a change in the slope of surface against dive times was similar to that of Kooyman and Kooyman (1995) except that we used a model-based approach to estimate the inflection point and gave equal weight to all dives.

We tested for differences among breeding categories and years in the proportion of individuals that made use of anaerobic diving by using contingency tables. Sample sizes were too small, however, to test for differences among all five breeding categories. We therefore pooled all non-nesting individuals for comparison with nesting individuals, because of clear differences in diving behavior between these groups (see below).

We used estimates of cADL in Jodice and Collopy (1999) that were calculated by dividing mass-specific oxygen stores (mL O$_2$ kg^{-1}) by mass-specific diving metabolic rates (mL O$_2$ kg^{-1} min^{-1}). Diving metabolic rates (DMR) were assumed to be a multiple of mass-based estimates of standard metabolic rates (SMR) calculated from models in Burger (1991) and Schreer and Kovacs (1997). We used a range of values from 1.5 to 6.0 for the increase in metabolic rate during diving to explore the sensitivity

of results to uncertainty in murrelets' DMR. To explore uncertainty in oxygen-storage capacity, we used values of 44.5 and 58.0 mL O$_2$ kg^{-1} for this parameter (Burger 1991, Schreer and Kovacs 1997). Values reported in the results section are means or least-squares means ± 1 SE, unless stated otherwise.

RESULTS

DISTRIBUTION AND MOVEMENT PATTERNS AT SEA

We located murrelets at sea primarily within 2500 m of the coast between Half Moon Bay and Santa Cruz (Fig. 1; $n = 2707$ radio-telemetry locations). Three birds made long-distance (>100 km) movements to the south and were not included in statistical analyses while south of Santa Cruz (Peery et al. 2008). From these data, we estimated (1) 565 movements between nighttime resting locations and foraging locations the subsequent day and (2) 1255 movements between locations on consecutive days for the 32 murrelets of known reproductive status. Murrelets were located an average of 7.9 km (SD = 7.7 km) and 5.1 km (SD = 6.6 km) from the mouth of drainages they used to reach nesting habitat in the Santa Cruz Mountains during the day and night, respectively. Murrelets reached nesting habitat primarily via Waddell Creek (80% of individuals) but also via Gazos Creek (20% of individuals; Fig. 3; Peery et al. 2004b). Breeders (when not incubating eggs at inland nest
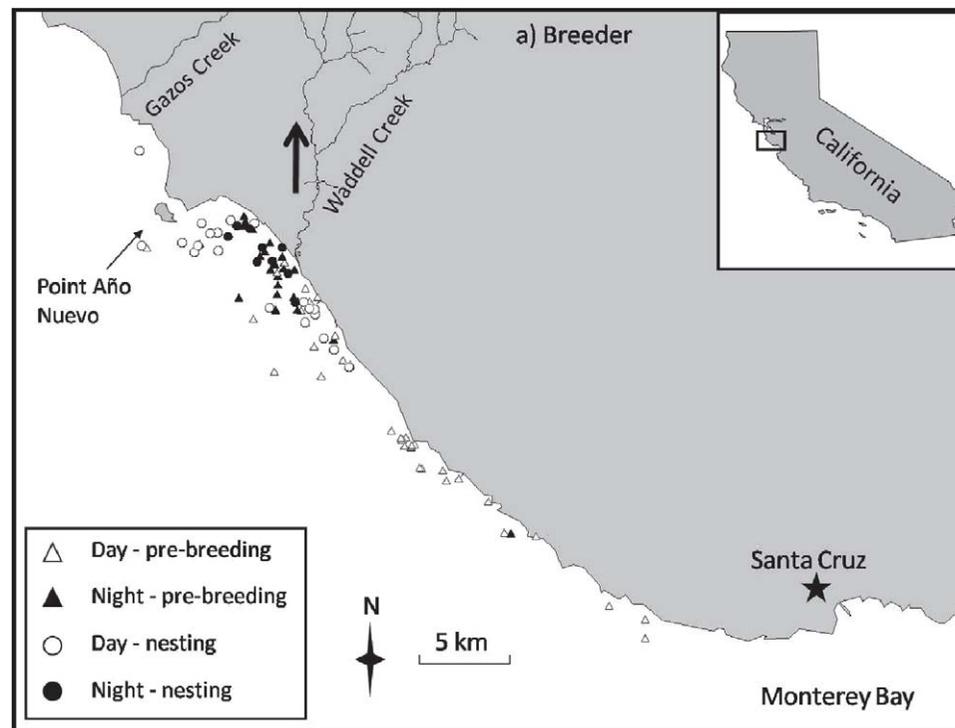

FIGURE 3.   Daytime and nighttime radio-telemetry locations for three representative Marbled Murrelets radio-marked in central California in 2000 and 2001: (a) a breeder during the pre-breeding and nesting period; (b) a potential breeder that did not nest but was physiologically in breeding condition; (c) a nonbreeder. The breeder and potential breeder typically flew up Waddell Creek early in the morning to reach nesting habitat (denoted by the black arrow; Peery et al. 2004a). The nonbreeder was never detected flying inland.
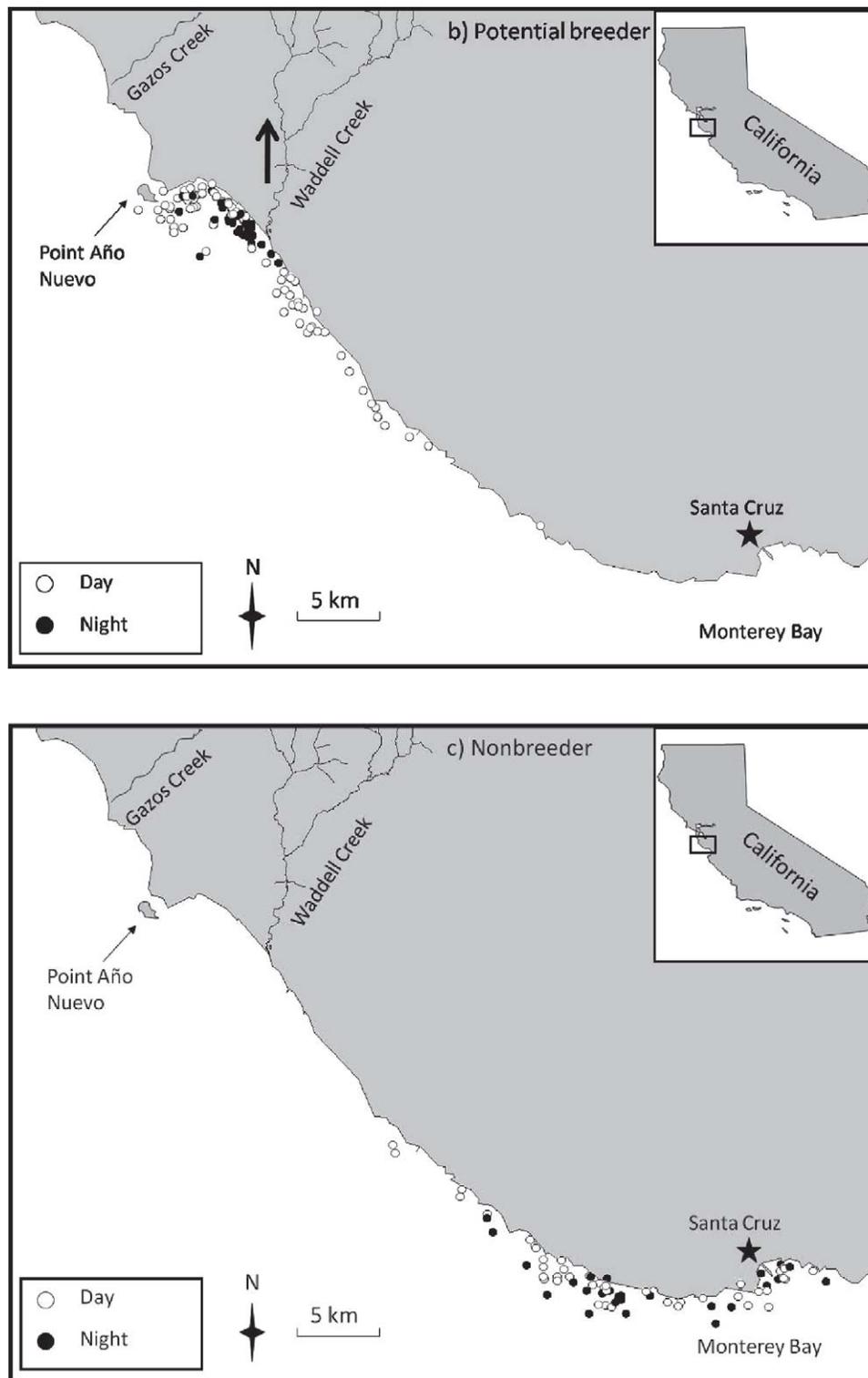
FIGURE 3.   Continued

sites) and potential breeders almost always spent the night near the mouth of these two inland flyways and tended to be located closer to inland flyways at night than during the day (Figs. 3a and 3b). Breeders foraged farther from flyways during the pre- and post-breeding periods, however, than they did while actively nesting. When nesting, breeders tended to forage closer to their nighttime resting locations in Año Nuevo Bay. Nonbreeders often did not spend the night in Año Nuevo Bay near flyways, instead remaining near daytime foraging areas located farther from nesting habitat (Figs. 3c and 4a).

Murrelets moved an average of 5.7 km (SD = 6.7 km) from nighttime resting locations to foraging locations the following day. According to the mixed model, night-to-day movements varied significantly from individual to individual ("individual" random effect: $z = 3.2$; $p < 0.01$) and differed by breeding category and upwelling condition (Table 1). Breeders in the pre-breeding (least-squares mean = 9.8 ± 1.3 km) and post-breeding (least-squares mean = 10.5 ± 2.0 km) stages moved significantly farther between their nighttime and daytime locations than did actively nesting breeders (least-squares mean = 4.7 ± SE = 1.8), potential breeders (least-squares mean = 5.6 km ± 1.0 km), and nonbreeders (least-squares mean = 3.4 ± 1.0 km), on the basis of t-tests of least-squares means ($p < 0.05$ in all cases; Fig. 4b). Although upwelling state was a significant term in the mixed model, least-squares means revealed no difference between periods of upwelling (6.7 ± 0.7 km) and relaxation (6.9 ± 0.7 km) ($t_{522} = 0.2$, $p = 0.74$). The absence of a statistical difference was a result of the strong interaction between upwelling state and the duration of the event (Table 1). Murrelets made relatively short movements when relaxation
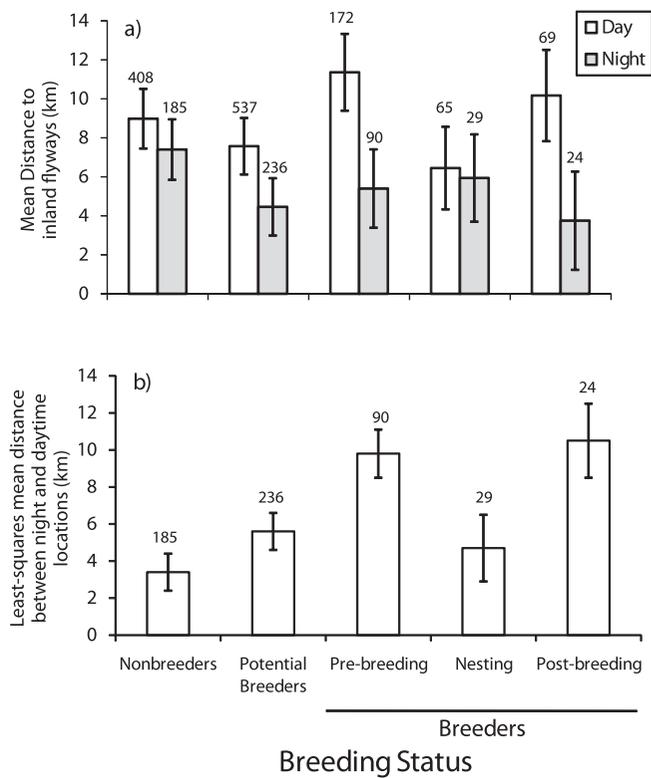

FIGURE 4.   Movements and distribution of 32 radio-marked Marbled Murrelets in central California in 2000 and 2001, by breeding status: (a) mean (± 1 SE) distance from flyways used to reach inland nesting habitat during the day and at night; (b) least-squares mean (± 1 SE) distance between nighttime locations and locations the following day. Sample sizes (number of movements) given above bars.

TABLE 1.   Results of mixed models testing the effect of breeding status and ocean conditions on the movement distances and the proportion time spent diving by 32 Marbled Murrelets radio-marked in central California, 2000–2001.

| Factor	Night-to-day movements			Day-to-day movements			Proportion time diving		
	df	F	P	df	F	P	df	F	P
Breeding status	4, 35	5.2	<0.01	4, 35	0.7	0.62	4, 36	4.4	<0.01
Sex	1, 521	1.0	0.33	1, 1209	2.7	0.10	1, 740	<0.1	0.86
Upwelling state	1, 522	4.8	0.03	1, 1209	10.5	<0.01	1, 755	7.2	<0.01
Upwelling duration	1, 522	0.8	0.39	1, 1209	1.7	0.19	1, 754	1.1	0.30
Year	1, 521	0.4	0.55	1, 1209	<0.1	0.93	1, 755	3.4	0.06
Day of year	1, 521	2.9	0.09	1, 1209	25.9	<0.01	1, 755	9.7	<0.01
Sea conditions	—	—	—	—	—	—	2, 752	0.5	0.63
Time of day	—	—	—	—	—	—	4, 771	0.3	0.91
Breeding status × upwelling state	4, 517	0.3	0.89	4, 1205	0.3	0.89	4, 740	0.8	0.52
Upwelling state × upwelling duration	1, 522	6.1	0.01	1, 1209	13.1	<0.01	1, 739	<0.1	0.88
Breeding status × time of day	—	—	—	—	—	—	16, 755	0.3	0.88
Breeding status × sea conditions	—	—	—	—	—	—	8, 744	1.2	0.25
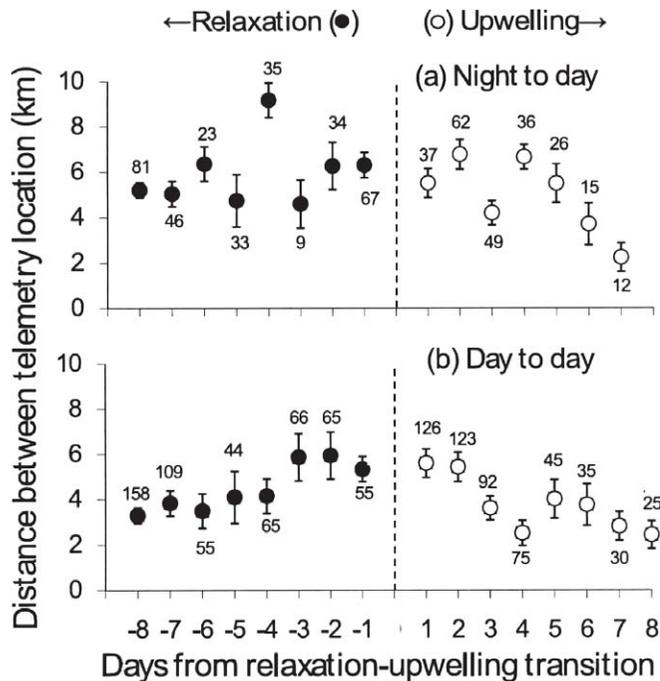
FIGURE 5.   Mean (± 1 SE) distance traveled by 32 radio-marked Marbled Murrelets in central California in 2000 and 2001 as a function of upwelling conditions: (a) between nighttime resting locations and foraging locations the following day; (b) daytime locations on consecutive days. Sample sizes (number of movements) given above and below symbols.

began but made longer movements as relaxation continued (Fig. 5a; slope = 0.43 ± 0.12 km day^{-1}). When relaxation transitioned into upwelling, murrelets initially made relatively long movements, but movement distances declined as upwelling continued (slope = −0.20 ± 0.23 km day^{-1}). Night-to-day movements were not significantly related to sex, year, day of year, or the breeding status by upwelling-state interaction (Table 1).

On the basis of the mixed model, day-to-day movements varied significantly from individual to individual ("individual" random effect: $z = 3.3$; $p < 0.01$). This distance was unrelated to breeding status, sex, and year but did depend on upwelling conditions (Table 1). No difference in least-squares means was detected between upwelling (4.4 ± 0.4 km) and relaxation (4.4 ± 0.4 km) events ($t_{1209} = 0.2$, $p = 0.83$), however, because of the strong interaction between upwelling state and the duration of the event. As with night-to-day movement, murrelets moved relatively short distances between consecutive daytime locations at the beginning of relaxation and began making longer movements as relaxation continued (Fig. 5b; slope = 0.39 ± 0.08 km day^{-1}). When relaxation transitioned into upwelling, murrelets initially made relatively long movements, but distances between consecutive locations declined as upwelling continued (slope = −0.18 ± 0.13 km day^{-1}). By the time upwelling ceased, movements were

as short as estimated at the beginning of relaxation (Fig. 5b). Day-to-day movements also declined with day of year (Table 1; slope = −0.04 ± 0.01 km day^{-1}).

FACTORS AFFECTING DIVING BEHAVIOR

We estimated the proportion of time spent diving, dive times, and post-dive surface times for the 32 murrelets of known reproductive status on the basis of 819 behavioral observations 1 hr long. The mean number of such observations per individual was 25.6 (SD = 13.4, range = 6−49). The mean proportion of time murrelets spent diving was 0.12 (SD = 0.05). Mean dive time was 23.5 sec (SD = 9.0 sec, $n = 9728$ dives), and mean post-dive surface time was 11.9 sec (SD = 9.3 sec, $n = 9728$ post-dive surface pauses).

According to the mixed model, the proportion time diving varied significantly from individual to individual ("individual" random effect: $z = 1.9$; $p = 0.03$). Diving was significantly related to breeding status, upwelling state, and day of year, and was marginally different between years (Table 1). Breeding murrelets spent a greater proportion of their time diving while nesting (least-squares mean = 0.19, SE = 0.02) than they did during the pre-breeding (least-squares mean = 0.11 ± 0.02; $t_{31} = 3.2$, $p < 0.01$) and post-breeding stages (least-squares mean = 0.11 ± 0.02; $t_{31} = 3.1$, $p < 0.01$; Fig. 6a). When nesting, breeders also spent proportionately more time diving than did nonbreeders (least-squares mean = 0.11 ± 0.01; $t_{31} = 3.5$, $p < 0.01$) and potential breeders (least-squares mean = 0.11 ± 0.01; $t_{31} = 3.7$, $p < 0.01$). No other comparisons among breeding categories were significant ($p > 0.87$ in all cases). The interaction between breeding status and time of day was not statistically significant (Table 1). A visual examination of means, however, suggests that the difference among breeding categories was largely due to nesting murrelets foraging more intensively in the early morning (06:00–09:00) than did other individuals (Fig. 6b). Murrelets spent a greater proportion of their time diving during periods of upwelling (least-squares mean = 0.14 ± 0.01) than during periods of relaxation (least-squares mean = 0.11 ± 0.01; Table 1). This difference was consistent among breeding categories (Fig. 6a), as evidenced by a lack of a significant interaction between upwelling state and breeding status (Table 1). Murrelets spent a nearly statistically significant ($p = 0.06$) greater proportion of time foraging in 2000 (least-squares mean = 0.14 ± 0.01) than in 2001 (least-squares mean = 0.11 ± 0.01). The proportion of time spent diving declined significantly over the breeding season (slope = −0.06% ± 0.02% day^{-1}).

AEROBIC VERSUS ANAEROBIC DIVING

Post-dive surface times were positively correlated ($p < 0.05$) with dive times in 93% of 41 cases (individual by breeding status combinations), on the basis of Pearson's correlation coefficients (mean $r = 0.28$, SD = 0.16). There was more support for
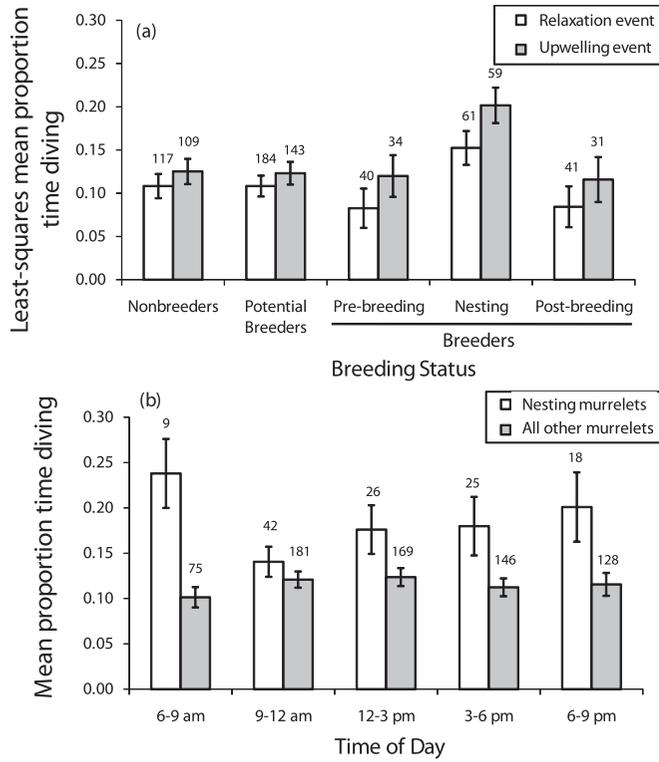
FIGURE 6.   Diving behavior of 32 radio-marked Marbled Murrelets in central California in 2000 and 2001: (a) least-squares mean (± 1 SE) proportion time spent diving by breeding status and upwelling state; (b) mean (± 1 SE) proportion time spent diving by time of day and nesting status. Sample sizes (number of 1-hr dive surveys) given above bars.

a two-slope model of post-dive surface time regressed against dive time (suggesting that some dives exceeded bADL) than for a one-slope model (indicative of aerobic diving only) in 27% of cases. Two cases with more support for each class of regression model are illustrated in Fig. 7. Mean bADL = 27 sec (SD = 7 sec) for the 11 cases in which anaerobic diving was
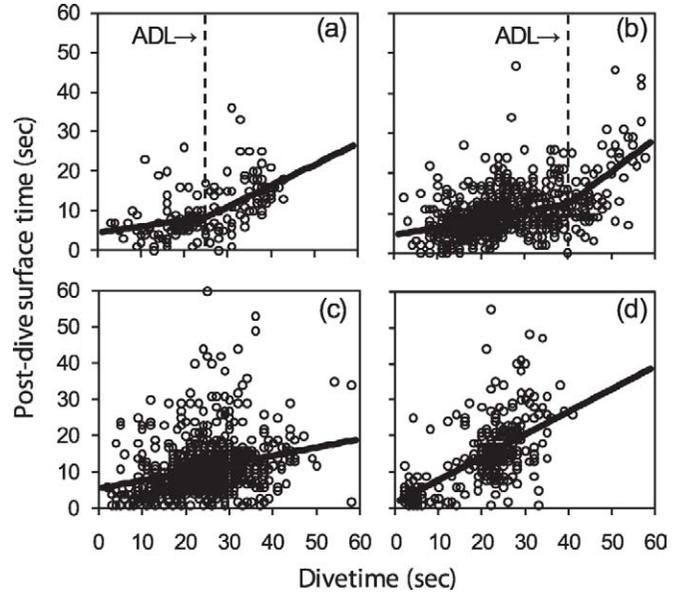

FIGURE 7.   Relationship between dive time and post-dive surface time for four representative Marbled Murrelets radio-marked in central California in 2000 and 2001. Competing one-slope (indicative of aerobic respiration only) and two-slope (indicative of aerobic and anaerobic respiration) regression models were fit to the data and evaluated with AIC_c. Two-slope models received more support for the two individuals in (a) and (b); one-slope models were better supported for the two individuals in (c) and (d). ADL = aerobic dive limit.

supported. The proportion of actively nesting and all other murrelets respiring anaerobically did not differ significantly (0.43 and 0.21, respectively, $\chi^2_2 = 0.9, p = 0.34$). Nor was there a difference in anaerobic respiration between 2000 and 2001 (0.20 and 0.33, respectively, $\chi^2_2 = 0.9, p = 0.24$).

The percentage of dives that exceeded cADL was ≤1% when DMR was ≤3× SMR regardless of the assumed oxygen-storage capacity (Table 2). However, the percentage of dives greater than the estimated cADL was sensitive to assumptions

TABLE 2.   Estimates of calculated aerobic diving limit (cADL) for Marbled Murrelets and the percentage of dives exceeding cADL for radio-marked individuals in central California, 2000 and 2001 (this study), and in central Oregon, 1995 and 1996 (Jodice and Collopy 1999). cADLs and percentage of dives exceeding cADLs are presented for a range of potential diving metabolic rates (DMR) as a multiple of standard metabolic rate (SMR) and two different possible oxygen-storage capacities for murrelets as described in Jodice and Collopy (1999).

	Oxygen capacity = 44.5 mL O_2 kg^{-1}				Oxygen capacity = 58.0 mL O_2 kg^{-1}			
		Percentage of observed dives > cADL				Percentage of observed dives > cADL		
		California		Oregon		California		Oregon
DMR × SMR	cADL (sec)	Nesting	Non-nesting	All birds	cADL (sec)	Nesting	Non-nesting	All birds
1.5	95.7	0	0	<0.1	124.7	0	0	0
2.0	71.8	0.1	0.2	<0.1	93.6	0	0	0.1
3.0	47.9	0.1	1.0	0.9	62.4	0.1	0.4	0.1
4.0	35.9	3.3	5.8	15.0	46.8	0.2	1.1	1.2
5.0	28.7	16.4	19.7	38.7	37.4	2.4	4.9	10.6
6.0	23.9	38.9	42.1	59.1	31.2	10.4	13.8	27.3

regarding oxygen-storage capacity and DMR when DMR was ≥4× SMR. For DMR 4×−6× SMR, the percentage of dives exceeding the cADL ranged from <1% to 39% and was significantly greater when oxygen-storage capacity was assumed to be relatively low. The percentage of dives exceeding cADL was very similar for nesting and non-nesting murrelets, regardless of assumed metabolic rates and oxygen-storage capacity. For high DMRs, the percentage of dives exceeding cADL we observed was lower than that estimated for murrelets in central Oregon (Table 2).

DISCUSSION

Transmitting devices have a variety of effects on the foraging behavior and vital rates of seabirds in general, and such effects need to be considered when information from marked seabirds is interpreted (Burger and Shaffer 2008). Previous work detected transmitter effects on the survival of Marbled Murrelets, but these effects were most evident in 1998 during a toxic algal bloom and a severe El Niño–Southern Oscillation event (Peery et al. 2006), and we excluded data from that year from the present study. Moreover, radio-marked murrelets detected dying during the tracking period were removed from analyses. Of course, more subtle effects on diving and movement behavior could certainly have occurred without being detected. Yet our hypotheses were relative in nature (e.g., we tested for difference between individuals with differing breeding commitments), and murrelets experienced the same capture and handling process and were outfitted with the same model of radio-transmitter. Thus, it seems implausible that transmitter effects are responsible for the main findings of this study, such as (1) breeding murrelets spend more time foraging while actively nesting than in other stages, (2) murrelets range farther when not constrained by the need to attend nest sites, and (3) diving rates are greater and foraging ranges are shorter during upwelling than during relaxation.

EFFECT OF REPRODUCTIVE CONSTRAINTS ON FORAGING BEHAVIOR

Breeders spent nighttime hours resting near flyways used to reach nesting habitat, flew inland early in the morning, and then flew to daytime foraging sites several kilometers from nighttime locations when they returned to sea. Once they initiated nesting, however, they remained near nesting habitat during the day and resumed traveling longer distances to foraging sites after nests failed. In the incubation and provisioning stages, breeders were detected in inland flyways on 100% of early morning surveys, whereas pre- and post-breeders were detected on only 70 and 77% of inland surveys, respectively (Peery et al. 2004b). Therefore, the shift toward nesting habitat during nesting likely reflected an attempt to reduce energy expenditure during stages requiring more frequent nest attendance.

In contrast, nonbreeders tended to spend the night farther from nesting habitat, probably because they rarely fly inland and are unconstrained by the need to attend nest sites. This flexibility allowed nonbreeders to make night-to-day movements shorter than those of pre- and post-breeders and to remain near foraging areas during both the day and night. Despite clear differences in movement patterns between breeders and nonbreeders, however, murrelets of all breeding categories remained within a few kilometers of nesting habitat during the breeding season (Figs. 3 and 4). During the nonbreeding season (October through March), murrelets disperse up to 300 km from waters adjacent to the Santa Cruz Mountains (Peery et al. 2008). Thus, nonbreeders return from wintering areas to forage in waters near nesting habitat even though they very rarely fly inland. Nonbreeders may move into the area during the breeding season to take advantage of seasonally abundant prey or, perhaps more likely, to participate in social interactions such as mate finding and pair bonding.

The influence of reproduction on the murrelets' foraging behavior was also clearly evident from the 71–73% increase in the proportion of time that breeders spent diving during nesting. We did not have a sample size sufficient to model incubating and nestling-provisioning murrelets separately, but both groups appeared to forage at rates higher (mean proportion time diving = 0.19, 95% CL = 0.14−0.23; mean proportion time diving = 0.15, 95% CL = 0.11−0.18, respectively) than those of non-nesting murrelets (mean proportion time diving = 0.11, 95% CL = 0.09−0.12). When at sea, incubating murrelets almost doubled their diving activity because the time available for foraging was half of what it was for nonincubating individuals. Elevated foraging during the nestling-provisioning stage almost certainly occurred because parents must provide for rapidly growing young in addition to meeting their own energy demands, as is typical of breeding seabirds (Chappell et al. 1993, Barlow and Croxall 2002, Shaffer et al. 2003). Parents with nestlings, however, may also have increased the proportion of time they spent foraging while at sea because delivering prey to inland nest sites reduces available foraging time. The reduction in available foraging time and hence its influence on diving behavior was probably relatively small during nestling provisioning because parents typically make one or two deliveries per day (Bradley et al. 2002) and commuting times to nests in central California are generally <1 hr (MZP unpubl. data), whereas foraging time is reduced by half during incubation.

Comparisons of breeders and nonbreeders indicate that the constraints and demands of reproduction require significant changes in foraging strategies while murrelets are actively nesting, but not immediately before or after nesting. Two conclusions can be drawn from this finding. First, energetic costs incurred prior to egg-laying did not translate into a measurable change in diving effort, as might be expected from the cost of egg production (Monaghan et al. 1998). Note

that the proportions of time spent diving by female pre-breeders and nonbreeders were similar (pre-breeder mean = 0.12, 95% CL = 0.08−0.16, n = 4; nonbreeder mean = 0.14, 95% CL = 0.08−0.20, n = 4). Second, the costs of reproduction apparently did not require that murrelets recover by foraging at greater than "baseline" rates following breeding. Nests of five of nine breeders failed within 9 days of initiation, and the cost of breeding may have been relatively minor in these cases. However, one murrelet that foraged at a high rate over the 44 days it nested (mean proportion time diving = 0.15) foraged at almost the exact same low rate before and after nesting (mean proportion time diving = 0.08 and 0.08, respectively). Thus, for some individuals, even extended periods of nesting may not require recovery via increased foraging.

In sum, to meet reproductive demands while nesting, murrelets adopted a combined strategy of reducing energy expended commuting to foraging sites and increasing aerobic dive rates. These results reflect a general pattern in breeding seabirds of foraging ranges being reduced when nest attendance is greatest and foraging effort increasing when energy demands are highest (Barlow and Croxall 2002, Shaffer et al. 2003, Walker and Boersma 2003). Apparently, the rewards of traveling to distant, but potentially profitable, foraging sites are outweighed by the benefits of increased diving at foraging areas near nest sites when nest attendance is high. When nest attendance is low, the rewards of traveling over greater areas seem to outweigh increased commuting costs and the potential benefits of increasing diving effort at local foraging sites.

FREQUENCY OF AEROBIC VERSUS
ANAEROBIC DIVING

We believe that murrelets exceeded their bADL in the 11 cases (27%) in which individuals were observed making extended post-dive surface pauses following long dives, and an average of 35% of dives exceeded bADL in these cases. Thus, we estimate that only about 9% (27% × 35%) of all murrelet dives exceeded bADL. The proportion of dives exceeding cADLs was sensitive to assumptions about the murrelets' oxygen-storage capacity and DMR (Table 2), as is typical in studies of marine divers (Schreer et al. 2001). Several authors have cautioned against estimating cADL and testing for anaerobic diving when field-based estimates of DMR are unavailable for the species under investigation (Nagy et al. 2001, Schreer et al. 2001), especially because a wide range of DMRs have been reported in the literature and DMRs as high as 10× SMR have been observed in penguins (Nagy et al. 1984, Chappell et al. 1993). However, maximum sustainable metabolic rates are likely ~4× SMR (Drent and Daan 1980), and in the only such study of alcids, the metabolic rates of the Common Murres (*Uria aalge*) and Thick-billed Murre (*U. lomvia*) were estimated to increase during diving by factors of 1.8 and 2.4, respectively (Croll and McLaren 1993). Even with an assumed DMR ≤4× SMR, <6% of murrelet dives exceeded cADL,

regardless of the assumed oxygen-storage capacity—a number that is reasonably similar to estimates based on bADL.

Despite uncertainty in ADL estimates, neither nesting nor non-nesting murrelets made regular use of anaerobiosis. Instead, nesting individuals increased diving effort by diving more often (mean = 29.2 dives hr^{-1}) than non-nesting murrelets (18.5 dives hr^{-1}) rather than by making longer dives (mean = 22.4 sec vs. 23.2 sec). A general pattern of aerobic diving in this species is supported by a low proportion of dives exceeding cADL in radio-marked individuals in Oregon (Jodice and Collopy 1999). Most studies demonstrating anaerobiosis in seabirds have been based on larger-bodied species such as penguins and large alcids (Croll et al. 1992, Kooyman and Ponganis 1998). A greater reliance on aerobic diving in murrelets, regardless of breeding status, may be attributable to the species' comparatively small size and shallow diving depth (<20 m in this study; Becker and Beissinger 2003). Foraging in shallow waters may allow murrelets to reduce the amount of time they spend descending and ascending to the depth of prey and obviate the need for extended anaerobic dives. The ability to assess prey availability and terminate dives early when prey are not detected may also reduce the frequency of anaerobic dives for shallow-diving species (Sparling et al. 2007).

EFFECT OF UPWELLING ON FORAGING BEHAVIOR

On annual time scales, the cooler water characteristic of upwelling affects the diet and improves the reproductive success of the Marbled Murrelet and other alcids in the California Current by stimulating primary productivity and increasing the availability of krill and forage fish (Becker et al. 2007, Lee et al. 2007, Thayer and Sydeman 2007). In this study, we showed that variability in upwelling intensity has an important influence on the foraging behavior of murrelets on shorter time scales. Upwelling measured in this study fluctuated on daily to weekly scales, indicating that murrelets responded to upwelling-mediated changes in the distribution of prey rather than to changes in prey populations via bottom-up processes, which occur over monthly to seasonal scales (Mann and Lazier 2006).

Whether murrelets responded to reduced or elevated prey availability during episodes of upwelling is uncertain without direct comparisons of prey abundance during upwelling and relaxation. Moreover, an apparent contradiction exists between the increase in diving and the reduction in foraging distances in response to upwelling. Numerous studies have demonstrated that diving seabirds respond to reductions in prey by increasing both foraging distances and diving rates (Monaghan et al. 1994, Davoren 2000). The relationship between foraging effort and prey availability is complex, however, and appears to be species and system specific. For example, in the Bering Sea Black-legged Kittiwakes (*Rissa tridactyla*) increase their daily energy expenditure when their preferred prey are abundant (Jodice et al. 2006) but in Glacier

Bay, Alaska, increase their expenditure when prey become scarce (Kitaysky et al. 2000).

A priori knowledge of the linkage between physical processes associated with upwelling in the California Current System and the distribution of zooplankton and forage fish does not necessarily provide insight into whether murrelets respond to reductions or increases in prey availability during upwelling. On one hand, upwelling advects invertebrates and small fishes away from nearshore murrelet foraging habitat via Ekman transport to deeper, offshore waters (Ainley et al. 1993, Larson et al. 1994). Reductions in prey may have been particularly acute in our study area because Point Año Nuevo is a major upwelling center from which a large plume of cold water frequently moves offshore during the breeding season (Schwing et al. 1991, Rosenfeld et al. 1994; Fig. 1). On the other hand, upwelling increases the velocity of along-shore currents, and the interaction of those currents with bathymetric features and coastal topography generates convergent fronts that can aggregate invertebrates and forage fish (Bjorkstedt et al. 2002, Shanks and McCulloch 2003). Despite these uncertainties, our results suggest that short-term variation in upwelling influences the distribution and availability of prey for nearshore seabirds in eastern boundary currents such as the California Current System. Concurrent studies of seabirds' foraging behavior, daily to weekly changes in oceanographic processes associated with upwelling, and spatio-temporal variability in prey distributions in such systems are merited.

ACKNOWLEDGMENTS

LITERATURE CITED

Ainley, D. G., W. J. Sydeman, R. H. Parrish, and W. H. Lenarz. 1993. Oceanographic factors influencing distribution of young rockfish (*Sebastes*) in central California: a predator's perspective California Cooperative Oceanic Fisheries Investigations Reports 34:133–139.

Ainley, D. G., L. B. Spear, C. T. Tynan, J. A. Barth, S. D. Pierce, R. Glenn Ford, and T. J. Cowles. 2005. Physical and biological variables affecting seabird distributions during the upwelling season of the northern California Current. Deep Sea Research Part II: Topical Studies in Oceanography 52:123–143.

Baker, L. M., M. Z. Peery, E. E. Burkett, S. W. Singer, D. L. Suddjian, and S. R. Beissinger. 2006. Nesting habitat characteristics of the Marbled Murrelet in central California redwood forests. Journal of Wildlife Management 70:939–946.

Bakun, A. 1973. Coastal upwelling indices, west coast of North America, 1946–1971. NOAA Technical Report NMFS SSRF 671.

Barlow, K. E., and J. P. Croxall. 2002. Seasonal and interannual variation in foraging range and habitat of Macaroni Penguins *Eudyptes chrysolophus* at South Georgia. Marine Ecology Progress Series 232:291–304.

Becker, B. H., and S. R. Beissinger. 2003. Scale-dependent habitat selection by a nearshore seabird, the Marbled Murrelet, in a highly dynamic upwelling system Marine Ecology Progress Series 256:243–255.

Becker, B. H., M. Z. Peery, and S. R. Beissinger. 2007. Ocean climate and prey availability affect the trophic level and reproductive success of the Marbled Murrelet, an endangered seabird. Marine Ecology Progress Series 329:267–279.

Bertram, D. F., C. V. J. Welham, and R. C. Ydenberg. 1996. Flexible effort in breeding seabirds: adjustment of provisioning according to nestling ages and mass. Canadian Journal of Zoology 74:1876–1881.

Bjorkstedt, E. P., L. K. Rosenfeld, B. A. Grantham, Y. Shkedy, and J. Roughgarden. 2002. Distribution of larval rockfishes *Sebastes* spp. across nearshore fronts in a coastal upwelling region. Marine Ecology Progress Series 242:215–228.

Boyd, I. L. 1997. The behavioural and physiological ecology of diving. Trends in Ecology & Evolution 12:213–217.

Bradley, R. W., L. A. McFarlane-Tranquilla, B. A. Vanderkist, and F. Cooke. 2002. Sex differences in nest visitation by chick-rearing Marbled Murrelets. Condor 104:178–183.

Burger, A. E., and J. F. Piatt. 1990. Flexible time budgets in breeding Common Murres as buffers against variable prey abundance. Studies in Avian Biology 14:71–83.

Burger, A. E. 1991. Maximum diving depths and underwater foraging in alcids and penguins. Canadian Wildlife Service Occasional Paper 68:9–15.

Burger, A. E., and S. A. Shaffer. 2008. Application of tracking and data-logging technology in research and conservation of seabirds. Auk 125:253–264.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach Springer-Verlag, New York.

Cairns, D. K., K. A. Bredin, and W. A. Montevecchi. 1987. Activity budgets and foraging ranges of breeding Common Murres. Auk 104:218–224.

Chappell, M. A., V. H. Shoemaker, D. J. Janes, S. K. Maloney, and T. L. Bucher. 1993. Energetics of foraging in breeding Adelie Penguins. Ecology 74:2450–2461.

Croll, D. A., A. J. Gaston, A. E. Burger, and D. Konnoff. 1992. Foraging behavior and physiological adaptation for diving in Thick-billed Murres. Ecology 73:344–356.

Croll, D. A., and E. McLaren. 1993. Diving metabolism and thermoregulation in Common and Thick-billed Murres. Journal of Comparative Physiology B–Biochemical Systemic and Environmental Physiology 163:160–166.

Croxall, J. P., J. R. D. Silk, R. A. Phillips, V. Afanasyev, and D. R. Briggs. 2005. Global circumnavigations: tracking year-round ranges of nonbreeding albatrosses. Science 307:249–250.

Davoren, G. K. 2000. Variability in foraging in response to changing prey distributions in Rhinoceros Auklets. Marine Ecology Progress Series 198:283–291.

Dewar, J. M. 1924. The bird as a diver. Witherby, London.

Drent, R. H., and S. Daan. 1980. The prudent parent: energetic adjustments in avian breeding. Ardea 68:225–252.

Gaston, A. J. 1985. Energy invested in reproduction by Thick-billed Murres (*Uria lomvia*). Auk 102:447–458.

GASTON, A. J., AND R. G. BROWN. 1991. Dynamics of seabird distributions in relation to variations in the availability of food on a landscape scale. Proceedings of the International Ornithological Congress 20:2306–2312.

GRANADEIRO, J. P., M. BOLTON, M. C. SILVA, M. NUNES, AND R. W. FURNESS. 2000. Responses of breeding Cory's Shearwater *Calonectris diomedea* to experimental manipulation of chick condition. Behavioral Ecology 11:274–281.

GREEN, J. A., I. L. BOYD, A. J. WOAKES, C. J. GREEN, AND P. J. BUTLER. 2005. Do seasonal changes in metabolic rate facilitate changes in diving behaviour? Journal of Experimental Biology 208:2581–2593.

HARDING, A. M. A., J. F. PIATT, J. A. SCHMUTZ, M. T. SHULTZ, T. I. VAN PELT, A. B. KETTLE, AND S. G. SPECKMAN. 2007. Prey density and the behavioral flexibility of a marine predator: the Common Murre (*Uria aalge*). Ecology 88:2024–2033.

HENKEL, L. A., E. E. BURKETT, AND J. Y. TAKEKAWA. 2003. At-sea activity and diving behavior of a radio-tagged Marbled Murrelet in central California. Waterbirds 26:9–12.

HENKEL, L. A., AND J. T. HARVEY. 2006. Potential prey resources for Marbled Murrelets in central California. California Fish and Game 92:191–206.

HICKS, C. R. 1993. Fundamental concepts in the design of experiments. Oxford University Press, UK., Oxford.

HUNT, G. L., JR, F. MEHLUM, R. W. RUSSELL, D. IRONS, M. B. DECKER, AND P. H. BECKER. 1999. Physical processes, prey abundance, and the foraging ecology of seabirds. Proceedings of the International Ornithological Congress 22:2040–2050.

HUSBY, D. M., AND C. S. NELSON. 1982. Turbulence and vertical stability in the California Current. California Cooperative Oceanic Fisheries Investigations Reports 23:113–129.

JODICE, P. G. R., AND M. W. COLLOPY. 1999. Diving and foraging patterns of Marbled Murrelets (*Brachyramphus marmoratus*): Testing predictions from optimal-breathing models. Canadian Journal of Zoology 77:1409–1418.

JODICE, P. G. R., D. D. ROBY, R. M. SURYAN, D. B. IRONS, K. R. TURCO, E. D. BROWN, J. F. THEDING, AND G. H. VISSER. 2006. Increased energy expenditure by a seabird in response to higher food abundance. Marine Ecology Progress Series 306:283–293.

KITAYSKY, A. S., G. L. HUNT, JR, E. N. FLINT, M. A. RUBEGA, AND M. B. DECKER. 2000. Resource allocation in breeding seabirds: Responses to fluctuations in their food supply. Marine Ecology Progress Series 206:283–296.

KOOYMAN, G. L. 1989. Diverse divers: physiology and behavior. Springer-Verlag, Berlin.

KOOYMAN, G. L., AND T. G. KOOYMAN. 1995. Diving behavior of Emperor Penguins nurturing chicks at Coulman Island, Antarctica. Condor 97:536–549.

KOOYMAN, G. L., AND P. J. PONGANIS. 1998. The physiological basis of diving to depth: birds and mammals. Annual Review of Physiology 60:19–32.

LARSON, R. J., W. H. LENARZ, AND S. R. RALSTON. 1994. The distribution of pelagic juvenile rockfish of the genus *Sebastes* in the upwelling region off of central California. California Cooperative Oceanic Fisheries Investigations Reports 35:175–221.

LEE, D. E., N. NUR, AND W. J. SYDEMAN. 2007. Climate and demography of the planktivorous Cassin's Auklet *Ptychoramphus aleuticus* off northern California: implications for population change. Journal of Animal Ecology 76:337–347.

LITTELL, R. C., G. A. MILLIKEN, W. W. STROUP, AND R. D. WOLFINGER. 1996. SAS System for mixed models. SAS Institute, Cary, NC.

MANN, K. H., AND J. R. N. LAZIER. 2006. Dynamics of marine ecosystems: biological–physical interactions in the oceans. Blackwell, Malden, MA.

MCFARLANE-TRANQUILLA, L. A., R. W. BRADLEY, D. LANK, T. D. WILLIAMS, L. W. LOUGHEED, AND F. COOKE. 2003a. The reliability of brood patches in assessing reproductive status in the Marbled Murrelet: words of caution. Waterbirds 26:108–118.

MCFARLANE-TRANQUILLA, L. A., T. D. WILLIAMS, AND F. COOKE. 2003b. Using vitellogenin to examine interannual variation in breeding chronology of Marbled Murrelets (*Brachyramphus marmoratus*). Auk 120:512–521.

MONAGHAN, P., P. WALTON, S. WANLESS, J. D. UTTLEY, AND M. D. BURNS. 1994. Effects of prey abundance on the foraging, diving efficiency, and time allocation of breeding guillemots *Uria aalge*. Ibis 136:214–222.

MONAGHAN, P., R. G. NAGER, AND D. C. HOUSTON. 1998. The price of eggs: increased investment in egg production reduces the offspring capacity of parents. Proceedings of the Royal Society of London B 265:731–735.

NAGY, K. A., W. R. SIEGFRIED, AND R. P. WILSON. 1984. Energy utilization by free-ranging Jackass Penguins, *Spheniscus demersus*. Ecology 65:1648–1655.

NAGY, K. A., G. L. KOOYMAN, AND P. J. PONGANIS. 2001. Energetic cost of foraging in free-diving Emperor Penguins. Physiological and Biochemical Zoology 74:541–547.

NELSON, S. K. 1997. Marbled Murrelet (*Brachyramphus marmoratus*), no. 276 *In* A. Poole and F. Gill [EDS.], The Birds of North America. The Academy of Natural Sciences and The American Ornithologists' Union.

NEWMAN, J. A., J. BERGELSON, AND A. GRAFEN. 1997. Blocking factors and hypothesis tests in ecology: is your statistics test wrong? Ecology 78:1312–1320.

NEWMAN, S. H., J. Y. TAKEKAWA, D. L. WHITWORTH, AND E. BURKETT. 1999. Subcutaneous anchor attachment increases retention of radio-transmitters on Xantus' and Marbled Murrelets. Journal of Field Ornithology 70:520–534.

PEERY, M. Z., S. R. BEISSINGER, S. H. NEWMAN, E. BURKETT, AND T. D. WILLIAMS. 2004a. Applying the declining population paradigm: diagnosing causes of poor reproduction in the Marbled Murrelet. Conservation Biology 18:1088–1098.

PEERY, M. Z., S. R. BEISSINGER, S. H. NEWMAN, B. H. BECKER, E. BURKETT, AND T. D. WILLIAMS. 2004b. Individual and temporal variation in inland flight behavior of Marbled Murrelets: implications for population monitoring. Condor 106:344–353.

PEERY, M. Z., S. R. BEISSINGER, E. BURKETT, AND S. H. NEWMAN. 2006. Local survival of Marbled Murrelets in central California: roles of oceanographic processes, sex, and radiotagging. Journal of Wildlife Management 70:78–88.

PEERY, M. Z., L. A. HENKEL, S. H. NEWMAN, B. H. BECKER, J. T. HARVEY, C. THOMPSON, AND S. R. BEISSINGER. 2008. Effects of rapid flight-feather molt on post-breeding dispersal in a pursuit-diving seabird. Auk 125:113–123.

PIATT, J. F., W. J. SYDEMAN, AND F. WIESE. 2007. Introduction: A modern role for seabirds as indicators. Marine Ecology-Progress Series 352:199–204.

RICKLEFS, R. E. 1983. Some considerations of the reproductive energetics of pelagic seabirds. Studies in Avian Biology 8:84–94.

RONCONI, R. A., AND A. E. BURGER. 2008. Limited foraging flexibility: increased foraging effort by a marine predator does not buffer against scarce prey. Marine Ecology Progress Series 366:245–258.

ROSENFELD, L. K., F. B. SCHWING, N. GARFIELD, AND D. E. TRACY. 1994. Bifurcated flow from an upwelling center: a cold water source for Monterey Bay. Continental Shelf Research 14:931–964.

SCHREER, J. F., AND K. M. KOVACS. 1997. Allometry of diving capacity in air-breathing vertebrates. Canadian Journal of Zoology 75:339–358.

SCHREER, J. F., K. M. KOVACS, AND R. J. O'HARA HINES. 2001. Comparative diving patterns of pinnipeds and seabirds. Ecological Monographs 71:137–162.

SCHWING, F. B., D. M. HUSBY, N. GARFIELD, AND D. E. TRACY. 1991. Mesoscale oceanic responses to wind events off central California in spring 1989: CTD surveys and AVHRR imagery. California Cooperative Oceanic Fisheries Investigations Reports 32:47–64.

SHAFFER, S. A., D. P. COSTA, AND H. WEIMERSKIRCH. 2003. Foraging effort in relation to the constraints of reproduction in free-ranging albatrosses. Functional Ecology 17:66–74.

SHAFFER, S. A., Y. TREMBLAY, H. WEIMERSKIRCH, D. SCOTT, D. R. THOMPSON, P. M. SAGAR, H. MOLLER, G. A. TAYLOR, D. G. FOLEY, B. A. BLOCK, AND D. P. COSTA. 2006. Migratory shearwaters integrate oceanic resources across the Pacific Ocean in an endless summer. Proceedings of the National Academy of Sciences of the USA 103:12799–12802.

SHANKS, A. L., AND A. McCULLOCH. 2003. Topographically generated fronts, very nearshore oceanography and the distribution of chlorophyll, detritus, and selected diatom and dinoflagellate taxa. Marine Biology 143:969–980.

SIMPSON, J. J. 1987. Transport mechanisms affecting the survival of pelagic fish stocks in the California Current. American Fisheries Society Symposium 2:39–60.

SPARLING, C. E., J.-Y. GEORGES, S. L. GALLON, M. FEDAK, AND D. THOMPSON. 2007. How long does a dive last? Foraging decisions by breath-hold divers in a patchy environment: a test of a simple model. Animal Behaviour 74:207–218.

THAYER, J. A., AND W. J. SYDEMAN. 2007. Spatio-temporal variability in prey harvest and reproductive ecology of a piscivorous seabird, *Cerorhinca monocerata*, in an upwelling system. Marine Ecology Progress Series 329:253–265.

WALKER, B. G., AND P. D. BOERSMA. 2003. Diving behavior of Magellanic Penguins (*Spheniscus magellanicus*) at Punta Tombo, Argentina. Canadian Journal of Zoology 81:1471–1483.

WEIMERSKIRCH, H. 1998. How can a pelagic seabird provision its chick when relying on a distance food source? Cyclic attendance at the colony, foraging decision and body condition in Sooty Shearwaters. Journal of Animal Ecology 67:99–109.

YDENBERG, R. C., AND C. W. CLARK. 1989. Aerobiosis and anaerobiosis during diving by Western Grebes: An optimal foraging approach. Journal of Theoretical Biology 139:437–449.